

# Evolution of community composition in several carnivore palaeoguilds from the European Pleistocene: the role of interspecific competition

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This study focuses on ecological processes such as competition or predation from an evolutionary perspective. First, we attempt to test the idea that species with similar feeding requirements tend to coexist by separating morphologically or behaviourally. Then, the Barton–David test was applied to several carnivore communities (felids and canids) separated in time. Although the preservation bias of the fossil record renders our conclusions tentative, the general equal size–ratio pattern in most of the guilds examined indicates that inter-specific competition for prey species seems to be a good candidate to explain the evolution of guild composition and morphological traits throughout the Pleistocene for the two groups considered, felids and canids. □ *Barton–David test, body size estimation, canids, character displacement, felids, size–ratios.*

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Palaeoecological studies explain how evolutionary patterns may be shaped by ecological processes such as competition, predation or abiotic factors (climate changes, large macro-geological processes). Nevertheless, most palaeoecological studies failed to analyze the role of these processes in shaping aspects such as the evolution of community patterns, character displacement or diversification events (Werdelin 1996).

Interspecific competition has been proposed as one of the main forces that may structure ecological communities and speciation events (e.g. Lack 1947; Connell 1983; Connor & Simberloff 1989; Schluter 1988; Keddy 2001). There are large numbers of field experiments that support the relevance of interspecific competition in shaping species composition through resource partitioning (Connell 1983; Roughgarden 1989; Keddy 2001). The theory of character displacement (Brown & Wilson 1956) established that two closely related species with overlapping geographical distributions (sympatry) showed more pronounced differences than in areas where each of the species showed allopatric distributions (Schoener 1970; Huey & Pianka 1974; Schluter *et al.* 1985; Losos 1990; Schluter 2000). Hence the observed phenomenon ‘character displacement’ would represent a *prima facie* evidence for interspecific competition. Schluter (2000) considers

necessary to include six criteria for testing character displacement in ecological communities. Nevertheless, only a few studies have used an experimental framework to test the character displacement hypothesis following all the criteria (reviewed in Schluter 2000; Pritchard & Schluter 2001). In contrast, most relevant studies only analyze that differences of the character states among the species living in sympatry were greater than expected by chance (e.g. Hutchinson 1959; Simberloff & Boecklen 1981; Dayan *et al.* 1990, 1991).

In this study, it is tested if character displacement might be the cause of the evolution of community patterns by analyzing if differences between sympatric species are greater than expected by chance. For this search, the character displacement is tested as equal size ratios between adjacent species in a size ranking of presumed competitors (Simberloff & Boecklen 1981; Dayan *et al.* 1989a, b), a pattern that is consistent with competition in the past (Case 1982). Community structure in several guilds (species using resources similarly, Root 1967) of carnivores of the European Pleistocene is analyzed. We used carnivores because they appear to be a taxonomic group where competition has played an important role in evolutionary diversification (Rosenzweig 1966; Valkenburg 1988, reviewed in Dayan & Simberloff 1996).

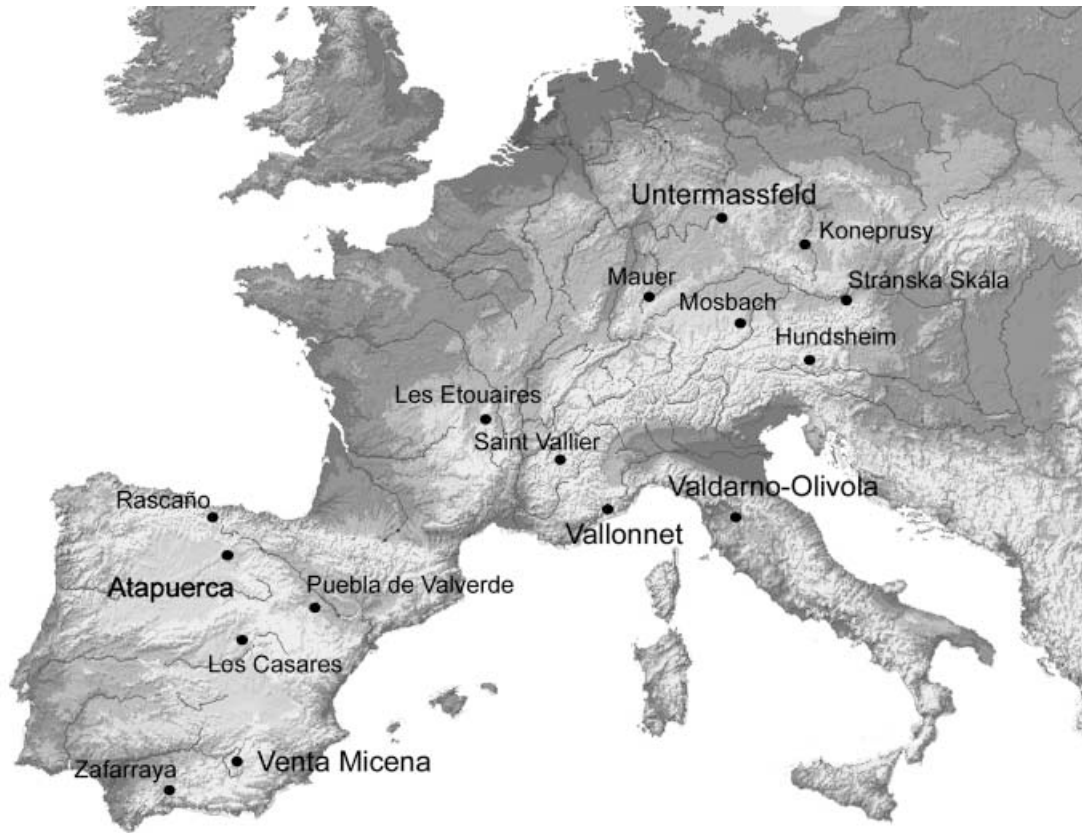


Fig. 1. Location map of the sites mentioned in this study. Atapuerca (Trinchera Galería and Trinchera Dolina), Puebla de Valverde, Rascaño, Zafarraya, Los Casares and Venta Micena (Spain), Saint Vallier, Les Etouaires and Le Vallonnet (France), Mauer, Mosbach and Untermassfeld (Germany), Hundsheim (Austria), Valdarno and Olivola (Italy), Koneprusy and Stránska Skála (Czech Republic).

