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Title: Niche overlap and competition potential among tigers (*Panthera tigris*), sabertoothed cats (*Homotherium ultimum*, *Hemimachairodus zwierzyckii*) and Merriam's Dog (*Megacyon merriami*) in the Pleistocene of Java

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Abstract: On Java during the Pleistocene, tigers of more than 300 kg occurred, but these are restricted to a single Late Pleistocene faunal unit, while Early and Middle Pleistocene tigers possessed body masses comparable to those of historic Javanese and extant Sumatran tigers. The aim of this study is to test if competition for prey with other hypercarnivorous taxa such as sabertoothed cats and the large Merriam's Dog was the driver for the increase in body mass of tigers. We calculated body masses and prey mass spectrum for tigers and potential competitors using linear regressions. Niche overlap was then estimated based on the prey mass spectrum after which niche overlaps were used as indicators for competition potentials. Reconstructed body mass for *Homotherium ultimum*, *Hemimachairodus zwierzyckii*, *Megacyon merriami* are 154 kg (comparable to *Homotherium* from Untermassfeld), 130 kg and 52 kg, respectively. The niche overlap between tigers and Merriam's Dog is highest (100%) while it is comparatively low (60 %) between tigers and *Homotherium ultimum*. In order to reduce competition, tigers seem to have increased body mass to avoid competition especially with Merriam's Dog whereas Merriam's Dog on its turn seems to have decreased body mass to avoid competition with tigers. The sabertoothed cats on the other hand seem to have been unable to adapt and went extinct.

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5

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20 prey mass spectrum – Sangiran – Southeast Asia

21 Abstract

22 On Java during the Pleistocene, tigers of more than 300 kg occurred, but
23 these are restricted to a single Late Pleistocene faunal unit, while Early and
24 Middle Pleistocene tigers possessed body masses comparable to those of
25 historic Javanese and extant Sumatran tigers. The aim of this study is to test if
26 competition for prey with other hypercarnivorous taxa such as sabertoothed
27 cats and the large Merriam's Dog was the driver for the increase in body mass
28 of tigers. We calculated body masses and prey mass spectrum for tigers and
29 potential competitors using linear regressions. Niche overlap was then
30 estimated based on the prey mass spectrum after which niche overlaps were
31 used as indicators for competition potentials. Reconstructed body mass for
32 *Homotherium ultimum*, *Hemimachairodus zwierzyckii*, *Megacyon merriami* are
33 154 kg (comparable to *Homotherium* from Untermassfeld), 130 kg and 52 kg,
34 respectively. The niche overlap between tigers and Merriam's Dog is highest
35 (100%) while it is comparatively low (60 %) between tigers and *Homotherium*
36 *ultimum*. In order to reduce competition, tigers seem to have increased body
37 mass to avoid competition especially with Merriam's Dog whereas Merriam's
38 Dog on its turn seems to have decreased body mass to avoid competition with
39 tigers. The sabertoothed cats on the other hand seem to have been unable to
40 adapt and went extinct.

41 1 Introduction

42 Body masses of tiger subspecies vary in accordance with latitude and
43 geographic distribution (Mazák, 1981). In Southeast Asia body masses of
44 tigers, for example, range from 80 to 120 kg while body masses of Siberian
45 tigers can reach up to 300 kg (Mazák, 1981). This variation in body masses is
46 regularly explained with Bergmann's rule according to which closely related
47 mammalian taxa tend to be larger in colder environments than in warmer ones
48 (Bergmann, 1847; Seidensticker et al., 1999; Meiri et al., 2007).

49 In the Pleistocene, however, tigers with body masses in excess of 300 kg also
50 occurred in lower latitudes, particularly in Java (Hertler and Volmer, 2008).

51 Such high body masses cannot be understood as an adaptation to cold
52 climate in the sense of Bergmann. Moreover, the large tiger individuals are
53 restricted to a single Late Pleistocene faunal unit Ngandong (Yokoyama et al.,
54 2008), while Early and Middle Pleistocene tigers of Java possess body
55 masses comparable to historic Javanese and extant Sumatran tigers (Hertler
56 and Volmer, 2008).

57 Competition with other hypercarnivorous taxa may provide an alternative
58 explanation for the observed shifts in body mass. The prey mass spectrum of
59 carnivores strongly correlates with body mass (Carbone et al., 1999; Hemmer,
60 2004) and shifts in body mass lead to shifts in prey mass spectra (Sinclair et
61 al., 2003). Extensive overlap in the prey mass spectra among any pair of
62 coexisting carnivores can therefore be reduced by increase or decrease in
63 body mass.

64 Body mass increases observed for tigers in the Late Pleistocene Ngandong
65 faunal stage may therefore have been induced by a strong niche overlap with

66 the short-faced hyena (*Pachycrocuta brevirostris*) during the preceding faunal
67 unit (Hertler and Volmer, 2008). Consequently, this would have led to a
68 reduction of competition. Niche overlap between tigers and other competitors
69 like Trinil Dog (*Mececyon trinilensis*, or *Cuon trinilensis* in Louys, 2014),
70 leopard (*Panthera pardus*) and the Asiatic wild dog (*Cuon alpinus*) are much
71 lower on the ground of their much lower body masses (Hertler and Volmer,
72 2008). These taxa are therefore not considered as ecologically significant
73 competitors for tigers in the Ngandong faunal unit.

74 Hertler and Volmer (2008) also mentioned additional large carnivore taxa that
75 co-occurred with tigers during the Pleistocene of Java, namely the
76 machairodonts *Homotherium ultimum* and *Hemimachairodus zwierzyckii*, as
77 well as a very large canid, *Megacyon merriami* (von Koenigswald, 1940;
78 Schütt, 1973). This raises the question whether competition between tigers
79 and the machairodonts and canids may have had an additional impact on tiger
80 body masses.

81 The succession of mammalian faunas at Sangiran illustrates a biostratigraphic
82 sequence (Fig. 1), which calibrates other Javanese fossil localities (Fig. 2) in
83 Central and East Java (Watanabe and Kadar, 1985). Von Koenigswald
84 collected a large number of mammalian fossils from Sangiran, including
85 specimens attributed to the machairodonts and Merriam's Dog (von
86 Koenigswald, 1940). However, the deposits at the Sangiran dome cover a
87 lithostratigraphic sequence extending possibly over a million years (Watanabe
88 and Kadar, 1985; Sémah et al., 2003). The lack of crucial stratigraphic
89 background information in Von Koenigswald's collection hampers the
90 assessment with whom *Homotherium ultimum*, *Hemimachairodus* and

91 *Megacyon* competed. Beside fossils collected by Von Koenigswald in
92 Sangiran, fossils from Teguan and Jeruk are found by Dubois and cannot be
93 attributed to one of the faunal levels (van den Bergh, 2001). Among these
94 fossils are also an ulna from a tiger found at Teguan and a maxilla found in
95 Jeruk (Brongersma, 1935). Reconstruction of body masses may help to
96 assign fossils from Teguan and Jeruk to a faunal level.

97 Nevertheless, it is evident that the machairodonts as well as Merriam's Dog
98 were collected from Early and/or Middle Pleistocene deposits. Von
99 Koenigswald (1934, 1974) further informs that *Megacyon merriami* was
100 collected from the black clays (von Koenigswald 1940). The black clays at
101 Sangiran encompass both the Satir and Ci Saat faunal unit (Watanabe and
102 Kadar, 1985). The Satir faunal unit represents an imbalanced island fauna
103 without carnivores (Sondaar, 1984), which implies that Merriam's Dog
104 occurred in the Ci Saat faunal unit. The machairodonts should be attributed to
105 either the Ci Saat faunal unit or the Kedung Brubus faunal unit. For
106 stratigraphic reasons, the Trinil H.K. faunal unit, which is bracketed by Ci Saat
107 and Kedung Brubus faunal units, cannot be excluded either for the
108 machairodonts. With respect to biostratigraphy, tigers are likely part of all
109 three faunal units (Fig. 2). Tigers must thus have competed with the
110 sabertoothed cats and Merriam's Dog.

111 Here, we will reconstruct body masses and prey mass spectra for all large
112 carnivores from Sangiran in order to address potential niche overlaps between
113 tigers (*Panthera tigris*), sabertoothed cats (*Homotherium ultimum*,
114 *Hemimachairodus zwierzyckii*) and Merriam's Dog (*Megacyon merriami*). Our
115 hypothesis is that extensive niche overlap among these taxa indicates strong

116 competition which subsequently resulted in body mass shifts observed in later
117 faunal units.

118 2 Material and Methods

119 Body masses were reconstructed for canids and felids from Sangiran (based
120 on regressions; details in Appendix A). Based on these body masses, we infer
121 prey mass spectra (PMS) using a second set of regressions. Finally, niche
122 overlaps (NO) between the taxa at Sangiran are reconstructed. Broad niche
123 overlap is used as a proxy for high competition potentials, because prey of the
124 same size is consumed by both competitors.

125

126 The fossil samples are stored in the Von Koenigswald collection
127 (Senckenberg Research Institute, Frankfurt am Main, Germany), the Dubois
128 Collection (Naturalis Biodiversity Center, Leiden, the Netherlands) and the
129 Museum of Geology (Bandung, Java) (**Error! Reference source not
130 found.)Error! Reference source not found..**

131 The tiger samples for reconstructing body mass come from the following sites:
132 Dubois Collection: Trinil (n=13), Pitu (n=1), Jeruk (n=1), Kebon Duren (n= 1),
133 Kedung Brubus (n=2), Teguan (n=1), von Koenigswald Collection: Sangiran
134 (n=14) and the Museum of Geology: Bumiayu (n=2), Ngasinan (n=1),
135 Ngandong (n=7), and Watualang (n=2). The sites of Ngandong, Ngasinan and
136 Watualang belong to the Ngandong Faunal stage (Weidenreich, 1951;
137 Sondaar, 1984; Hertler and Volmer, 2008), whereas all other samples are
138 classified as pre-Ngandong-samples. The samples from Pitu and Trinil are
139 classified as Trinil H.K. sample and Kedung Brubus and Kebon Duren as

140 Kedung Brubus sample. All samples are shown in Table 2 and their
141 stratigraphic background in Table 1. The 40 tiger fossils from Sangiran
142 (Hemmer, 1971) originate from Early and/or Middle Pleistocene deposits.
143 Because of the absence of stratigraphic background we excluded specimens
144 from the Sangiran dome from our previous studies (Hertler and Volmer, 2008).
145 Nonetheless, all specimens were retrieved from deposits at Sangiran, which
146 implies that they are geographically congruent and are thus included in this
147 study.

148 The samples of the *Homotherium ultimum* (n=1), *Hemimachairodus*
149 *zwierzyckii* (n=1) and *Megacyon merriami* (n=3) are stored in the Von
150 Koenigswald-Collection and originate from the Sangiran Dome. The
151 machairodonts and *Megacyon merriami* are here attributed to the Ci Saat
152 faunal stage (see section 1).

153

154 2.1 Body mass and prey mass spectrum reconstructions

155 For reconstruction of body masses on the basis of long bones (humerus,
156 femur, tibia, ulna) the regressions of Christiansen and Harris (2005) are used.