## Materials

### *Selected sites and taxa*

We have selected several European sites (Fig. 1) ranging from the Early Pleistocene to the late Middle Pleistocene, where a sufficiently large carnivore sample could be employed in our test. The chronology and source for each site are included in Tables 1 and 2. Nevertheless, within the Middle Pleistocene we have distinguished two time ranges for a better comprehension of the felid guild evolution: (1) from the Cromer Complex (early Middle Pleistocene) to the Holstein period (middle Middle Pleistocene), and (2) from the Holstein to the Eem interglacial (late Middle Pleistocene). In certain cases, some of the archaeopalaeontological levels from different sites located very close to one another are also chronologically contemporaneous such as Trinchera Galería and Sima de los Huesos in the Sierra de Atapuerca (Bischoff *et al.* 2003; C. Falguères, personal communication, 2001) or Valdarno and Olivola (Gliozzi *et al.* 1997) in Italy. We have treated these sites as a whole to manage their fossil taxa as part of the same carnivore association.

Part of the fossil material was originally measured by the authors (Tables 1 and 2), with the exception of the Valdarno, Venta Micena and Untermassfeld sites, which values were taken from the literature. Tables 1 and 2 show all the raw values of the fossil elements available for the analysis and also the chronology attributed to that site as well as the bibliographic source.

The recent carnivores selected for this study were measured in several institutions: Institute d'Anatomie Comparée (Paris) (*Acinonyx jubatus*, *Panthera pardus*, *Panthera uncia*, *Panthera tigris*, *Felis wiedii*, *Felis temmincki*, *Felis pardalis*, *Felis yagouaroundi*, *Alopex lagopus*, *Canis aureus*, *Canis latrans*, *Dusicyon magellanicus*, *Fennecus zerda*); National Museum of Natural History (Madrid) (*Lynx lynx*, *Lynx pardinus*, *Lynx rufus*, *Felis silvestris*, *Canis lupus*, *Vulpes vulpes*); Animal Biology Department Complutensis University of Madrid (Madrid) (*P. tigris*, *F. silvestris*, *V. vulpes*); Doñana Biological Station (Sevilla) (*L. pardinus*); Anatomy Department – School of Medicine-Valladolid University (Valladolid) (*Panthera leo*, *Panthera onca*, *P. pardus*, *Puma concolor*, *Caracal caracal*, *Felis serval*, *F. geoffroyi*, *F. wiedii*, *F. zerda*, *Nyctereutes*

Table 1. Measurements of the Canidae fossil remains ( $M_1$ ) included in this study from selected Early to Middle Pleistocene localities. The chronology attributed to the sites and the bibliographic sources are also included.

Taxa	Site	Location label	Chronology	Variable	Value (mm)	Mean
Middle Pleistocene						
<i>Canis lupus</i>	TG (Unit II–III)	TG10a-G16-60	300–400 ka (4)	$LM_1$	25.4	25.4
	Iberian (northern Spain)	$n = 42$	Extant	$LM_1$	$26.86 \pm 1.6$	26.9
<i>Cuon alpinus</i>	TG (Unit II–III)	TG-GSU11 F17 1	300–400 ka (4)	$LM_1$	22.2	23.1
		TG-GSU11 F18 15			22	
		TG10a			23.8	
		TG-GSU12 F26 1			24.2	
<i>Vulpes vulpes</i>	Asian (several regions)	$n = 42$	Extant	$LM_1$	$21.42 \pm 1.1$	21.4
	Sima de los Huesos	SH ( $n = 36$ )	400 ka (5)	$LM_1$	$15.86 \pm 0.83$	15.9
	North American <sup>1</sup>	$n = 50$	Extant	$LM_1$	$15.4 \pm 0.7$	15.4
Early Pleistocene						
<i>Canis etruscus</i>	Valdarno Sup.-Olivola <sup>2</sup> Venta Micena <sup>3</sup>	Valdarno ( $n = 23$ )	1.7 Ma (6)	$LM_1$	$24.72 \pm 0.97$	24.7
		IPS VM2253	1.4–1.2 Ma (7)	$LM_1$	21.2	22.3
		IPS VM2260			24.1	
		IPS VM85C32B12			21.8	
		Valdarno ( $n = 16$ )	1.7 Ma (6)	$LM_1$	$21.9 \pm 1.1$	21.9
<i>Canis arnensis</i>	Valdarno Sup. + Tasso <sup>2</sup>	Valdarno ( $n = 16$ )	1.7 Ma (6)	$LM_1$	$21.9 \pm 1.1$	21.9
		Venta Micena <sup>3</sup>	1.4–1.2 Ma (7)	$LM_1$	14.3*	14.3
<i>Vulpes praeglacialis</i>	Valdarno <sup>2</sup>	IGF 865	1.7 Ma (6)	$LM_1$	28.3	28.3
		IPS VM2255	1.4–1.2 Ma (7)	$LM_1$	24.5	26.1
		IPS VM2256			25.3	
<i>Xenocyon falconeri</i>	Venta Micena <sup>3</sup>	IPS VM2257			28.6	

(1) Gingerich & Wrinkler 1979; (2) Rook 1993; (3) Martínez Navarro 1992; (4) C. Falguères, personal communication, 2006; (5) Bischoff *et al.* 2003; (6) Torre *et al.* 1993; (7) Agustí & Moyà-Solà 1991.

\*Value estimated from another element from that site:  $M^1$  ( $LM^1 = 8.7$ ;  $WM^1 = 10.7$ ). The sample used to estimate the  $LM_1$  value (by a regression equation includes a sample of 15 Pleistocene specimens of *Vulpes praeglacialis* ( $n = 8$  from L'Escaie and  $n = 7$  from Villány-Kalkberg). The resulted value is very close to those from other sites as Le Vallonnet ( $LM_1 = 14$  mm) or Petralona ( $n = 3$ ;  $LM_1 = 13.7$  mm). Even if slight variability in this estimation occurs this would not affect the test result due to the low size of this canid (*Vulpes praeglacialis*  $LM_1$  range = 12.3–14.8 mm)

*procyonoides*, *Lycaon pictus*, *Canis mesomelas*); National Museum of Natural History-Smithsonian Institution (Washington) (*P. leo*, *P. onca*, *P. pardus*); and Natural History Museum (London) (*C. lupus*, *Cuon alpinus*). The weights of the different carnivore species were obtained from published sources based on mean values (Couturier 1954; Notario 1970; Grizmeck 1988; Eisenberg 1989, 1992, 1999; Nowak 1991; Beltrán & Delibes 1993; Blanco 1998).

## Methods

### Selected measurements

We studied carnivore communities by using two different guilds: canids and felids. We tested separately canids and felids following the recommendations of Dayan *et al.* (1989b, 1990, 1992; Dayan & Simberloff 1996). To test character displacement we used those dental measurements previously suggested as related to prey catching by the different guilds (Dayan *et al.* 1989a, b, 1990, 1992). In particular, we measured anterior–posterior (maximal) diameter of the upper canine (APD-C<sup>s</sup>) for felids and length (maximal) of the lower first molar ( $LM_1$ ) for canids (Dayan *et al.* 1989b, 1990, 1992, 1996), assuming a morpho-functional

relation between the canine or carnassial size and the size of the potential preys (Dayan & Simberloff 1996). The morpho-functional relation between the large canine diameter of *Homotherium* and of *Meganteron* and the size of their potential prey is a basic assumption in order to apply the character displacement test. The theory that saber-toothed felids used their upper canines to stab their prey was very preliminarily put forth by Warren (1853) and then was subsequently explicitly developed by a number of authors (Matthew 1901; Simpson 1941; Kurtén 1952; Gonyea 1976). Other authors have rejected the stabbing theory and tried to show that the machairodonts were not predaceous but actually carrion feeders (Marinelli 1938; Bohlin 1940). Subsequent studies have speculated that the powerful front limbs of saber-toothed felids were employed to immobilize prey while the long sabers were used to stab the victim (Schultz *et al.* 1970). Biknevicius & Valkenburg (1996) and Turner & Antón (1996) have proposed that *Smilodon* and *Homotherium*, respectively, may have killed their prey using a throat hold similar to that employed by felids today. All these data support the killing-behaviour hypothesis of *Homotherium* and *Meganteron* having had access to large-bodied prey such as giant camelids, bison and perhaps even proboscideans (Biknevicius & Valkenburg 1996). At

Table 2. Measurements of the Felidae fossil remains (canines) included in this study from selected Early to Middle Pleistocene localities. Also the chronology attributed to the sites and the bibliographic sources are included.

Taxa	Site	Location label	Chronology	Variable	Value (mm)	Mean
Middle Pleistocene						
<i>Panthera leo</i>	Atapuerca (TG; TD)	TG11-GSU2-I16-1 TG10a-G17-9	300–400 ka (7)	APDC <sup>s</sup> APDC <sub>i</sub>	22.5 22.3	22.5 23.7
		TD10 <sub>(3)</sub> G11-229	300–400 ka (8)		25.1	
<i>Lynx p. spelaeus</i>	Atapuerca (SH; TG)	SRM SH-L1	~400 ka (9)	APDC <sub>i</sub>	8 8	7.7
		TZ GIII Q2 1	300–400 ka (7)			
		TN6 F23 36		APDC <sup>s</sup>	8.3	8.6
		TG11 GSU6 F20 16			8.9	
<i>H. latidens</i>	Atapuerca (TD)	TD10 <sub>(3)</sub> G12 240	300–400 ka (8)	APDC <sub>i</sub>	33	33
<i>Felis silvestris</i>	Atapuerca (TG)	TG-2 Z N4 G7-4	300–400 ka (7)		5.6	5.6
Early Pleistocene						
<i>Panthera gombaszoegensis</i>	Atapuerca (TD)	TDW4-48	~0.8 Ma (10)	APDC <sub>i</sub>	16.9	16.9
	Valdarno-Olivola <sup>1</sup>	IGF 10032	~1.7 Ma (11)	APDC <sup>s</sup>	22.6	19.6
		IGF-1225V			18	
		IGF-4376			20	
		IGF-4376			20.5	
		IGF-1226V			17	
		IGF 853		APDC <sub>i</sub>	18	19
		IGF 851			20*	
		IGF-4374			18*	
		IGF-4375			20	
	Untermassfeld <sup>2</sup>	Mei. 19788	0.99–1.05 Ma (12)	APDC <sup>s</sup>	20.8	20.8
		Mei. 18689		APDC <sub>i</sub>	18.5	18
		Mei. 23666			18.2	
		Mei. 24872			17.3	
	Vallonnet <sup>3</sup>	C6 192	0.99–1.05 Ma (13)	APDC <sup>s</sup>	23.4	21.7
		B8 B2 289			20	
<i>Homotherium latidens</i>	Valdarno-Olivola <sup>1</sup>	IGF 817	~1.7 Ma (11)	APDC <sup>s</sup>	36	33.1
		IGF 12480			32	
		IGF 824			27.6	
		IGF 832			35	
		IGF 820			34.5	
		IGF 6090			34	
	Untermassfeld <sup>2</sup>	Mei. 23929	0.99–1.05 Ma (12)		37.7	37.7
	Vallonnet <sup>3</sup>	G G9 J1 100	0.99–1.05 Ma (13)		35	35
<i>Megantereon cultridens</i>	Valdarno <sup>1</sup>	IGF 821	~1.7 Ma (11)	APDC <sup>s</sup>	26	25.4
		IGF 830			24.5	
		IGF 816			25.8	
	Untermassfeld <sup>2</sup>	Mei. 23560	0.99–1.05 Ma (12)		21.98	
<i>Acinonyx pardinensis</i>	Valdarno <sup>4</sup>	IGF 12477	~1.7 Ma (11)	APDC <sup>s</sup>	14.2	14.2
	Untermassfeld <sup>2</sup>	Mei. 15861	0.99–1.05 Ma (12)	APDC <sup>s</sup>	15.4	15.4
		Mei. 15016		APDC <sub>i</sub>	14	
	Vallonnet <sup>3</sup>	C6-195	0.99–1.05 Ma (13)	LP4	20	15.4*
		C6-195		LP3	16.2	
<i>Puma pardoides</i>	Untermassfeld <sup>2</sup>	Mei. 18376	0.99–1.05 Ma (12)	APDC <sup>s</sup>	12.4	12.4
<i>Felis cf. silvestris</i>	Atapuerca (TD)	TDW4	~0.8 Ma (10)	APDC <sub>i</sub>	4.5	4.5
<i>Lynx sp.</i>		TDW4-195		APDC <sup>s</sup>	6.1	6.1
<i>Felis lunensis</i>	Olivola <sup>5</sup>	IGF 4298	~1.7 Ma (11)	APDC <sub>i</sub>	7.8	7.8
<i>Lynx issiodorensis</i>	Valdarno <sup>6</sup>	IGF 898		APDC <sup>s</sup>	8	9.3
		IGF 892			8.5	
		IGF 896			10	
		IGF 4396			9.5	
		IGF 893			11	
		IGF 13894			9	
	Untermassfeld <sup>2</sup>	Mei. 24220	0.99–1.05 Ma (12)	APDC <sup>s</sup>	7.7	7.85
		Mei. 16094			8	
	Vallonnet <sup>3</sup>	G210	0.99–1.05 Ma (13)	LP <sup>4</sup>	16.9	8.5
<i>Panthera cf. pardus</i>	Vallonnet <sup>3</sup>	RR10195		LM <sub>1</sub>	19.4	13.04**
		RR20050		LM <sub>1</sub>	16.7	

\*Value estimated with two premolars from that site (LP3 = 16.2; LP4 = 20). The values for P<sub>3</sub> and P<sub>4</sub> from the Untermassfeld specimen (skull: Mei. 15861; mandibles: Mei. 15016 + Mei. 15015, same individual) are identical to the Vallonnet ones (LP<sub>3</sub> = 16; LP<sub>4</sub> = 19.8, Hemmer 2001), for what we have applied the same upper canine value of the Untermassfeld specimen (15.4), also very close to those from other Early Pleistocene site as Les Etouaires or Valdarno.