157 Since for teeth only regressions based on M1 length are published, we
158 calculated regressions for other tooth positions based on samples of extant
159 felids and canids. We also calculated a tiger specific regression based on the
160 correlation between skull length and body mass in extant tiger subspecies.

161 The samples and the procedure of calculating these regressions (**Error!**
162 **Reference source not found.**) can be found in the supplementary material of
163 this paper (Appendix A Supplementary data).

164 Body mass is reconstructed for each fossil. For skulls, mandibles and teeth,
165 the computed regressions as given in **Error! Reference source not**
166 **found.Error! Reference source not found.**Table 3 are used. For mandibles and
167 skulls, body mass is estimated for each usable parameter after which the
168 means of all estimated body masses was calculated for the respective
169 specimen.

170 For each sample the mean body mass was calculated. For Javanese tigers,
171 the mean body mass of the pre-Ngandong and Ngandong samples were
172 compared by a t-test. In addition, the means of the samples from Trinil,
173 Kedung Brubus, Sangiran and Ngandong were compared with ANOVA.

174 Each sample/taxon is then characterized by its minimum (BM_{min}), mean
175 (BM_{mean}) and maximum body mass (BM_{max}). We applied the mean percentage
176 prediction error (%PE) to calculate a range of reconstructed body masses. For
177 each sample the minimum and the maximum body mass including errors were
178 determined ($BM_{min\%PE}$ und $BM_{max\%PE}$).

179 All taxa included in this study have a hypercarnivorous diet, according to the
180 definition of Van Valkenburgh (1988), who defined a hypercarnivorous diet as a
181 diet of which at least 70% of consumed biomass comes from self-hunted
182 vertebrate prey (van Valkenburgh, 1988, 2007; Wesley-Hunt, 2005).

183 Felids are characterized by hypercarnivorous dentitions; especially
184 machairodonts show a kind of “carnassialisation” of their premolars (Thenius,
185 1989; Ewer, 1998). Accordingly, the tiger and the maicharodonts are treated
186 as hypercarnivores in this study.

187 In case of canids, the diet varies from hypocarnivorous (e.g. *Chrysocyon*) to
188 hypercarnivorous (e.g. *Lycaon pictus*) and this is reflected in both tooth and

189 skull morphology (Ewer, 1998). Dental morphology can be used to reconstruct
190 the diet of fossil taxa (Ewer, 1998). Lyras et al. (2010) consider Merriam's Dog
191 as hypercarnivorous, because its dentition is most comparable to the
192 hypercarnivorous morphology of the molars of *Xenocyon* and *Lycaon pictus*.
193 Also Schütt (1973) mentioned the similarity of *Megacyon* to *Xenocyon* and
194 that both likely belong to the same genus.

195 Hunting strategies may also differ and can have a significant impact on the
196 prey mass spectra in canids (Nudds, 1978). Most hypercarnivorous canids
197 hunt in packs. Due to energetic constraints, carnivores with body masses of
198 21 kg or more hunt on prey larger than themselves (Carbone et al., 1999;
199 Bogusch, 2002), which is achieved by canids by hunting in a group (van
200 Valkenburgh et al., 2003). Therefore, we compare *Megacyon* here with the
201 pack-hunting hypercarnivorous canid *Cuon alpinus*.

202 Prey mass spectrum is required in order to calculate the potential niche
203 overlap. The prey mass spectrum of carnivores is often demonstrated by body
204 mass classes following logarithmic steps (Hemmer, 2004; Hertler and Volmer,
205 2008). The total hunted prey biomass is distributed over these body mass
206 classes. Some classes contribute relatively more to the total hunted prey
207 biomass than others (Volmer, 2013). These classes are the focus classes of
208 the top predators and it is assumed that the predator mainly subsists on prey
209 of these classes. The focus classes can be reconstructed using regressions
210 terms to calculate the mean prey mass (Hemmer, 2004; Hertler and Volmer,
211 2008).

212 A regression term is known only for felids (Hemmer, 2004), whereas such a
213 regression is missing for canids. But also in case of the regression term for
214 felids, it remains unclear on which sample it has been computed.

215 In order to reconstruct the prey mass spectra of Felidae and Canidae, we
216 computed new regressions based on the correlation between body mass and
217 prey mass of predators using data and samples of field studies of extant
218 members of these families. These regressions were calculated for felids and
219 canids separately, because both follow different hunting techniques. In case of
220 felids we included only large cats (> 10 kg) in our sample, because small cats
221 use different hunting styles (Schaller, 1972; Leyhausen, 1979; Ewer, 1998)
222 focusing on prey smaller than themselves (Carbone et al., 1999).

223 The mean prey mass of each taxon is calculated from prey counts of several
224 studies listed in
225 Table 4. The advantage of using more than one study from one study area to
226 calculate the mean body mass of a species, is that the influence of other
227 factors – e.g. prey offer, small sample size of kills/scats – which affect the
228 prey mass spectrum can be reduced. The body masses of the comparative
229 predators are taken from the literature (Jerdan, 1984; Kingdon, 1997;
230 Eisenberg and Redford, 1999; Smith and Xie, 2008).

231 The focus classes were calculated from the calculated regression terms (
 232 Table 5) and the reconstructed body masses from
 233 Table 6. The mean prey mass was calculated by the regression term and determines
 234 the focus class. Prey masses were calculated for each species using the minimum
 235 (BM_{min}), average (BM_{mean}), maximum (BM_{max}) body mass. To account for the
 236 statistical error of body mass reconstructions the prey mass was also calculated for
 237 BM_{min%PE} and BM_{max%PE} and prey mass classes will be assigned. These are called
 238 FC_{Min}, FC_{Mean}, FC_{Max} and FC_{Min%PE}, FC_{Max%PE}.
 239 Since the regression terms for calculation of prey masses also yield statistical
 240 errors, the reconstructed focus classes were compared to prey mass spectra
 241 of comparable extant family members with comparable size and a
 242 hypercarnivorous diet.

243

244 2.2 Calculation of niche overlap (NO)

245 Niche overlap was calculated as the percentage of overlap following
 246 Renkonen and Schoener (Renkonen, 1938; Schoener, 1970; Krebs, 1999),
 247 which is a measure of the actual area of overlap of the resource utilization
 248 curves of two species (Krebs, 1999).

249 Its equation is:

$$250 p_{jk} = [L \sum_{i=1}^n (p_{ij}, p_{ik})] \times 100, \text{ where}$$

251 p_{ik} = percentage overlap between species j and species k

252 p_{ij} = proportion resource i is of the total resources used by species j

253 p_{ik} = proportion resource i is of the total resources used by species k

254 n = total number of resource states

255 In this study the resources were reflected by the prey mass classes according
256 to Hertler and Volmer (2008). The total of focus classes for a sample is
257 assumed to represent 100% and each focus class contributes equally. For
258 example, if the reconstructed focus classes of predator A are 3a, 3b, 3c and
259 4a, and those of predator B are 3c, 4a, 4c, 5a and 5b, it follows that predator
260 A experiences a niche overlap of 50% with predator B, but predator B
261 experiences an niche overlap of only 20% by predator A.
262 The higher the niche overlap, the higher is the potential competition between
263 the competing taxa.

264 3 Results

265 3.1 Reconstructed body masses

266 Reconstructed body masses are shown in
267 Table 6 and Figure 3. Sangiran tigers have a mean body mass of 121 kg and
268 differ not significantly from other pre-Ngandong tigers. The largest Sangiran
269 tigers virtually reach the mean body mass of Ngandong tigers (182 and 184
270 kg, respectively).
271 The means of the single pre-Ngandong samples (Bumiayu, Trinil H.K.,
272 Kedung Brubus and Sangiran sample) vary between 87 and 122 kg.
273 The mean body mass for the Ngandong sample is 184 kg and for the pre-
274 Ngandong sample 114 kg. The Ngandong tiger is significantly larger than the
275 pre-Ngandong tiger regarding its body mass (ANOVA $p=0,0073$, Table 8). The
276 reconstructed body mass of *Homotherium ultimum*, *Hemimachairodus*
277 *zwierzyckii* and *Megacyon merriami* is 154 kg, 130 kg and 52 kg respectively.
278

279 3.2 Prey Mass Spectra and niche overlaps

280 The regressions for mean prey mass reconstruction show correlations
281 between mean body mass and prey mass (
282 Table 5). The prey mass spectra are shown in

283 Table 7. pre-Ngandong tigers and Sangiran tigers focus on the same prey
284 classes (3a to 4b). The prey mass spectrum of Ngandong tigers is shifted and
285 focusses on classes 3b to 5a. *Megacyon merriami* focuses on classes 3b to
286 4b which coincide with those of Sangiran tigers.

287 *Homotherium ultimum* and *Hemimachairodus zwierzyckii* focus on classes 3c
288 to 4c and 3b to 4b, respectively.

289 Prey mass spectra of Merriam's Dog overlap strongest with Sangiran and pre-
290 Ngandong tigers (NO = 100%) and vice versa (Figs 4 and 5).

291 *Hemimachairodus* also overlaps with the tiger by 100%, but *Homotherium*
292 only by 60%. Therefore, the highest competition potential is observed
293 between Sangiran tigers and pack-hunting Merriam's Dog.

294 Niche overlaps between tigers from Ci Saat, Trinil H.K. or Kedung Brubus and
295 the three other carnivores from Sangiran show slightly different results:

296 Merriam's Dog and *Hemimachairodus* both overlap all tigers by 100%.

297 *Homotherium ultimum* overlaps the tiger from Bumiayu by 66–67% and both,
298 the Trinil H.K. and Kedung Brubus tigers by 75%.

299 Niche overlap experienced by the competitors show similar results. *Megacyon*
300 *merriami* is overlapped by the Sangiran tiger by 100% (Fig. 5). The

301 Machairodonts experience smaller niche overlaps (60–80%) by the Sangiran
302 tiger. Niche overlaps with the Ngandong tiger are smaller for *Megacyon*

303 *merriami* and *Hemimachairodus zwierzyckii*, but larger for *Homotherium*

304 *ultimum*.

305 4 Discussion

306 4.1 Reconstructed body masses

307 All regressions for body mass reconstruction show a significant correlation
308 between tooth/skull length and body mass. The strongest correlations are
309 found for the carnassials (lower M1 and upper P4) in both felids and canids.
310 In felids, the upper P2 gives strong statistical errors ($r^2 = 0.314$, %SEE = 177,
311 %PE = 76%). The reason for this remains unclear, but this premolar is
312 reduced in felids –in some species it is even completely lacking–and shows
313 generally a high variability in its morphology (Thenius, 1989; Ewer 1998).
314 Tooth positions with a high variability usually show low correlation with body
315 mass (van Valkenburgh, 1990). Thus we excluded the upper second
316 premolars from the body mass reconstructions in this study and cannot
317 recommend using this tooth position in other studies.

318 Regressions based on dental elements have on average higher statistical
319 errors in comparison to the regressions for long bone elements developed by
320 Anyonge (1993) and Christiansen and Harris (2005). Christiansen and
321 Harris's regressions (2005) show %SEEs of 16–55 and Anyonge regressions
322 show %SEEs of 24–39 for felids and 23–41 for canids (1993). Our %SEE for
323 felids range from 14–50 % with the exception of the upper P2. The
324 regressions based on skull length of tigers, lower M1 and upper P4 have
325 statistical errors that fall into the range of error of limb bone regressions.

326 Therefore, we consider these two tooth positions (the carnassials) as well as
327 skull length as reliable as limb bones for body mass reconstruction.

328 %SEE of the canid regressions for lower P3, lower P4 and lower M1 also fall
329 within the range of the limb bone regressions by Anyonge (1993), which
330 makes them in our view as reliable as the limb bone measurements.
331 If tooth morphology differs strongly from that in the sample used for the
332 calculation of the regressions, the reconstructed body mass may vary widely
333 from its actual body mass, since teeth are no weight bearing structures
334 (Fortelius, 1990). This may apply to the reconstructed body masses of
335 *Homotherium* and *Hemimachairodus*. The lower P3 of *Homotherium ultimum*
336 is strongly reduced and we therefore excluded this position for the
337 reconstruction of its body mass. Application of the regression equation to the
338 lower P3 of *H. ultimum* would result in a body mass of only 24 kg. Obviously,
339 this value underestimates body mass, since other body mass reconstructions
340 of *Homotherium crenatidens* from Untermassfeld (Early Pleistocene,
341 Germany) range between 180 kg and 300 kg and those of *Homotherium*
342 *serum* range between 134 kg and 236 kg (Anyonge, 1993; Hemmer, 2001).
343 The 218 kg for *Homotherium ultimum* from Java as the means of regressions
344 based on the carnassials thus confirms the estimations for the other two
345 species of *Homotherium* from Untermassfeld.
346 Estimated body masses for Merriam's Dog vary around 52 kg which is
347 comparable to the size of extant gray wolves (*Canis lupus*). The reconstructed
348 masses based on measurements of the upper and lower first molars do not
349 differ much (49–55 kg) and thus both of them have been applied for the
350 reconstruction of prey mass spectra.
351 The body masses of tigers do not differ significantly among the pre-Ngandong
352 samples. Variation in body mass is low, although some fossils from Sangiran

353 fall in a range above the mean body mass of Ngandong tigers. This illustrates
354 that single large individuals existed already in the Middle Pleistocene, but the
355 majority of individuals was smaller than those of the Late Pleistocene.

356 The wide range of body masses in Ngandong tigers likely reflects sexual
357 dimorphism of these tigers. Females of all subspecies do not differ strongly in
358 body size in contrast to males (Seidensticker et al., 1999). This sexual
359 dimorphism increases with size, for example males are 185% larger than
360 females in *P. t. tigris* and 206% larger in *P. t. altaica* (Mazák, 1981).

361 Our study confirms the increase in tigers' body mass from the Middle to the
362 Late Pleistocene. The t-test comparing the mean reconstructed body mass of
363 pre-Ngandong and Ngandong samples indicates a significant difference at the
364 1%-level ($p= 0.0073$).

365 Two tiger fossils from the sites Teguan and Jeruk could not be attributed to a
366 certain faunal stage in earlier studies (van den Bergh et al., 2001). The tiger
367 fossil of Teguan has a reconstructed body mass of 86 kg and is comparable
368 with body masses reconstructed from the pre-Ngandong sample. In addition,
369 the presence of *Pachycrocuta brevirostris* in Teguan suggests an attribution of
370 this site to the Kedung Brubus faunal stage (de Vos pers. comm.). The
371 reconstructed body mass does not exclude this, but cannot confirm the
372 assumption either.

373 On the other hand, the tiger fossil of Jeruk has a reconstructed body mass of
374 228 kg. This body mass only falls in the range of the Ngandong tiger sample,
375 and thus suggests the attribution of Jeruk to the Ngandong faunal stage. The
376 presence of *Panthera pardus* at this site (Brongersma, 1935; Hemmer and

377 Schütt, 1972) further confirms this, because *Panthera pardus* is known only
378 from the Ngandong faunal stage and onwards.

379

380 4.2 Prey mass spectra (PMS)

381 The regressions for reconstruction of the mean prey masses show high
382 statistical errors (%PE 68 and 95, %SEE 138 and 192). Since other studies
383 about correlations between body mass and prey mass do not provide any
384 information about their statistical errors (Carbone et al., 1999; Hemmer, 2004)
385 we cannot compare our regressions with similar ones.

386 In order to cope with this shortcoming and to reduce the errors, we applied a
387 classification system. In addition, we compared the reconstructed focus
388 classes with results from comparable members of the respective families. This
389 method can also be used on itself for estimating the focus classes of fossil
390 carnivores. However, in some cases data for species or comparable family
391 members are unavailable. In addition, in case of fossil taxa we cannot be
392 certain about their hunting behavior. As we have shown here, Merriam's Dog
393 likely was a pack hunter.

394 In the case of extant cats, hunting strategy has no strong effect on prey mass
395 spectrum (Hemmer, 2004). The only pack hunting felids are lion and cheetah,
396 whose females or males respectively hunt in packs. Calculation of the prey
397 mass on the basis of regression F-1 would lead to an overestimation by 24%
398 for the lion (predicted: prey mass 295 kg, prey class 4b; observed: prey mass
399 238 kg, prey class: 4b) and for the cheetah to a underestimation of 46 %
400 (predicted: prey mass 20 kg, prey class: 3b; observed: prey mass 36 kg, prey
401 class: 3b). Since over- and underestimation occur in solitary taxa as well, we

402 cannot conclude that pack hunting on itself leads to an underestimation of
403 prey mass by regression F-1. In both cases, the prey class of the observed
404 and predicted prey mass is identical and illustrates that the regression is
405 applicable for reconstruction of prey mass spectra.

406 Whether machairodont taxa like *Homotherium* and *Hemimachairodus* were
407 pack hunters or solitary hunters will probably never be revealed. *Homotherium*
408 *latidens* is generally considered as a pack hunter, because of its cursorial
409 adaptations and reduced claws (Antón et al., 2005). *Hemimachairodus* is only
410 known from the Pleistocene of Java and no postcranial material was found.
411 But even if it would have focused on prey larger than reconstructed, this would
412 only have further reduced its competition potential with the tigers.

413

414 4.3 Competition potential among Sangiran carnivores and its impacts

415 The Sangiran tiger and Pre-Ngandong tiger have the same prey mass
416 spectra and thus also the same niche overlaps with the other three potential
417 competitors. The pre-Ngandong sample includes body masses from all Middle
418 Pleistocene sites in Java where the tiger occurred. Thus, there was no
419 geographic variation in body mass and prey spectrum. The pre-Ngandong
420 tiger focuses on classes 3a–4b according to prey from 10–200 kg.

421 From pre-Ngandong to Ngandong we can observe a shift to the classes 3b–
422 5a (20–1000 kg). This shift in the prey mass spectrum is caused by the shift in
423 body masses of the Ngandong tiger. Thus, the increased body mass of the
424 tiger had an impact on its prey spectrum and thus consequences for
425 competition relations, independent of whether competition was the main
426 driver for the body mass increase or not. The prey mass spectrum of the

427 Ngandong tiger includes class 5a, which is not hunted by any other potential
428 competitor. This applies also to *Pachycrocuta brevirostris*, *Cuon alpinus* and
429 *Panthera pardus* whose prey mass spectra were reconstructed in our former
430 study (Hertler & Volmer, 2008). Further, its prey mass spectrum includes class
431 4c which is hunted only by *Homotherium ultimum*. The Ngandong tiger thus
432 has the lowest niche overlap with *H. zwierzyckii* and Merriam's Dog.
433 It focuses on the same prey classes as *Megacyon merriami* and thus
434 experienced a niche overlap of 100% by *M. merriami*. The Ngandong tiger
435 would have experienced a smaller niche overlap by Merriam's dog (67%) than
436 the pre-Ngandong tiger. Thus, the increase in the body mass of the tiger
437 would have lowered the competition potential between both species.
438 Merriam's Dog also experienced a niche overlap of 100% by the tiger. As a
439 solitary hunter, *Megacyon* would have had no niche overlap with tigers at all. It
440 could have avoided niche overlap and competition with tigers by adopting a
441 solitary hunting style. More likely is the strategy proposed by Lyras et al.
442 (2010), who suggest that Merriam's Dog eventually reduced its body size and
443 evolved into the jackal-sized *Mececyon trinilensis*. In this way, there is no
444 competition with tigers. An alternative scenario is that *Megacyon* could not
445 adapt, went extinct and was replaced by a second, much smaller
446 hypercarnivorous canid with no niche overlap with the tigers.
447 Both scenarios are supported by our data, because Merriam's Dog had the
448 same reconstructed focus classes as the tiger whereas that of *Mececyon* falls
449 well below this class. The derived *Mececyon* would not have suffered from
450 niche overlap with the other carnivores from Sangiran because the clouded

451 leopard is significantly larger and the Bengal cat, mustelids and viverrids
452 significantly smaller.

453 Competition between tigers and *Homotherium ultimum* is not likely to have
454 had an impact on the extinction of the sabertoothed cats or shifts in body
455 masses of the tigers. *Homotherium ultimum* has the largest body mass and
456 thus focused on larger prey classes having a PMS of 3c–4c. The pre-
457 Ngandong tiger got overlapped by *Homotherium* only by 60%. This is the
458 lowest niche overlap the pre-Ngandong tiger would experience if it would have
459 competed to Sangiran carnivores. In contrast, the Ngandong tiger would have
460 been overlapped by *Homotherium ultimum* by 83%. This is 23% more and
461 thus, the increase in the body mass of the tiger likely did not evolve in
462 response to competition with *Homotherium ultimum*.

463 *Hemimachairodus zwierzyckii* shows an overlap of 80% with Sangiran and
464 pre-Ngandong tigers. This is as strong as the short-faced hyena and tigers in
465 Kedung Brubus (Hertler and Volmer, 2008). The observed increase in body
466 mass of the tiger in the Late Pleistocene would lead to a decrease in niche
467 overlap to 67%. Thus, competition between *Hemimachairodus zwierzyckii*
468 may have been the reason for body mass increase in the tiger to avoid
469 competition.

470 In summary, in the Ci Saat faunal level the coexistence of Merriam's Dog,
471 *Hemimachairodus zwierzyckii* and *Panthera tigris* implied a high degree of
472 competition which likely led to competition avoidance strategies. This is in
473 case of *Hemimachairodus zwierzyckii* its extinction, while *Panthera tigris*
474 increased its body mass and thus shifted its prey mass spectrum. Indeed,
475 *Hemimachairodus zwierzyckii* is already extinct in the following Trinil H.K.

476 faunal level. Merriam's Dog on the other hand was replaced by *Mececyon*
477 *trinilensis* in the Trinil H.K. faunal unit. The extinction of *Homotherium ultimum*
478 cannot be explained by competition between any of the other large carnivores.