\*\*Value estimated from two lower carnassials from the same site (LM<sub>1</sub> = 19.4; 16.7). The estimation of the APDCs value (by regression equation), was calculated with a modern sample of 40 *Panthera pardus* specimens.

(1) Del Campana 1915; (2) Hemmer 2001; (3) Moullé 1992; (4) Ficarelli 1984; (5) Ficarelli & Torre 1975; (6) Fabrini 1896; (7) C. Falguères, personal communication, 2001; (8) Falguères *et al.* 1999; (9) Bischoff *et al.* 2003; (10) Parés & Pérez González 1999; (11) Torre *et al.* 1993; (12) Kahlke 2001; (13) Yokoyama *et al.* 1988.

Freisenhahn Cave in Texas, a large bone accumulation of infant proboscideans (*Mammuthus americanus* and *Mammuthus columbi*) has been attributed to the activities of *Homotherium serum* (a descendent of the Eurasian form) (Rawn-Schatzinger 1992; Marean & Ehrhardt 1995).

### *Weight predictions (regression equation and ratio estimator (RE))*

Competition for preys can be predicted from the size of feeding structures. Considering body size may enhance a whole understanding of the community structure and its dynamics. This is related to a large number of life-history traits related to potential competition (Peters 1983).

The weight estimations of fossil species were calculated using 36 extant carnivore taxa from the two families studied: Canidae (16 species represented by 44 individuals of both sexes) and Felidae (20 species represented by 61 individuals of both sexes) (Table 3). In most cases, body weight predictions for the fossil taxa are based on post-cranial elements (using the most accurate regression equation in each case) and, when not available, tooth elements were used. Least squares regressions of  $\log_{10}$ -transformed data are used to model the association between body weight and skeletal elements. The equations used for estimating body weight are of the form:  $\log Y = b(\log X) + \log a$ ; where  $X$  is a metric variable taken on the fossil specimen and  $Y$  the unknown body weight. During this estimation procedure, variables were measured on a linear scale, transformed to logarithms, and estimated values were subsequently transformed back to a linear scale. Because this procedure biases the estimate of  $Y$ , several methods of transformation have been suggested. Among them, the ratio estimator (RE) seems to reduce the underestimate of  $Y$  as compared to other procedures for what it is recommended when logarithmic transformation procedures are applied to body measurements (Smith 1993a, b). Calculation of the estimated weight and RE is only carried out with the variable showing the best Pearson correlation coefficient ( $r$ ) value in all the cases (Table 3).

### *Barton–David test for character displacement*

The Barton–David test is applied to analyze the character displacement. Several tests are available for determining the degree to which a series of points may be seen as randomly located along a line versus being seen as equally spaced (Barton & David 1956; Poole & Rathcke 1979; Hopf & Brown 1986). Simberloff (1989) discussed the relative merits of each one,

but not the relative power of these tests in relation to several kinds of data. This study used the Barton–David test proposed by Simberloff & Boecklen (1981), which was extensively used in similar studies (e.g. Dayan *et al.* 1989a, b, 1990, 1992). It is especially powerful for detecting whether any two points are too close on a line to be viewed as part of a random throw. In brief, values are log transformed, with the difference between contiguous logs recorded as the log ratio of the two numbers:  $g_1$  (the difference between the smallest and the following smaller) through  $g_n$  (the difference between the largest and the following larger); then logs of  $n + 1$  sizes are ranked from the smallest to the largest. These logarithms divide a line into  $n$  segments of increasing size. The explicit distribution for any ratio of these  $g$  statistics is described by the formula,  $G_{ij} = g_i/g_j$  (for  $i < j$ ) (Barton & David 1956), and any one of these statistics can be used to test the hypothesis as for example the  $G_{1n}$  ratio of the smallest to the largest segment (Barton & David 1956; Dayan *et al.* 1989a, b; Dayan & Simberloff 1996).

## Results

### *Canids*

The size ratios obtained from the Valdarno and Venta Micena Early Pleistocene sites (chronology in Table 1) yield different results. According to the Barton–David test, the Valdarno canid guild (*Xenocyon falconeri*, *Canis etruscus*, *Canis arnensis*) would be evenly spaced (Fig. 2A), whereas the Venta Micena association (*X. falconeri*, *C. etruscus*, *Vulpes praeglacialis*) would not (Fig. 2B). *Canis arnensis* is present at Valdarno, while it is lacking at Venta Micena where *V. praeglacialis* was documented.

At the Middle Pleistocene site of Trincheria Galería, the canid guild appears not to be evenly spaced (Fig. 2C). This guild comprises an (early) *C. lupus*, *Cu. alpinus* and *V. vulpes*. Nevertheless, in a hypothetical Upper Pleistocene guild, composed of extant Iberian wolves and foxes as well as Asiatic dholes, a nearly evenly spaced structure is obtained ( $P = 0.1$ ) (Fig. 2D). These three canid species co-occurred in this period in most of the Iberian territory (as evidenced by several sites), but we did not find a representative site which canid sample (with a significant record of all these species) could be used to conduct the test. Thus, values from lower carnassial length of extant Asiatic dholes were used, (*C. alpinus*<sub>(n=42)</sub> =  $21.4 \pm 1.1$  mm) which show values very similar to the last (Upper Pleistocene) European representatives of this species – LM<sub>1</sub>: Rascaño = 21 mm (Altuna 1981); Los Casares = 20.2 mm (Altuna 1973); L'Observatoire = 21 mm (Boule & Villeneuve

Table 3. Estimated body weights for adults of each species and sites calculated from regression equations (including only individuals of the same family) of weights on raniodental/postcranial variables in recent species.