479

480 Conclusion

481 Our results confirm that tigers increased their body mass between the Middle
482 and Late Pleistocene. While tigers from the sites of Teguan have body
483 masses comparable to those of pre-Ngandong tigers, the tiger from Jeruk falls
484 in the range of the large Ngandong tigers and suggests an attribution of this
485 site to the Ngandong faunal stage.

486 There was no strong niche overlap between tigers and *Homotherium ultimum*
487 which makes it unlikely that competition with *Homotherium* forced tigers to
488 increase their body masses.

489 Interestingly, Merriam's Dog shows complete niche overlap with the tiger and
490 this constituted a high competition potential. After the short-faced hyena and
491 *Hemimachairodus zwierzyckii*, Merriam's Dog had the highest competition
492 potential. The hypothesis that Merriam's Dog was replaced by the much
493 smaller Trinil Dog, which had a lower niche overlap with the tiger, is thus
494 supported by our data.

495 If competition forced the tiger to increase its body mass, the short-faced
496 hyena and/or Merriam's Dog followed by *Hemimachairodus zwierzyckii* are
497 the most parsimonious candidates with high competition potential for the tiger.

498

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513

514 Appendix A. Supplementary data

515

516 References

517 Antón, M., Galobart, A., Turner, A., 2005. Co-existence of scimitar-toothed
518 cats, lions and hominins in the European Pleistocene. Implications of the post-
519 cranial anatomy of *Homotherium latidens* (Owen) for comparative
520 palaeoecology. *Quat. Sci. Rev* 24, 1287–1301.

521 Anyonge, W., 1993. Body mass in large extant and extinct carnivores. *J. Zool.*
522 231, 339–350.

523 Bergmann, C., 1847. Über die Verhältnisse der Wärmeökonomie der Thiere
524 zu ihrer Grösse. *Göttinger Studien* 3, 595–708.

525 Bogusch, C., 2002. Zum Sozialverhalten rudellebender Wildcaniden in
526 Gefangenschaft. Vergleichende Untersuchungen an *Canis lupus*, *Cuon*
527 *alpinus*, *Lycaon pictus* und *Speothos venaticus*. Philipps-Universität Marburg,
528 Marburg an der Lahn.

529 Bouteaux, A., Moigne, A.-M., Sémah, F., Jacob, T., 2007. Les assemblages
530 fauniques associés aux sites à *Homo erectus* du dôme de Sangiran
531 (Pléistocène moyen, Java, Indonésie). C.R. Palevol. 6, 169–179.

532 Brongersma, L.D., 1935. Notes on some recent and fossil cats, chiefly from
533 the Malay Archipelago. Zool. Med. 18, 1–89.

534 Carbone, C., Mace, G.M., Roberts, S.C., Macdonald, D.W., 1999. Energetic
535 constraints on the diet of terrestrial carnivores. Science 402, 286–288.

536 Caro, T.M., 1994. Cheetahs of the Serengeti Plains: group living in an asocial
537 species. The University of Chicago Press, Chicago.

538 Christiansen, P., Harris, J., M., 2005. Body size of *Smilodon* (Mammalia:
539 Felidae). J. Morphol. 266, 369–384.

540 Corbett, L.K., Newsome, A.E., 1987. The feeding ecology of the Dingo. III.
541 Dietary relationships with widely fluctuating prey populations in arid Australia:
542 an hypothesis of alternation of predation. Oecologia 74, 215–227.

543 de Azevedo, F.C.C., Murray, D.L., 2007. Spatial organization and food habits
544 of jaguars (*Panthera onca*) in a floodplain forest. Bio. Cons. 137, 391–402.

545 de Vos, J., Long, V.T., 2001. First settlements: Relations between Continental
546 and Insular Southeast Asia, in: Sémah, F., Falguères, C., Grimaud-Hervè, D.,
547 Sémah, A.-M. (Eds.), Origine Des Peuplements et Chronologie des Cultures
548 Paléolithiques dans le Sud-Est Asiatique, Semarang, Paris, pp. 225–249.

549 Eaton, R.L., 1974. The Cheetah - The Biology, Ecology, and Behaviour of an
550 Endangered Species. van Nostrand Reinhold Company, New York,
551 Cincinnati, Chicago, Millbra, Dallas.

552 Eisenberg, J.F., Redford, K.H., 1999. Mammals of the Neotropics – The
553 Central Neotropics, Volume 3. The University of Chicago Press, Chicago and
554 London.

555 Estes, R.D., Goddard, J., 1967. Prey selection and hunting behavior of the
556 African Wild Dog. J. Wildl. Manage. 31, 52–70.

557 Ewer, R.F., 1998. The Carnivores. Comstock Publishing Associates, Ithaca,
558 N.Y.

559 Fortelius, M., 1990. Problems with using fossil teeth to estimate body sizes of
560 extinct mammals, in: Damuth, J., MacFadden, B.J. (Eds.), Body Size in
561 Mammalian Paleobiology: Estimation and Biological Implications. Cambridge
562 University Press.

563 Hemmer, H., 2001. Die Feliden aus dem Epivillafranchium von Untermassfeld,
564 in: Kahlke, R.-D. (Ed.), Das Pleistozän von Untermassfeld bei Meiningen
565 (Thüringen) - Teil 3. Dr. Rudolf Habelt GMBh, Bonn.

566 Hemmer, H., 2004. Notes on the ecological role of European cats (Mammalia:
567 Felidae) of the last two million years., in: Baquedano, E., Rubio Jara, S.
568 (Eds.), Miscelánea en Homnaje a Emiliano Aguirre, Vol. II, Paleontología. Zona
569 Arqueológica, 4, Museo Arqueológico Regional, Alcalá de Henares.

570 Hemmer, H., Schütt, G., 1972. Pleistozäne Leoparden (*Panthera pardus*) aus
571 Java und Südchina. Proc. Kon. Acad. Wet., Ser. B 76, 37–49.

572 Hertler, C., Volmer, R., 2008. Assessing prey competition in fossil carnivore
573 communities -- a scenario for prey competition and its evolutionary

574 consequences for tigers in Pleistocene Java. *Palaeogeogr. Palaeoclimatol.*
575 *Palaeoecol.* 257, 67–80.

576 Jerdan, T.C., 1984. *Handbook of the Mammals of India – A natural History of*
577 *all the Animals Known to Inhabit Indian Sub-continent.* Mittal Publications,
578 Delhi.

579 Johnsingh, A.J.T., 1983. Large mammalian prey-predators in Bandipur. *J.*
580 *Bombay Nat. Hist. Soc.* 80, 1–57.

581 Karanth, K.U., Sunquist, M.E., 1995. Prey selection by tiger, leopard and
582 dhole in tropical forests. *J. Anim. Ecol.* 64, 439–450.

583 Kingdon, J., 1997. *The Kingdon Field Guide to African Mammals.* Academic
584 Press, London.

585 Krebs, C.J., 1999. *Ecological Methodology*, 2 ed. University of British
586 Columbia.

587 Kruuk, H., Turner, M., 1967. Comparative notes on predation by lion, leopard,
588 cheetah and wild dog in the Serengeti area, East Africa. *Mammalia* 31, 1–27.

589 Leinders, J.J.M., Aziz, F., Sondaar, P.Y., De Vos, J., 1985. The age of the
590 hominid-bearing deposits of Java: state of the art. *Neth. J. Geosci.* 64, 167–
591 173.

592 Leyhausen, P., 1979. *Katzen - Eine Verhaltenskunde*, Berlin.

593 Louys J., 2014. The large terrestrial carnivore guild in Quaternary Southeast
594 Asia. *Quat. Sci. Rev.* 96, 86–97.

595 Lyras, G.A., van der Geer, A.A.E., Rook, L., 2010. Body size of insular
596 carnivores: evidence from the fossil record. *J. Biogeogr.* 37, 1007–1021.

597 Mazák, V., 1981. *Panthera tigris.* *Mamm. Species*, 1–8.

598 Mech, L.D., Boitani, L., 2003. *Wolves: Behavior, Ecology, and Conservation*.
599 The University of Chicago Press, Chicago and London.

600 Meiri, S., Yom-Tov, Y., Geffen, E., 2007. What determines conformity to
601 Bergmann's rule? *Glob. Ecol. Biogeogr.* 16, 788–794.

602 Mills, M.G.L., 1990. *Kalahari Hyaenas: Comparative Behavioural Ecology of*
603 *Two Species*. Unwin Hyman, London.

604 Mills, M.G.L., Broomhall, L.S., du Toit, J.T., 2004. Cheetah *Acinonyx jubatus*
605 feeding ecology in the Kruger National Park and a comparison across African
606 savanna habitats: is the Cheetah only a successful hunter on open grassland
607 plains? *Wildl. Biol.* 10, 177–186.

608 Nudds, T.D., 1978. Convergence of group size strategies by mammalian
609 social carnivores. *Am. Nat.* 112, 957–960.

610 Pienaar, U.D.V., 1969. Predator-prey relationships amongst the larger
611 mammals of the Kruger National Park. *Koedoe* 12, 108–176.

612 Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M.E., Eisenberg,
613 J.F., 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological
614 interpretations of a management problem. *Biol. Conserv.* 109, 297–310.

615 Power, R.J., 2002. Prey selection of lions *Panthera leo* in a small, enclosed
616 reserve. *Koedoe* 45, 67–75.

617 Renkonen, O., 1938. Statistisch-ökologische Untersuchungen über die
618 terrestrische Käferwelt der finnischen Bruchmoore. *Ann Zool Soc Zool-Bot*
619 *Fenn 'Vanamo'* 6, 1–231.

620 Ruggiero, R.G., 1991. Prey selection of the lion (*Panthera leo* L.) in the
621 Manovo-Gounda-St. Floris National Park, Central African Republic. *Mammalia*
622 55, 23–44.

623 Schaller, G.B., 1972. The Serengeti Lion: A Study of Predator-Prey Relations.
624 The University of Chicago Press, Chicago and London.

625 Schoener, T.W., Roughgarden, J., Fenchel, T., 1986. The body-size-prey-size
626 hypothesis: A defense. Ecology 67, 260–261.

627 Schütt, G., 1973. Fossil Mammals of Java V: Pleistozäne Caniden (Carnivora,
628 Mammalia) aus Java. Proc. Kon. Acad. Wet., Ser. B 76, 446–471.

629 Seidensticker, J., Christie, S., Jackson, P., 1999. Riding the Tiger - Tiger
630 conservation in human-dominated landscapes. Cambridge University Press,
631 Cambridge.

632 Sémah, F., Sémah, A.M., Simanjuntak, H.T., 2003. More than a million years
633 of human occupation in insular Southeast Asia: the early archaeology of
634 eastern and Central Java. , in: Mercader, J. (Ed.), Under the Canopy: The
635 Archaeology of Tropical Rainforests. Rutgers University, New Brunswick, pp.
636 161–190.

637 Sillero-Zubiri, C., Gottelli, D., 1995. Diet and Feeding Behavior of Ethiopian
638 Wolves (*Canis simensis*). J. Mammal. 76, 531–541.

639 Sinclair, A.R.E., Mduma, S., Brashares, J.S., 2003. Patterns of predation in a
640 diverse predator-prey system. Nature 425, 288–290.

641 Smith, A.T., Xie, Y., 2008. A guide to the Mammals of China. Princeton
642 University Press, Princeton and Oxford.

643 Smith, J.M., 1981. Interpretation of correlations in intraspecific and
644 interspecific allometry. Growth 45, 291–297.

645 Smith, R.J., 1984. Allometric scaling in comparative biology: problems of
646 concept and method. Am. J. Physiol. 246, R152–R160.

647 Sondaar, P.Y., 1984. Faunal evolution and the mammalian biostratigraphy of
648 Java. *Cour. Forsch.-Inst. Senckenberg* 69, 219–235.

649 Swisher, C.C., Rink, W.J., Antón, S.C., Schwarcz, H.P., Curtis, G.H., Suprijo,
650 A., 1996. Latest *Homo erectus* of Java: potential contemporaneity with *Homo*
651 *sapiens* in southeast Asia. *Science* 274, 1870.

652 Thenius, E., 1989. *Handbuch der Zoologie: Zähne und Gebiß der Säugetiere.*
653 De Gruyter, Berlin.

654 van den Bergh, G.D., de Vos, J., Sondaar, P.Y., 2001. The Late Quaternary
655 palaeogeography of mammal evolution in the Indonesian Archipelago.
656 *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 171, 385–408.

657 van Valkenburgh, B.V., 1988. Trophic diversity in past and present guilds of
658 large predatory mammals. *Paleobiology* 14, 155–173.

659 van Valkenburgh, B., 1990. Skeletal and dental predictors of body mass in
660 carnivores., in: Damuth, J., MacFadden, B.J. (Eds.), *Body size in Mammalian*
661 *Paleobiology: Estimation and Biological Implications.* Cambridge University
662 Press, Cambridge.

663 Van Valkenburgh, B., 2007. Déjà vu: the evolution of feeding morphologies in
664 the Carnivora. *Integr. Compar. Biol.* 47, 147–163.

665 van Valkenburgh, B., Sacco, T., Wang, X., 2003. Chapter 7: Pack hunting in
666 Miocene Borophagine dogs: evidence from craniodental morphology and body
667 size. *Bull. Am. Mus. Nat. Hist.*, 147–162.

668 Volmer, R., 2013. *Struktur und gemeinsame Nutzung von*
669 *Nahrungsressourcen in fossilen Carnivoren-Gilden.* Goethe University,
670 Frankfurt.

671 von Koenigswald, G.H.R., 1933. Beitrag zur Kenntnis der fossilen Wirbeltiere
672 Javas - Teil I. Wet. Meded. K. Ned. Natuurhist. 23, 1–127.

673 von Koenigswald, G.H.R., 1934. Zur Stratigraphie des javanischen Pleistocän.
674 De Ing. Ned.-Ind. 11, 185–201.

675 von Koenigswald, G.H.R., 1940. Neue *Pithecanthropus*-Funde 1936-1938.
676 Wet. Meded. K. Ned. Natuurhist. 28, 1–132.

677 von Koenigswald, G.H.R., 1974. Fossil Mammals of Java VI:
678 Machairodontinae from the lower Pleistocene of Java. Proc. Kon. Acad. Wet.,
679 Ser. B 18, 267–273.

680 Watanabe, N., Kadar, D., 1985. Quaternary Geology of the Hominid Fossil
681 Bearing Formations in Java. Special Publication 4, Geological Research and
682 Development Centre, Bandung.

683 Weidenreich, F., 1951. Morphology of Solo Man. Anthropol. Pap. Am. Mus.
684 Nat. Hist. 43, 205–290.

685 Wesley-Hunt, G.D., 2005. The morphological diversification of carnivores in
686 North America. Paleobiology 31, 35–55.

687 Zuercher, G.L., Gipson, P.S., Carrillo, O., 2005. Diet and habitat associations
688 of bush dogs *Speothos venaticus* in the Interior Atlantic Forest of eastern
689 Paraguay. Oryx 39, 86–89.

690 Table 1 Faunal stages and the samples for body mass reconstruction and
 691 calculation of niche overlaps. Shown are the carnivora taxa for each faunal
 692 stage after van den Bergh et al. (2001); Hertler and Volmer (2008) and Lyras
 693 et al. (2010) and the attributed samples. For the felid samples from Sangiran,
 694 the exact faunal stage remains unknown (see explanation in text). The Pre-
 695 Ngandong sample is a summary of the Sangiran Sample, the attributed Tiger
 696 sample. The samples Teguan and Jeruk cannot be attributed to one of the
 697 faunal stages. The fossils included in the samples are shown in Table 2. The
 698 biostratigraphic sequence is based on Sondaar (1984), Leinders et al. (1985)
 699 and includes later revisions by de Vos and the Long (2001) and van den
 700 Bergh et al. (2001).

701 * Swisher et al. (1996) suggests dates from 27–53 ka based on electron-spin
 702 resonance and U-series dating of fossil bovid teeth. However, Westaway et al.
 703 (2007) dated the subsequent Punung fauna to the Last interglacial (between
 704 128 +/- 15 and 118 +/- 3 ka) and conclude that the Ngandong Fauna must be
 705 older than the Last Interglacial. Yokoyama et al. (2008) dated the *Homo*
 706 *erecuts* skulls from Ngandong to around 40 ka, with an upper limit of around
 707 60 to 70 ka by gamma-ray spectrometry.

Faunal Stages	Age	Carnivora taxa	Sangiran stratigraphy	Samples		
Ngandong	Late Pleistocene*	<i>Panthera tigris</i> <i>Panthera pardus</i> <i>Cuon alpinus</i>	sterile layers	Ngandong-Sample (<i>Panthera tigris</i> n=10,) Sites: Ngandong, Ngasinan, Waturalang	-	
Kedung Brubus	0,7-0,8 ma	<i>Panthera tigris</i> <i>Pachycrocuta brevirostris</i> <i>Lutrogale palaeoleptonyx</i>	upper Bapang	Kedung Brubus Sample (<i>Panthera tigris</i> , n=3) Sites: Kedung Brubus and Kebon Duren	Sangiran-Tiger-Sample n=14,	Pre- Ngandong -Sample (n=26) Sites: Kedung Brubus, Kebon Duren, Trinil, Pitu, Bumiyayu,
Trinil H.K.	0,9 ma	<i>Panthera tigris</i>	lower Bapang	Trinil H.K.-Sample		

		<i>Mececyon trinilensis</i> <i>Prionailurus bengalensis</i>		(<i>Panthera tigris</i> , n=7) Trinil and Pitu	(<i>Homotherium ultimum</i> , n=1) Hemimachairodus-Sample (<i>Hemimachairodus zwierzyckii</i> , n=1) Megacyon-Sample (<i>Megacyon merrimami</i> , n=3)	Sangiran Teguan-Sample (<i>Panthera tigris</i> n=1) Jeruk-Sample (<i>Panthera tigris</i> n=1)
Ci Saat	1,0 ma	<i>Panthera sp.</i> <i>Megacyon merriami</i> <i>Lutrogale palaeoleptonyx</i>	black clays	Ci Saat-sample (<i>Panthera tigris</i> , n=2) Sites: Bumiayu		
Satir	1,2 ma	no carnivores	black clays			

708

709 Table 2 Fossil material for body mass reconstruction and prey focus

710 calculation. Shown are the sample name, Collection Number (Coll. No.): NM =

711 Ned.D.v/d Mijnbouw, Museum Geologi Bandung (measurements taken from

712 von Koenigswald, 1933); DUB = Collectie Dubois, Naturalis Biodiversity

713 Center, Leiden; SMF/PA/F = von Koenigswald Sammlung, Senckenberg

714 Research Institute, Frankfurt; Site, anatomical element (Element), portion and

715 side of anatomical element (Portion), reconstructed body mass [kg] (BM);

716 standard deviation (sd). The Pre-Ngandong sample is a summary of the

717 Sangiran Sample, the Ci Saat , Trinil H.K., Kedung Brubus Sample.

Sample Name (from Table 1)	Coll. No.	Site	Element	Portion	BM [kg]	sd
Ngandong-Sample	NM 5497	Ngandong	Mandibula	P3 P4 M1 sin+dex	119	
	NM 49	Ngasinan	Radius	dex	134	
	NM 504	Ngandong	Mandibula	C P3fragm. P4 M1 inf dex	147	20
	NM 13776	Ngandong	Cranium	P3 P4 M1 sup dex	151	17
	NM 1184	Ngandong	Cranium	(C) (P2) P3 P4 sup dex	163	34
	NM 1933	Watualang	Humerus	sin	189	
	NM 2811	Ngandong	Cranium	complete	194	46
	NM 2671	Watualang	Mandibula	sin	212	
	NM 9554	Ngandong	Humerus	sin	235	
2641	Ngandong	Femur	dex	298		
Kedung Brubus-Sample	DUB 1499	Kedung Brubus	Mandibula	P4 M1 inf dex	134	
	DUB 1498	Kedung Brubus	Mandibula	(C) (P3) P4(M1) inf dex	135	
	DUB 89	Kebon Duren	Femur		69	

Trinil H.K.-Sample	DUB 8411	Trinil	Tibia	sin	99	
	DUB 1494	Trinil	Maxilla	I2 C (P2) P3 P4 (M1) sup sin	103	3
	DUB 1495	Trinil	Maxilla	(C) (P2) P3 P4 sup dex	103	5
	NM 5	Trinil	Cranium	(M1),P4,P3,(P2),(C),(I) sin M1 fragm.	133	
	DUB 1871	Trinil	Ulna	sin	117	
	DUB 1479	Trinil	Mandibula	C P3 P4 M1 inf dex	118	
	NM 61	Pitu	Mandibula	C P3 fragm. P4 M1 inf dex	114	
Ci Saat-Sample	NM 1533a	Bumiayu	Femur	sin	93	
	1209	Bumiayu	Mandibula	C1 P3 P4 M1 inf sin	96	
Teguan-Sample	DUB 90	Teguan	Ulna	dex	86	
Jeruk-Sample	DUB 6219	Jeruk	Maxilla	P3 P4 sup dex	228	10
Sangiran-Tiger-Sample	SMF/PA/F6683	Sangiran	Praemolar	P4 sup dex	64	
	DUB 11699	Sangiran	Mandibula	P3-M1 inf sin	77	14
	SMF/PA/F 6658	Sangiran	Mandibula	P3-M1 inf dex	81	8
	SMF/PA/F 6674	Sangiran	Praemolar	P4 sup sin	103	
	SMF/PA/F 6677	Sangiran	Maxilla	P4 sup sin	108	
	SMF/PA/F 6673	Sangiran	Praemolar	P4 sup dex	109	
	CD 1168 a	Sangiran	Praemolar	P3 inf sin	125	
	F6668	Sangiran	Praemolar	P4 sup sin	126	
	F6670	Sangiran	Praemolar	P4 sup dex	138	
	CD 1168 b	Sangiran	Praemolar	P4 inf sin	139	
	CD 1168 c	Sangiran	Molar	M1 inf sin	140	
	SMF/PA/F 6660	Sangiran	Maxilla	P3 P4 sup dex	143	
	SMF/PA/F 6671	Sangiran	Maxilla	P4 sup sin	153	
	SMF/PA/F 6659	Sangiran	Maxilla	P3 sup dex	182	
	<i>Homotherium-Sample</i>	SMF/PA/F 6676	Sangiran	Mandibula	P3-M1 inf dex	154
<i>Hemimachairodus-Sample</i>	SMF/PA/F 6679	Sangiran	Mandibula	P4 M1 inf dex	130	
<i>Megacyon-Sample</i>	F6785	Sangiran	Molar	M1 sup sin	49	
	F6792	Sangiran	Molar	M1 sup sin	51	
	F6786	Sangiran	Molar	M1 inf dex	55	

718

719

Table 3 Regressions for reconstruction of body masses. Shown are the

720

regression number (Reg. No.), the parameter (SKL = skull length), intercept

721

(a), slope (b), correlation coefficient (r^2), standard error of estimation (SE),

722

percentage standard error of estimate (%SEE) and percentage standard error

723

of the estimate (%PE) after Smith (1981, 1984).