Taxa	Site/Location	Chronology	Variable	Value (mm)	<i>r</i>	Estimated weight (kg)	RE	
<b>Felidae</b>								
Middle Pleistocene								
<i>Panthera leo</i>	Atapuerca (TG)	TG G19 18	~300–400 ka	APD-DT-RA	42.2	0.96	299.2	1.004
		TZ GIIC L2 92		APD-PX-FE	45.3	0.98	372.2	0.993
	Atapuerca (SH)	SRB 1176	~400 ka	TD-DT-TI	67.3	0.97	325.4	1.014
		SRB 8219		APD-PX-RA	33.2	0.96	317.7	0.957
<i>Lynx p. spelaeus</i>	Atapuerca (TG)	G5U0	~300–400 ka	APD-PX-FE	17.1	0.98	18.8	0.993
		G5U8 F17 8		APD-DT-HU	22.4	0.98	26.6	0.993
		TG-6D		APD-PX-RA	12.2	0.97	24.9	0.957
<i>Felis silvestris</i>	Atapuerca (TG)	TG2 Z N4 G7-4	~300–400 ka	APDC <sub>1</sub>	5.6	0.94	6.3	0.976
Early Pleistocene								
<i>Panthera gombaszoegensis</i>	Valdarno		1.7 Ma	APDC <sup>s</sup>	19.6 ( <i>n</i> = 5)	0.94	122 (average)	0.976
	Vallonnet		0.99–1.05 Ma		22; 25.8	0.94	152 (average)	0.976
	Untermassfeld	Mei. 15758	0.99–1.05 Ma	TD-DP-HU	27		160 (1)	
		Mei. 15025			26.5		170 (1)	
<i>Homotherium</i>	Olivola and Valdarno		1.7 Ma	Several values (different elements): 210–300 kg (1)				
	Untermassfeld		0.99–1.05 Ma	Three values (different elements): 210; 300; ~400 kg (1)				
<i>Megantereon cultridens</i>	Olivola		1.7 Ma	TD-DP-HU			170 (1)	
	Untermassfeld	Mei. 16120	1.07–0.99 Ma	TD-DP-HU			160 (1)	
		Mei. 23560		TD-DP-FE			100 (1)	
<i>Acinonyx pardinensis</i>	Valdarno (Casa Frata)		1.7 Ma	TD-DP-FE			120–90 kg (1)	
	Untermassfeld	Mei. 15503	0.99–1.05 Ma	LM <sub>1</sub> /TD-DP-HU	23.9		110 (1)	
		Mei. 15160		TD-DP-FE	26		140	
<i>Puma pardoides</i>	Vallonnet		0.99–1.05 Ma	Same P <sub>3</sub> -P <sub>4</sub> values than Untermassfeld: 110–140				
	Untermassfeld		0.99–1.05 Ma	TD-DP-FE	18.5		40–45 kg (1)	
				LM <sub>1</sub>	16.9			
<i>Lynx issiodorensis</i>	Valdarno		1.7 Ma	APDC <sup>s</sup> ( <i>n</i> = 8)	9.3		21	
	Untermassfeld		0.99–1.05 Ma	TD-DP-HU	12.3		15 (1)	
	Vallonnet		1.07–0.99 Ma	APDC <sup>s</sup> ( <i>n</i> = 1)	8.5		17	
<b>Canidae</b>								
Middle Pleistocene								
<i>Canis lupus</i>	Atapuerca TG	TG10a-G16-60	~300–400 ka	LM <sub>1</sub>	25.4	0.91	18.1	0.94
<i>Cuon alpinus</i>		G5U11-G17-8		APD-PX-RA	14	0.98	22	1.01
		G5U11b-G16			11.5		14.1	
<i>Vulpes vulpes</i>	Atapuerca SH	( <i>n</i> = 5)	~400 ka	APD-PX-FE	26.7	0.94	6	1.05
	Atapuerca SH	( <i>n</i> = 9)		TD-DT-FE	20.6	0.94	5.1	1.01
Early Pleistocene								
<i>Vulpes praeglacialis</i>	Venta Micena	( <i>n</i> = 23)	~1.3 Ma				3–5 kg (2)	
<i>Canis etruscus</i>	Valdarno		1.7 Ma	LM <sub>1</sub>	24.72	0.91	16.82	0.94
	Venta Micena		~1.3 Ma				9.9 kg (9.3–11.5) (2)	
<i>Canis arnensis</i>	Valdarno		1.7 Ma	LM <sub>1</sub>	21.93	0.91	13.2	0.94
<i>Xenocyon falconeri</i>	Valdarno		1.7 Ma	LM <sub>1</sub>	28	0.91	22.12	0.94
	Venta Micena		~1.3 Ma				29.8 kg (24.7–34.7) (2)	

Bibliographic references of the sites chronology are given in Tables 1 and 2. (1) Hemmer 2001; (2) Palmqvist *et al.* 1996.

*r*, correlation; RE, ratio estimator; estimated weight is calculated considering RE.

Atapuerca sites abbreviations: Trinchera Galería: TG, TZ and TN; Sima de los Huesos: SH, SRM and SRB.

PX, proximal epiphysis; DT, distal epiphysis; DP, diaphysis; APD, anteroposterior diameter; TD, transversal diameter; HU, humerus; RA, radius; FE, femur; TI, tibia; LM<sub>1</sub>, length of LM<sub>1</sub>; APDC<sup>s</sup>, anteroposterior diameter of the upper canine.

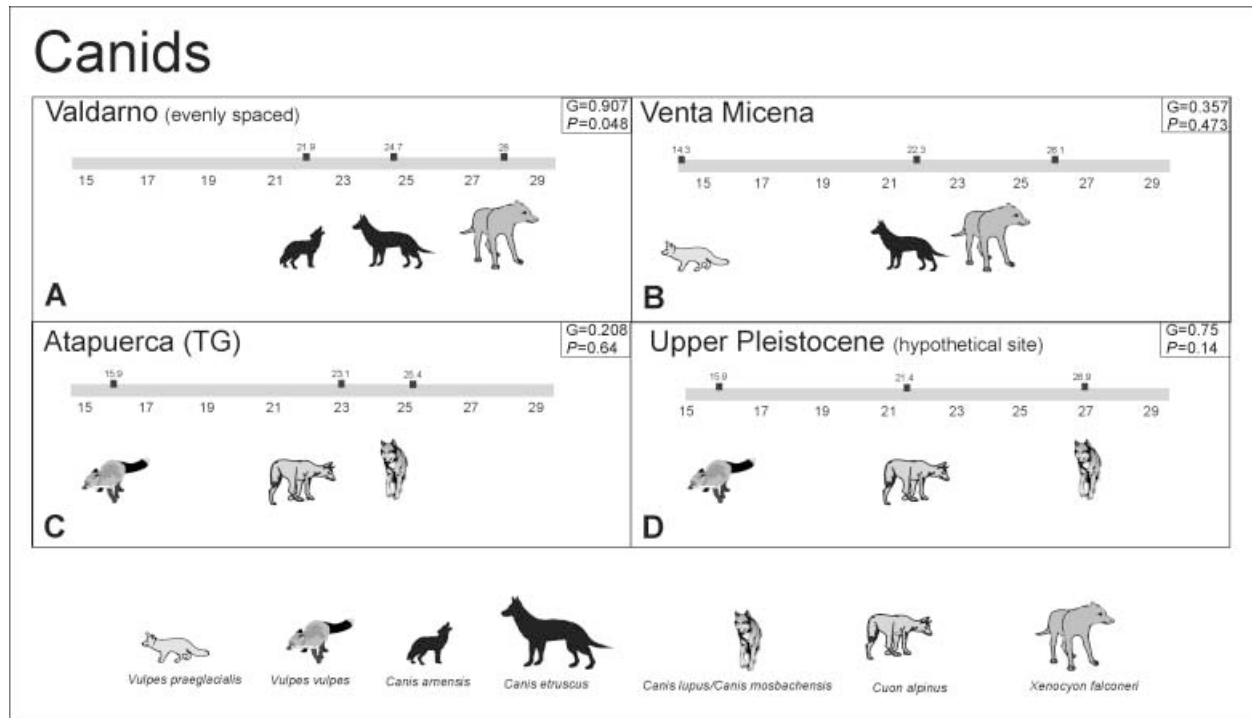


Fig. 2. Length of the lower carnassial (M1) in several canid paleoguilds. A, B and C represent Pleistocene sites while D is a hypothetical guild (representing an upper Pleistocene community) composed of modern Iberian wolves and foxes together with modern Asian dholes. The Barton–David test was applied in all cases resulting evenly-spaced ( $P + 0.05$ ) in the Valdarno association, and nearly in the hypothetical Upper Pleistocene guild ( $P = 0.1$ ).

1927); Isturitz = 22.3 mm (Bouchud 1951); and Zafarraya = 22.4, 22.3, 22, 22.2 mm (Geraads 1995) – and hence differ from the larger Middle Pleistocene form (*C. alpinus fossilis*) (García 2003, p. 158).

### Felids

Valdarno-Olivola represents an initial Early Pleistocene guild with six taxa (*Homotherium crenatidens*, *Megantereon cultrindens*, *Panthera gombaszoegensis*, *Lynx issiodorensis*, *Felis lunensis*), which would have been evenly spaced (Fig. 3A). In contrast, the results from more recent Early Pleistocene sites, such as Le Vallonnet and Untermassfeld, which preserve some of these taxa, in addition to *P. pardus* (which makes its first appearance in Europe at roughly this time), do not show an even spacing (Fig. 3B). The Barton–David test was applied to a hypothetical early Middle Pleistocene site including *Homotherium latidens*, *P. gombaszoegensis*, *P. pardus*, *Lynx spelaeus* and *F. silvestris* (as those are all felid taxa recovered from several Middle Pleistocene, we presume their co-existence). The values for these species were taken from Le Vallonnet for *H. latidens*, *P. gombaszoegensis* and *P. pardus*; a female *L. lynx* sample average ( $n = 15$ ) was used for *L. spelaeus* (with a similar range of values), and either the Trincheria Galería

site value for *F. silvestris* (5.8 mm) or the Olivola site *F. lunensis* value (4.5 mm) for the hypothetical wild cat species (*F. silvestris/lunensis*). The result would be an evenly spaced guild (using whatever value) (Fig. 3D). A hypothetical guild for the latter part of the Middle Pleistocene felids, after the entrance in Europe of *Panthera leo* – chronologically placed at around 0.5–0.6 Ma (García & Arsuaga 1999) – could be represented by *P. leo*, *Homotherium*, *P. pardus* (or *P. gombaszoegensis*), *Lynx* and *Felis*. An example for this approximate chronology may be the base of TD10 level (TD10<sub>(3)</sub>) at the Trincheria Dolina (TD) site dated to  $373 \pm 33$  ka (Falgüeres *et al.* 1999) where both lion and the saber-toothed cat are present (Fig. 3E). *Felis silvestris* and *L. pardinus* values were taken from the Trincheria Galeria (TG) site (contemporaneous with and placed only a few meters from TD) given a more complete record than those from TD. Leopard values (instead of jaguar) were included in the association, given that the last occurrence of *P. gombaszoegensis* in Western Europe is placed around 450 ka ago (García & Arsuaga 1999). Moreover, *P. pardus* was in maximum expansion, and present throughout a wide geographical range by Upper Pleistocene times. The *P. pardus* value applied in the test is taken from a modern sample ( $n = 40$ ), whose values overlap precisely with the European Middle