Reg. No.	Parameter	a	b	r^2	p	SE	%SEE	%PE
----------	-----------	---	---	-------	---	----	------	-----

Reg. No.	Parameter	a	b	r ²	p	SE	%SEE	%PE
F-1	SKL*	-5,983	3,25	0,878	<0,0001	0,058	14	11
F-2	P2 sup	+0,632	1,389	0,314	0,02	0,442	177	76
F-3	P3 sup	-2,128	3,187	0,915	<0,0001	0,171	48	28
F-4	P4 sup	-2,775	3,239	0,948	<0,0001	0,135	36	24
F-5	P3 inf	-1,936	3,333	0,933	<0,0001	0,175	50	29
F-6	P4 inf	-2,209	3,178	0,938	<0,0001	0,158	44	26
F-7	M1 inf	-2,281	3,151	0,954	<0,0001	0,106	28	17
Reg. No.	Parameter	a	b	r ²	p	SE	%SEE	%PE
C-1	P3 inf	-2,137	3,288	0,897	<0,0001	0,039	36	26
C-2	P4 inf	-2,172	3,153	0,906	<0,0001	0,039	35	23
C-3	M1 inf	-2,436	2,775	0,919	<0,0001	0,041	32	22
C-4	M2 inf	-2,035	3,346	0,831	<0,0001	0,049	51	35

724

725 Table 4 Samples for calculation of prey mass regressions. Listed is taxon,
726 mean body mass (BM) taken from literature (see text), pack size (PS), pack
727 weight (BMxPS=PW), mean prey mass (PM), number of kills used for
728 calculation of mean prey mass (n) and studies:

729 1= Mech and Boitani, 2003; 2 = Ruggiero, 1991; 3 = Sillero-Zburi and Gottelli,
730 1995; 4 = Pienaar, 1969; 5 = Power, 2002; 6 = Karanth and Sunquist, 1995; 7
731 = Estes and Goddard, 1967; 8 = Corbett and Newsome, 1987; 9 = Zuercher et
732 al., 2005; 10 = Johnsingh, 1983; 11= de Azevedo and Murray, 2007; 12 =
733 Polisar et al., 2003; 13 = Kruuk and Turner, 1967; 14 = Eaton, 1974; 15 =
734 Mills et al., 2004; 16 = Mills, 1990; 17 = Caro, 1994.

735 *Zuercher et al. (2005) provide no list of prey items. We therefore provide the
736 mean prey mass as calculated by them.

737

Taxon	BM [kg]	PS	PW	PM [kg]	n	Studies
<i>Acinonyx jubatus</i>	50	-	-	35,91	1071	4,13,14,15,16,17

Taxon	BM [kg]	PS	PW	PM [kg]	n	Studies
<i>Panthera leo</i>	197	-	-	238,36	2840	1,4,5,16,
<i>Panthera onca</i>	71	-	-	15,93	61	12,11
<i>Panthera pardus</i>	59	-	-	48,22	1088	4,6,10,13,16,
<i>Panthera tigris tigris</i>	179	-	-	401,4	157	6,10
<i>Puma concolor</i>	53	-	-	13,24	23	12
<i>Canis lupus</i>	49	9,5	465,5	251,6	248	1
<i>Canis lupus dingo</i>	12,5	3,3	41,25	12,7	348	8
<i>Canis simensis</i>	15,25	1	15,25	0,3	362	3
<i>Cuon alpinus</i>	15	10,5	157,5	33,4	395	6, 10
<i>Lycaon pictus</i>	27	11,5	310,5	44,8	859	4, 7,13
<i>Speothos venaticus</i>	6,5	4,5	29,25	2,2	u*	9

738

739 Table 5 Regressions for calculation of prey mass. Shown are intercept (a),
740 slope (b), correlation coefficient (r), standard error of estimation (SE),
741 percentage standard error of estimate (%SEE) and percentage standard error
742 of the estimate (%PE) after Smith (1981, 1984).

Nr.	Sample	Intercept	slope	r ²	p	SE	%SEE	%PE
P-1	Felidae	-2,0795	1,9831	0,7922	0,017	0,138	86	60
P-2	Canidae	-2,082	1,634	0,895	0,004	0,377	138	68

743

744 Table 6 Reconstructed body masses of the fossil carnivores. Shown are
745 sample name (see Table 2), minimum reconstructed body mass (BM_{min}),
746 mean body mass (BM_{mean}), maximum Body mass (BM_{max}) and the range of
747 statistical errors: minimum reconstructed body mass - %PE (BM_{min}%PE) and
748 maximum reconstructed body Mass + %PE (BM_{max}%PE).

Sample name	BmminPE % [kg]	BM min [kg]	BM mean [kg]	BM max [kg]	BM max %PE [kg]
<i>Megacyon</i>	38	49	52	55	68
<i>Hemimachairodus</i>	61	24	130	308	209
<i>Homotherium</i>	17	83	154	178	255
Tiger Samples (<i>Panthera tigris</i>)					
pre-Ngandong	49	64	114	182	233
Sangiran	49	64	121	182	233
Ci Saat	63	81	87	93	113
Trinil H.K.	68	96	110	133	171
Kedung Brubus	54	69	113	135	171
Ngandong	79	119	184	298	363
Teguan	63	86	86	86	109
Jeruk	159	228	228	228	292

749

750 Table 7 Competitors and the reconstructed prey mass spectra. The focus
 751 classes are framed and the percentage contribution of each focus class to the
 752 complete focus area is displayed.

Competitor	3a	3b	3c	4a	4b	4c	5a
<i>Homotherium ultimum</i>			25	25	25	25	
<i>Machairodus zwierzyckii</i>		25	25	25	25		
<i>Megacyon merriami</i>	20	20	20	20	20		
SangiranTiger	20	20	20	20	20		
Ci-Saat Tiger		33,33	33,33	33,33			
Trinil H.K .Tiger		25	25	25	25		
Kedung Brubus Tiger		25	25	25	25		
pre-Ngandong Tiger	20	20	20	20	20		
Ngandong Tiger		16,67	16,67	16,67	16,67	16,67	16,67

753

754 Table 8 Results of unpaired t-test between mean body mass of the Sangiran
 755 sample and the Ngandong sample executed by Graph Pad “Quick Calcs”
 756 <http://www.graphpad.com/quickcalcs>

P value and statistical significance:		
The two-tailed P value equals 0.0073	By conventional criteria, this difference is considered to be statistically significant.	
Confidence interval:		
The mean of Group One minus Group Two equals	-55.14	
95% confidence interval of this difference	From -94.59 to -15.69	
Intermediate values used in calculations:		
standard error of difference	19.520	
t	2.8246	
df	40	
Group	Sangiran sample	Ngandong sample
Mean	129.06	184.20
SD	53.92	53.74

SEM	9.53	16.99
N	32	10

757 Figures

758 Figure 1

759 Large carnivore assemblages from several faunal levels of the Pleistocene of
760 Java. Shown are only carnivores weighing more than 10 kg. The Sangiran v.K
761 assemblage reflects taxa collected in the Sangiran dome by von Koenigswald
762 and excludes finds by the team of Sémah (Bouteaux et al., 2007).

763 Figure 2

764 Map of Java and the sites of the fossil assemblages.

765

766 Figure 3

767 Reconstructed body masses of the Pleistocene tiger samples, the
768 Machairodonts and *Megacyon merriami* in Java. Each reconstructed body
769 mass value is displayed as a black dot for the samples. The sample name is
770 provided at the x-axis. Composition of the samples is given in Tables 1 and 2.

771

772 Figure 4

773 Niche overlap by hypercarnivorous carnivores from Sangiran with tigers.

774 Shown are the different tigers and their niche overlap with *Homotherium*

775 *ultimum*, *Hemimachairodus zwierzyckii* and *Megacyon merriami*.

776 * The samples Sangiran and pre-Ngandong have the same PMS and thus the
777 same niche overlap in percent.

778 ** the samples Ci Saat, Trinil H.K. and Kedung Brubus have the same PMS

779 and thus the same niche overlap.

780

781 Figure 5

782 Niche overlap by tigers with other hypercarnivores from Sangiran. Shown are
783 *Homotherium ultimum*, *Hemimachairodus zwierzyckii* and *Megacyon merriami*
784 and their niche overlap with tigers in percent. * The samples Sangiran and
785 pre-Ngandong have the same PMS and thus the same niche overlap.
786 ** The samples Ci Saat, Trinil H.K. and Kedung Brubus have the same PMS
787 and thus the same niche overlap.

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Amsterdam
Netherlands

Manila, 19 July 2015

Dear editors,

We hereby submit our manuscript with the title “Niche overlap and competition potential among tigers (*Panthera tigris*), sabertoothed cats (*Homotherium ultimum*, *Hemimachairodus zwierzyckii*) and Merriam’s Dog (*Megacyon merriami*) in the Pleistocene of Java”.

We investigated the role of competition in a case of dramatic body mass increase in Late Pleistocene tigers. During the Late Pleistocene, tigers with a body mass in excess of 300 kg inhabited Java, whereas tigers from the Early and Middle Pleistocene of Java range in body mass between 63 until 121 kg. The question is what drove this size increase in tigers?

In order to answer this question, we estimated body mass of tigers from all periods, and of its potential competitors. Based on body mass and new regressions for both felids and canids derived from extant species, we calculated prey mass spectrum and niche overlap. Niche overlap was then used as proxy for degree of competition. We found that Merriam's dog, a very large wolf-like canid, had a 100% niche overlap with tigers. We concluded that in order to minimize competition, tigers increased in size whereas Merriam's dog decreased in size (ecological character displacement). The sabertoothed felids, which also had a considerable overlap, went extinct.