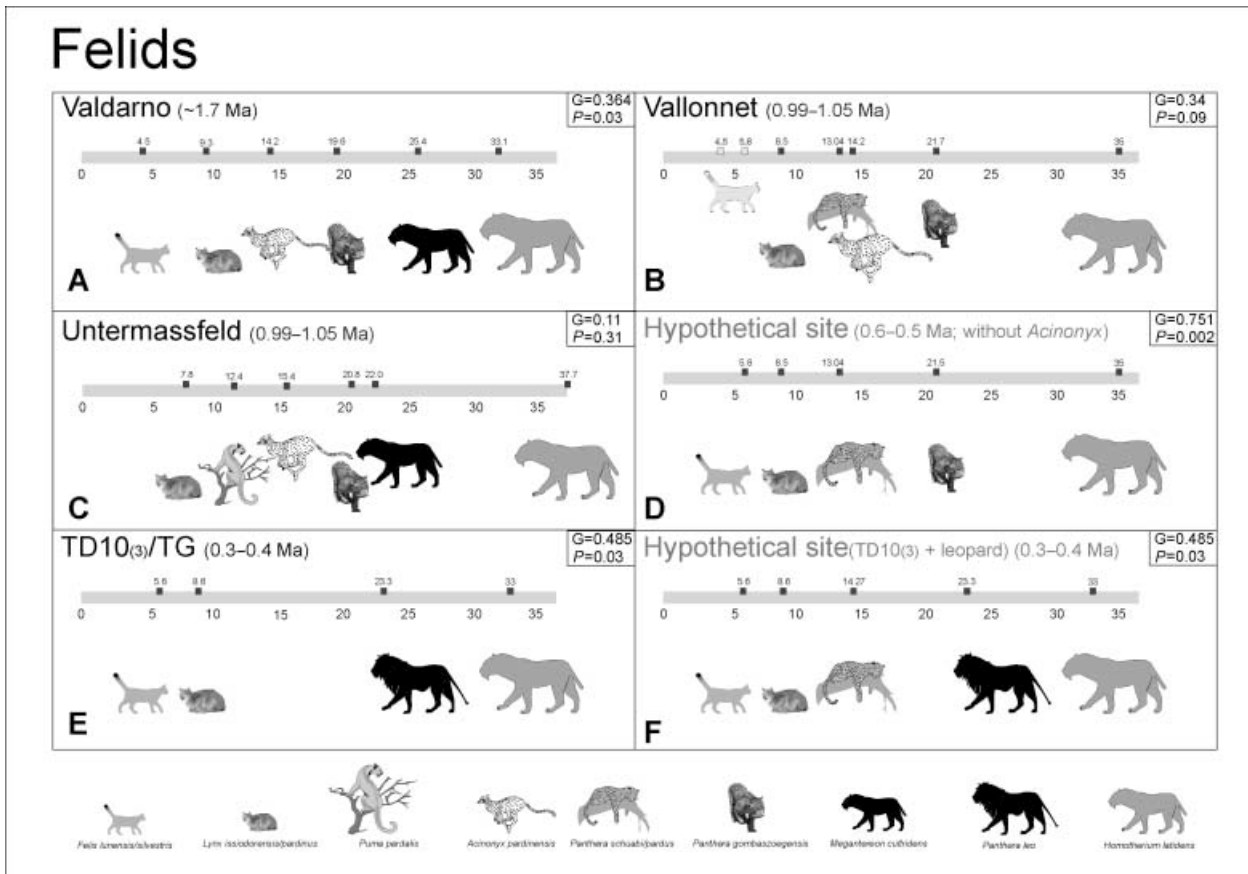


Fig. 3. Anterior-posterior diameter of the upper canine (Cs) in several felid paleoguilds and the Barton–David test results. A, B, C and E represent Pleistocene sites while D and F are hypothetical guilds. D could be a hypothetical early Middle Pleistocene felid guild in Europe; and F represents a hypothetical middle Middle Pleistocene felid guild yielding, both evenly spaced results ( $P + 0.05$ ).

Pleistocene specimens (as at Mauer, Schütt 1969). The results when the Barton–David test was applied to this hypothetical > type community = are evenly spaced, and same result was obtained when the leopard was substituted by the jaguar (Fig. 3F).

## Discussion

During the last 2 Myr, community compositions have changed both in felid and in canid guilds. Sympatric species showed character displacement in feeding structures in most of the cases of the European Pleistocene felid and canid guilds. Both families differ in their killing behaviours and consequently, in the morphological traits used in the analyses (canines in felids and carnassials in canids), which strengthens the observed patterns.

### Early Pleistocene canids

The Venta Micena association, which lacks *C. arnensis* but has *Vulpes preglacialis*, is not homogeneously

spaced. A large spacing between *Canis* and *Xenocyon* on the one hand, and between *V. preglacialis* and *Canis* on the other, is observed. Furthermore, a size decrease is evidenced in *C. etruscus* and *X. falconeri*. This size modification in both species could be the result of the absence of *C. arnensis* and could be interpreted as a case of ‘niche release’ as in modern canid communities (Dayan & Simberloff 1996). One alternative is that the differences observed between both sites are because of their diverse geographical location (Spain and Italy). However, the body sizes of extant Italian and Spanish wolves fail to show any significant differences (Blanco 1998; Ciucci & Boitani 1998). All *C. etruscus* individuals at Valdarno ( $n = 23$ ) exhibit a larger  $M_1$  than do the majority of the Venta Micena specimens; the latter have a lower average and range of values than that observed in the Valdarno sample. (Valdarno values:  $\bar{x}_{(n=23)} = 24.7 \pm 1.03$  mm; range = 22.9–27.1 mm; Venta Micena values:  $\bar{x}_{(n=3)} = 22.3$  mm (21.1, 21.8 and 24.1 mm)). At the Early Pleistocene site of Olivola, where *C. etruscus* co-existed with *C. arnensis* and *X. falconeri*, the  $M_1$  dimensions ( $\bar{x}_{(n=6)} = 25.3 \pm 0.49$  mm; range:



24.9–26.2 mm) are larger than those of Venta Micena, which could be due to a character displacement as a consequence of competition pressure with *C. arnensis*. Larger differences of species living in sympatry than those living in allopatry have been proposed as evidences in favour of character displacement in ecological communities (Schoener 1970; Huey & Pianka 1974; Schluter 2000).

### *Middle and Late Pleistocene canids*

The analysis of the Middle Pleistocene Trinchera Galería (TG) canid community includes *C. lupus* (early form), *C. alpinus* and *V. vulpes* and fails to reveal an even spacing. The length of  $M_1$  in the TG sample of *Canis* and *Cuon* is very similar, while *Vulpes* is clearly smaller. In contrast, the hypothetical community composed by *C. lupus*, *V. vulpes* and *C. alpinus* in the late Pleistocene was almost evenly spaced (Fig. 2D). The difference observed between this later modern canid community and that from the Middle Pleistocene (TG) (some 300 ka older) could be interpreted as a consequence of character displacement between *Cuon* and *Canis*. Both genera apparently lived in a competitive context during the Middle Pleistocene, as interpreted from their similar carnassial sizes. After this period, a size increase in *Canis* and a size decrease in *Cuon* were observed in the Upper Pleistocene populations. This suggests that competition during the previous period may be implied in the variations in size observed further and would allow for their coexistence. *Vulpes vulpes* shows no significant size change, perhaps because of a lack of competitive pressure from these larger canids. Therefore, whole disappearance in Europe at the end of the late Pleistocene might have not been because of competition with other social canids of similar size, such as the wolf, but to other possible causes (climatic, genetics, human pressure). During the end of the late Pleistocene, several other carnivores suffered a drastic reduction in their geographical ranges or vanished altogether (*Ursus spelaeus*, *P. pardus*, *P. leo* and *Crocota crocuta*). The extinctions might be related to some environmental event or increasing human activities.

### *Early Pleistocene felids*

The extinction of *Megantereon cultridens* and the nearly complete disappearance of *Acinonyx pardinensis* (with the exception of Mosbach 2 and Hundsheim, in the case of the latter species) after the Jaramillo magnetosubchron (C1r.1n) cannot be explained as a consequence of interspecific competition during the Early Pleistocene. Nevertheless, when comparing the

Valdarno (Plio-Pleistocene age) and Untermassfeld (Jaramillo age) sites (Table 2), a canine reduction is observed within *Megantereon*, approaching the canine size values of *P. gombaszoegensis* from (Vallonnet and Untermassfeld (Fig. 3A–C) and also from the slightly younger TDW4 site at Atapuerca (Table 2). This size displacement in *Megantereon* invading the jaguar ‘space’ could have produced a strong competition between these two felids, ultimately resulting in the extinction of *Megantereon*.