On behalf of all authors,
Sincerely yours,

Rebekka Volmer

Figure 1

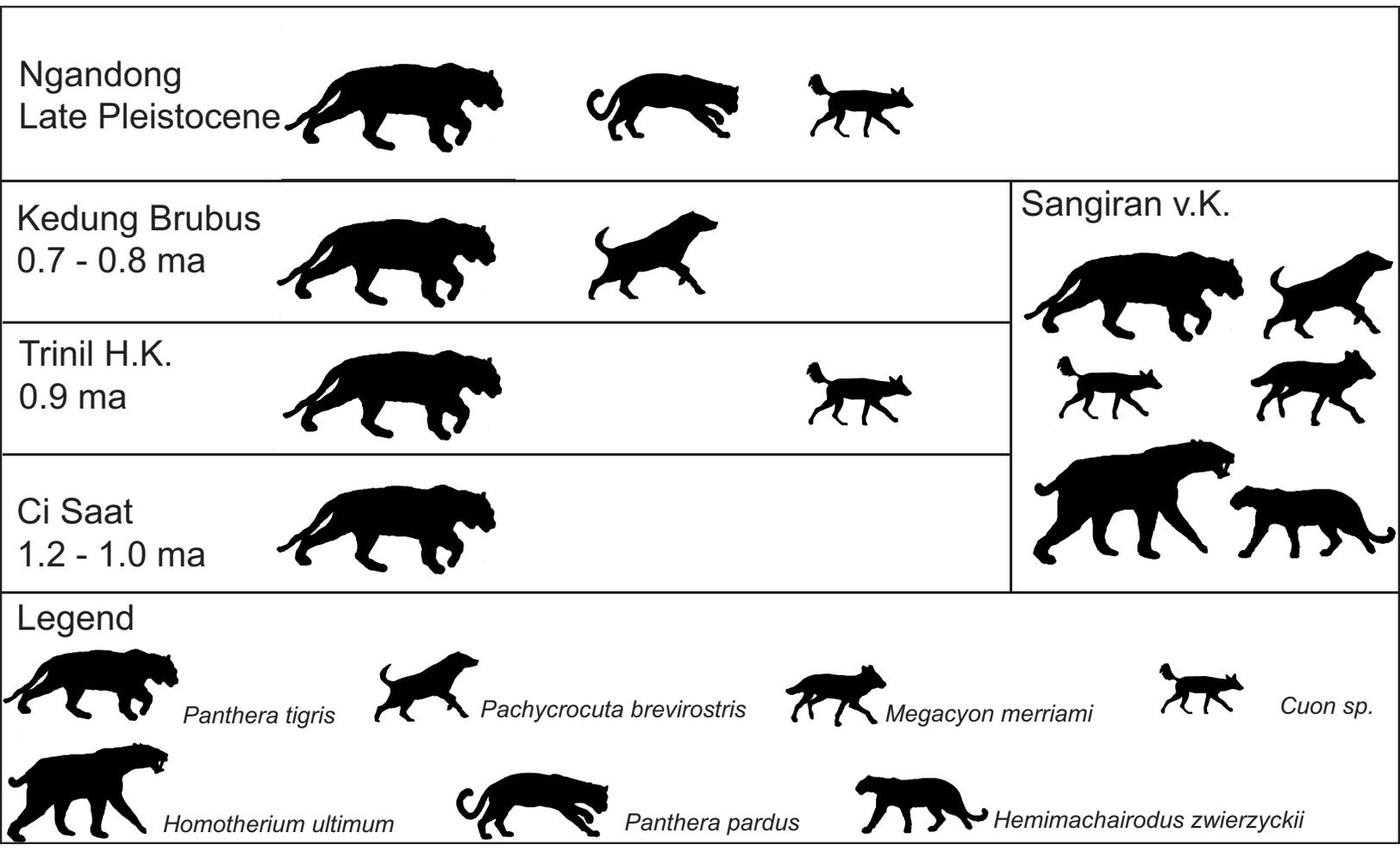


Figure2

[Click here to download high resolution image](#)



Figure3

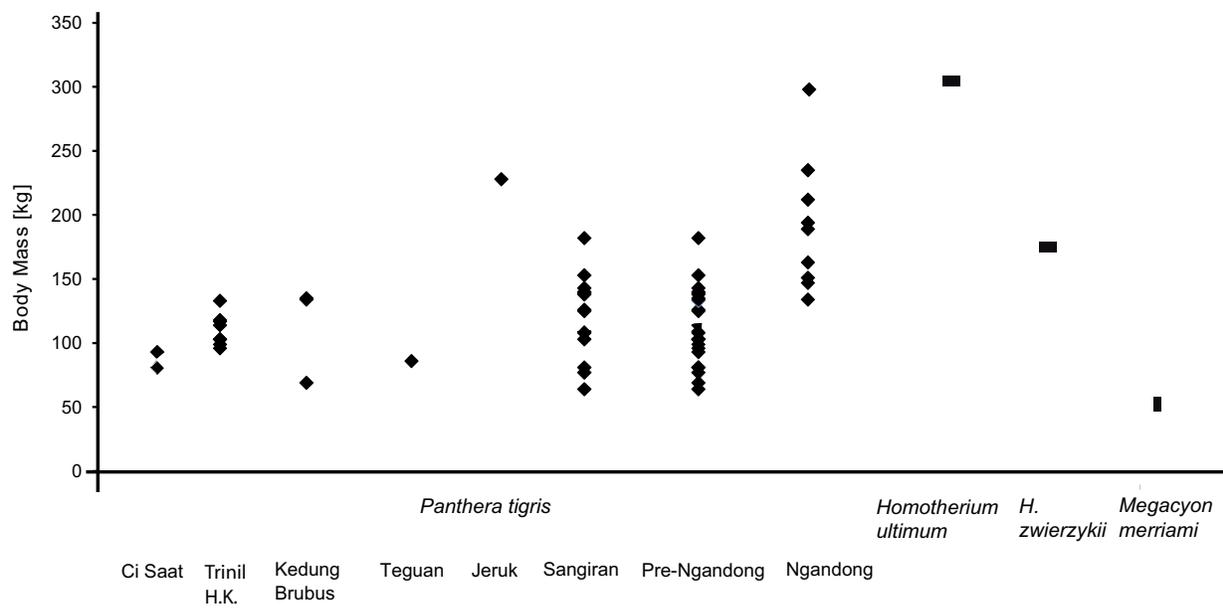


Figure4

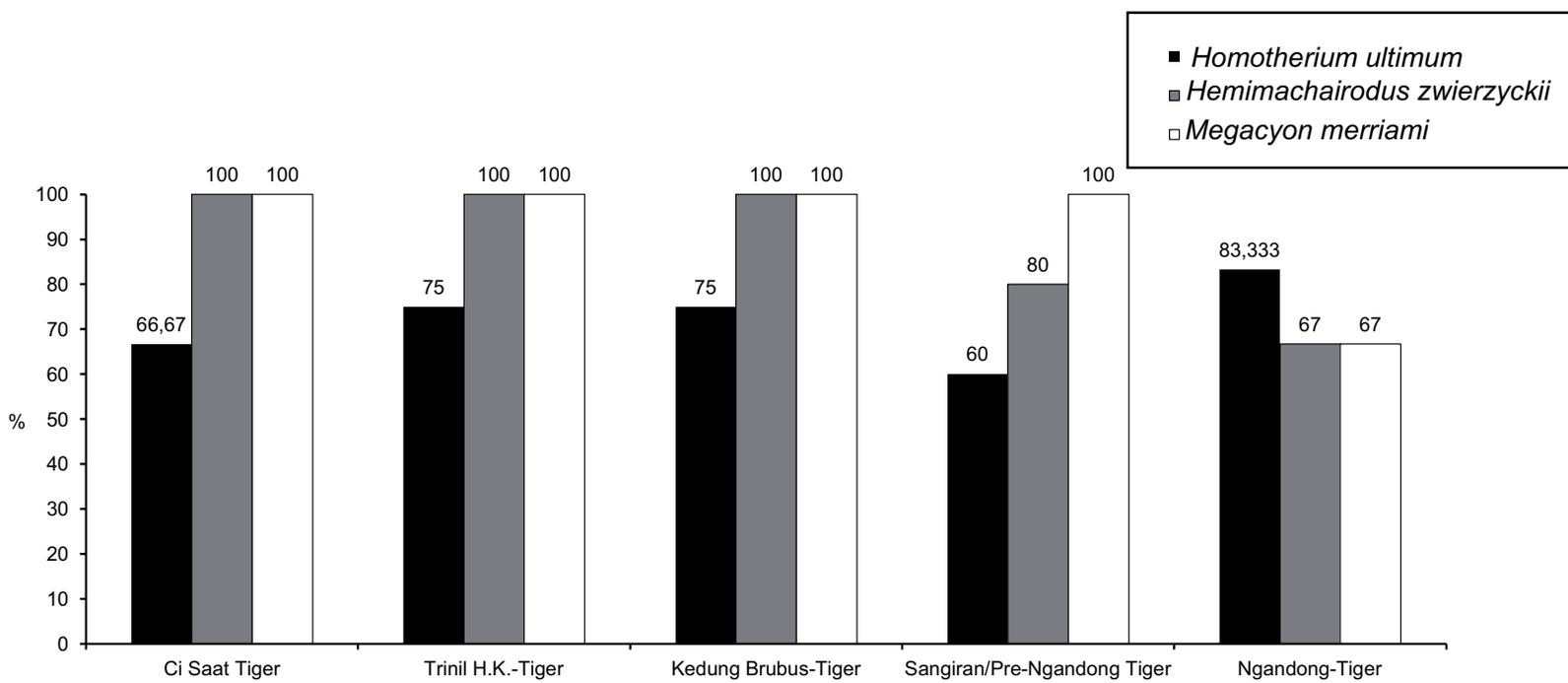
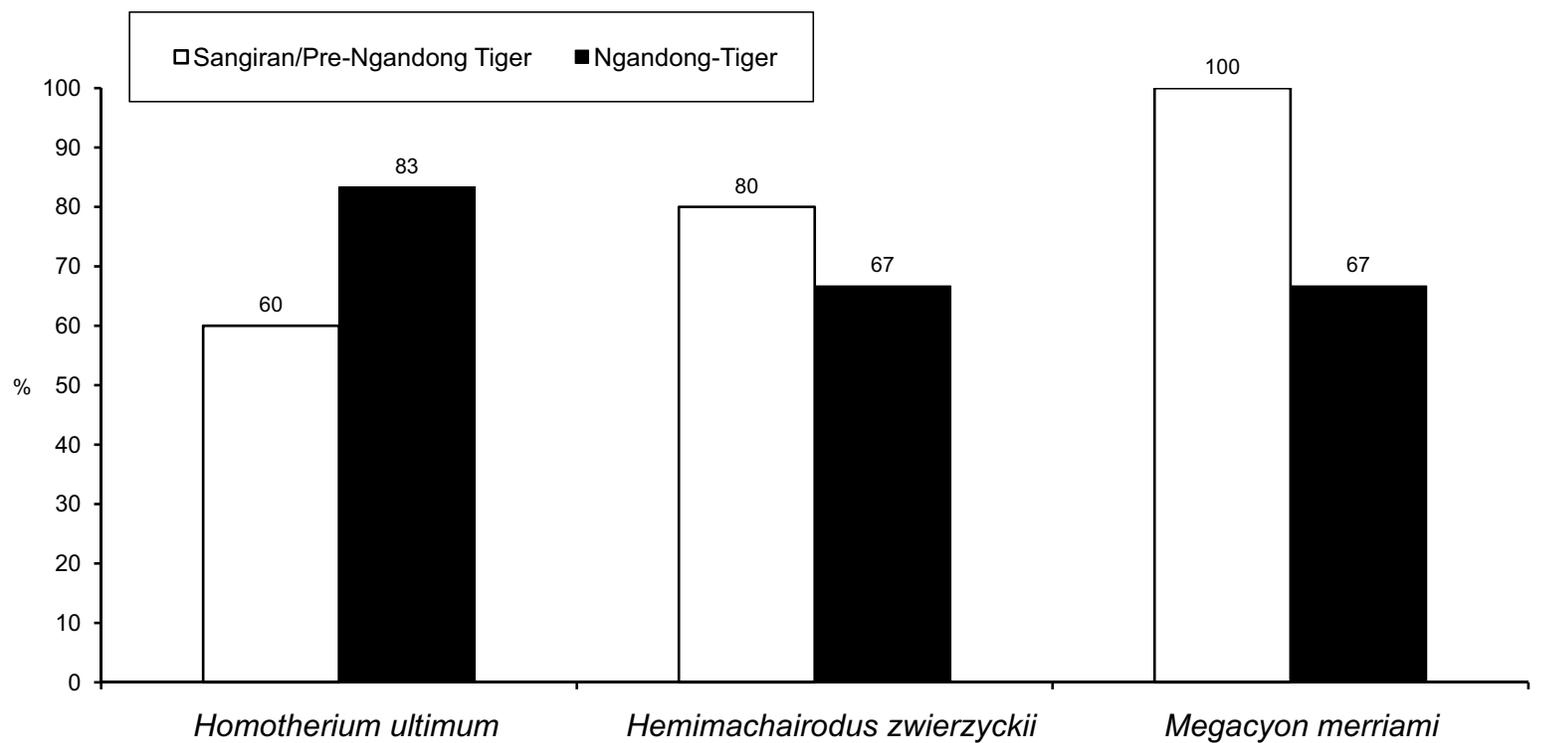