In order to understand the decline of *Acinonyx* (during the latest Early Pleistocene), we simulated an assemblage including the leopard (*P. pardus*), which first appears in Europe roughly 1.0 Ma ago, into the Valdarno-Olivola one, an older felid guild previous to the *Acinonyx* disappearance. The simulation was calculated using the *P. pardus* value from Vallonnet. *Megantereon*, which very latest occurrence is at Untermassfeld around 1 Ma ago, is not considered when applying the Barton–David test: the result is *not evenly spaced* as also observed in the Vallonnet site (Fig. 3B). This suggests a maximum competition focused in the mid-sized species, particularly between *P. gombaszoegensis*, *P. pardus* and *A. pardinensis*. The *Acinonyx* extinction or decline might have been brought about by several causes, including changes in ungulate communities and/or habitats (Turner 1992) and which finally led to intense ecological competition. *Acinonyx pardinensis* is not rare in pre-Jaramillo sites such as Saint Vallier (Viret 1954), Puebla de Valverde (Kurtén & Crusafont 1977), Les Etouaires (Schaub 1949), Olivola and Valdarno (Ficarelli 1984), and Jaramillo localities such as Untermassfeld or Vallonnet, whereas younger occurrences of *Acinonyx* in Europe are definitely rare, only Mosbach (Schütt 1970) and Hundsheim (Thenius 1954) being known. These might represent relict populations of a species already on its way to extinction and which was finally to disappear around 0.5 Ma ago (Fig. 4). The Vallonnet and Untermassfeld fossil assemblages of similar age (around 1 Ma) have not yielded any fossil remains corresponding to a ‘wild cat’, either *F. lunensis* (the species from Valdarno-Olivola, early Pleistocene sites) or *F. silvestris* (described at a number of Middle Pleistocene sites). In both cases the outlook after applying the Barton–David test is *not evenly spaced* (Fig. 3B, C).

### *Middle Pleistocene felids*

The Middle Pleistocene interval extends from the Matuyama-Brunhes boundary ( $775 \pm 10$  ka; Bassinot *et al.* 1994) to the base of the Eemian interglacial, at around 130 ka. We have divided this interval for a better understanding of the guilds evolution:

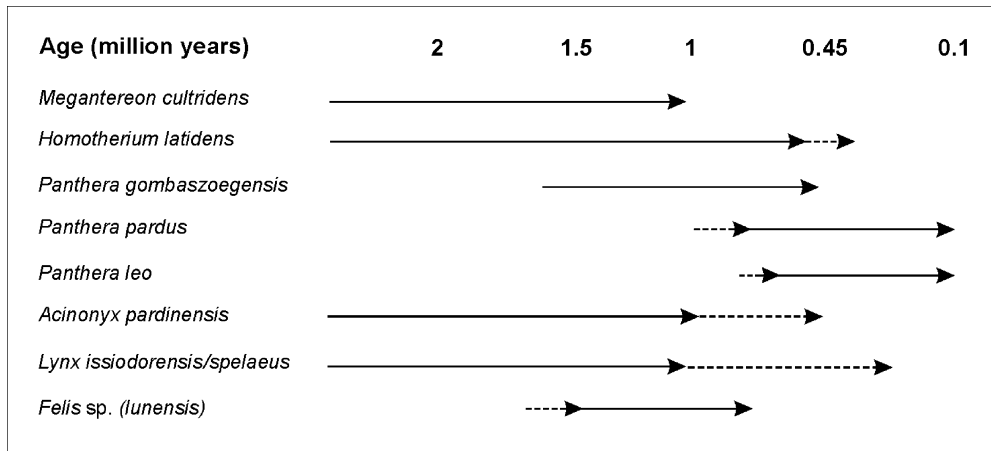


Fig. 4. Chronological distribution of European Felidae. From the late Early Pleistocene to the middle Middle Pleistocene (1 Ma to ca 500 ka) several species disappear while others appear into Europe.

1. From the Cromer Complex (early Middle Pleistocene, at around 780 ka) to the Holstein interglacial (middle Middle Pleistocene, at around 450 ka), and hence prior to the *P. leo* dispersal into Europe: The entrance of the leopard in Europe seems to constitute an alteration of the felid guild. This difference might be because of the co-existence of the leopard with both the jaguar and the cheetah (of roughly body similar size). With the entrance of the leopard into Europe and ‘occupying’ the previously-held *Acinonyx* size range, the hypothetical early Middle Pleistocene guild in Europe would be composed of *H. latidens*, *P. gombaszoegensis*, *P. pardus*, *L. spelaeus* and *F. silvestris*, yielding evenly spaced results (Fig. 3D). The Koneprusy C718 site (Czech Republic) is chronologically placed during the Elsterian period (Kahlke 1975) (Elsterian ca. 550 to 450 Ka) and includes the five latter felid species. This represents the first definite documented co-occurrence of *P. gombaszoegensis* and *P. pardus*, and in subsequent sites (Mauer 5, Mosbach 2, Stránská Skála) there is evidence as well of both felid species.
2. From the Holstein (middle Middle Pleistocene, at around 450 ka), after the entrance of *P. leo*, to the base of Eem interglacial, at around 130 ka: In this period, the typical Middle Pleistocene felid community after the entrance of *P. leo* into Europe (Fig. 4) might be made up of *H. latidens*, *P. leo*, *P. pardus* (or *P. gombaszoegensis*), *L. pardinus/lynx* and *F. silvestris*. The results from Barton–David test indicated that this guild could be structured because of interspecific competition (Fig. 3F). Therefore, these ecosystems might ‘support in balance’ six species within the Felidae family, as observed in the Valdarno–Olivola sites. Nevertheless, the degree of competition between the species,

and the consequent pressure within the guild, is determined by the specific composition of that particular community, and can even eventuate in the extinction of some of the species.

## Conclusions

The hypothesis that the observed size–ratio relationships are selected for interspecific competition is supported by the presented data. The results are similar to previous studies on extant felid and canid guilds (Dayan *et al.* 1989b, Dayan *et al.* 1990), and on hyaenid paleo guilds (Werdelin 1996). The results of this study support some suggestions about the importance of coevolution in shaping communities. Roughgarden (1989) has pointed out that evenly spaced communities are only possible when time allows for coevolutionary equilibria to be attained between successive invasions. This may be the case in most of the felid and canid guilds analyzed, where communities shifted from non-equilibrium to evenly spaced communities with time. Nevertheless, given the prevalent scarcity within the fossil record, it has not been possible to separate felid species by sex in the analyses, and it has been necessary to afford a single value for each species. It is possible that intraspecific competition (e.g. between the sexes) may also shape communities and size ratios (Slatkin 1980, 1984; Dayan *et al.* 1990, 1993).

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