Figure5



Highlights

- Late Pleistocene tigers of Java belong to the largest known tigers
- Shifts in body masses of tigers are probably caused by competition.
- Tigers on Java had highest competition potential with Merriam's Dog.
- *Homotherium ultimum* had the lowest competition potential with tigers.
- New regressions for body mass and prey mass reconstruction for large carnivores were calculated.

1 Supplementary data

2 Material

3 A variety of studies provides regression terms for parameters like upper M1 length
4 and long bones for the estimation of body mass (van Valkenburgh, 1990; Anyonge,
5 1993; Hemmer, 2001; Christiansen and Harris, 2005). Skull length and lower M1
6 length are used as well. Teeth other than M1 have not yet been studied for
7 correlation with body mass. We were therefore unable to reconstruct a large portion
8 of the specimens in the collections (Hertler and Volmer, 2008). Many fossil samples
9 only encompass dental material, for example, samples from the Sangiran dome.
10 The Ngandong sample includes a tiger cranium based on which Hertler and Volmer
11 (2008) reconstructed a large body mass of 470 kg using the felid specific regression
12 of van Valkenburgh (1990). Because body size and skull length of tigers varies
13 hugely (Mazák, 1981), it is advisable to calculate a species-specific regression term
14 based on tigers only (*Panthera tigris*) of Mazák's dataset (Mazák, 1981). In our
15 present study additional regressions were calculated to include additional tooth
16 positions in the reconstruction of body masses for Felidae and Canidae .
17 Furthermore, a tiger specific regression term is calculated.

18

19 Body mass regressions

20 A sample of extant skeletons, representing 31 felid and 16 canid species, of the
21 Senckenberg Collection were measured for the regression terms. Only fully erupted,
22 complete, permanent teeth are measured. In order not to confuse intra- and
23 interspecific allometry, averages of each species with multiple individuals were used
24 for statistical analysis. For some taxa and parameters larger samples than available
25 in the Senckenberg Institute were already measured and published by Schmid
26 (1940). In these cases the samples are used instead.

27 The length of the teeth is defined as the largest mesio-distal length and was
 28 measured with digital vernier calipers. For each taxon and parameter the means of
 29 the measurements is calculated. The mean tooth length and the mean body mass,
 30 taken from literature are defined as a pair of values.

31 For the regression for tiger skull length the data from Mazák (1981) were used. Here
 32 the pair of values is the minimum and maximum skull lengths and body masses,
 33 including the sex. For example: the maximum body mass for male Sumatra Tiger is
 34 paired with the maximum body mass for male Sumatra Tiger. This method gives a
 35 higher sample size.

36 The samples are shown in Supplementary Tables 1–3. The linear regressions for
 37 reconstruction of body masses are computed by Systat 12 using tooth/skull length as
 38 known variable and body mass as the unknown variable.

39

40 Regressions for Reconstruction of Body Masses

41 The calculated regressions for body mass reconstruction are shown in Table 5. A
 42 statistically relevant correlation with body mass is present for all parameters ($P \leq$
 43 $0,02$). All parameters show a strong correlation ($r^2 > 0,878$), except for the upper P2
 44 length. The percentage estimation errors vary between 14–177%, the %PE between
 45 11–76 %.

46

47 Supplementary Tables

48

49 Supplementary Table 1 Sample for calculation the regression for body mass reconstruction of
 50 skull length of *Panthera tigris* (Regression F-1). Listed are the subspecies, sex, minimal body mass
 51 (BM min), maximal body mass (BM max) and minimal and maximal skull length (SKL min, SKL max).
 52 BM min and SKL min of one sex of a subspecies is used as a pair of values and BM max and SKL
 53 max respectively. All data taken from Mazák (1981).

Subspecies	Sex	BM min	BM max	SKL min	SKL max
<i>P.t. altaica</i>	M	180	306	341	383
<i>P.t. altaica</i>	F	100	167	279	318
<i>P.t. amoyensis</i>	M	130	175	318	343
<i>P.t. amoyensis</i>	F	100	115	273	301

Subspecies	Sex	BM min	BM max	SKL min	SKL max
<i>P.t. balica</i>	M	90	100	295	298
<i>P.t. balica</i>	F	65	80	263	269
<i>P.t. corbetti</i>	M	150	195	319	365
<i>P.t. corbetti</i>	F	100	130	279	302
<i>P.t. sondaica</i>	M	100	141	306	349
<i>P.t. sondaica</i>	F	75	115	270	292
<i>P.t. sumatrae</i>	M	100	140	295	335
<i>P.t. sumatrae</i>	F	75	110	263	294
<i>P.t. tigris</i>	M	180	258	329	378
<i>P.t. tigris</i>	F	100	160	275	311
<i>P.t. virgata</i>	M	170	240	316	369
<i>P.t. virgata</i>	F	85	135	268	305

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55
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61

Supplementary Table 2 Samples for calculation of body mass regressions based on dental parameters for Felidae. Listed are taxon, mean body mass (BM) [kg], the tooth length [mm] (P2 sup, P3 sup, P4 sup, P3 inf, M1 inf) and abbreviation of the regression (F-2 – F-7), n= sample size. Source of data (S) :1= parameters taken from specimens housed at Research Institute Senckenberg, 2 = Schmid (1940), 3 = Hooijer (1947), 4 = Mazlaghani (2005), 5 = Hemmer (1971), 6 = Brongersma (1935).

* = only female individuals, mean body mass of females is used

		F-2		F-3		F-4		F-5		F-6		F-7		
Taxon	BM [kg]	P2 sup	n	P3 sup	n	P4 sup	n	P3 inf	n	P4 inf	n	M1 inf	n	S
<i>Leopardus pardalis</i>	9,9	4,53	1	11,13	1	12,27	1	9,55	1	12,08	1	12,71	1	1
<i>Neofelis nebulosa</i>	15,5	2,45	1	12,6	16	18,5	16	8,5	16	13,8	16	14	16	1,2
<i>Panthera leo</i>	197	8,49	2			33,59	13	15,76	10	23,96	12	24,65	12	1
<i>Panthera onca</i>	71	6,94	9			27,18	12	14,23	12	19,76	12	20,56	13	1
<i>Panthera tigris balica*</i>	72,5	18,98	1	19,1	1	30,05	1					21,57	1	1
<i>Panthera tigris corbetti</i>	147,5	6,9	1	20,9	1	33,4	1	21,8	1			26	1	4
<i>Panthera tigris tigris</i>	179	5,72	1	22,3	u	35,65	u	16,5		23,5		26,9	u	3
<i>Prionailurus planiceps</i>	2,25	4,34	1	8,34	1	11,4	1	6,2		8,35	u			1,6
<i>Prionailurus viverrinus</i>	9	2,89	1	8,64	1	13,68	1	6,81	1	9,38	1	10,57	1	1
<i>Panthera tigris altaicus</i>	203	7,83	1	23,01	3	33,15	4	17,38	3	23,94	4	25,92	4	1,3
<i>Acinonyx jubatus</i>	50	2,8	3	13,04	6	21,51	6	13,86	4	15,1	6	18,2	6	3
<i>Panthera pardus</i>	59	5	82	16,3	113			11,8	94	17,3	99	18	104	2
<i>Panthera pardus fusca</i>	45,5	5,2	9	16,4	12	25,1	12	11,7	12	17,8	12	17,8	11	2
<i>Panthera pardus melas</i>	35	3,7	12	14,8	23	22,2	22	10,5	22	15,3	24	16	25	2
<i>Panthera pardus orientalis</i>	36,5	5,4	1							18,75	1	18,65	1	2
<i>Puma concolor</i>	53	5,5	6	15,23	13	21,53	15	11,79	11	14,76	13	17,81	12	1
<i>Uncia uncia</i>	45	6,3	28	15	30	24,1	29	12,3	29	16,6	29	18	28	2
<i>Panthera</i>	107,5	8,3	13	20,8	13	31,35	13	14,55	13	21,95	13	23,74	13	1

<i>tigris sumatrae</i>														
<i>Lynx lynx</i>	19,85	x		11,9	20	18,8	22	9,9	29	12,2	29	15,7	31	2
<i>Catopuma temincki</i>	11,75							8,1	3					1
<i>Felis chaus</i>	10							7,75	4	10	4	10,55	4	5
<i>Panthera leo*</i>	152					32,87	5	16,28	3					1
<i>Panthera pardus</i> (Africa)	59					24,5	109							2
<i>Panthera tigris amoyensis</i>	137,5			21,9	5	33,5	5	16,15	5	22,65	5	24,75	5	3
<i>Panthera tigris sondaica</i>	108			20,65	8	32,31	12	14,9	8	21,74	14	24,18	15	1,3
<i>Pardofelis badia</i>	4							5,9		7,8	u			6
<i>Pardofelis marmorata</i>	3,5			7,48	1	11,84	1	5,55		8	u			6
<i>Pardofelis temminckii</i>	11,75			9,95	3	16,42	3			10,66	3	11,84	3	1
<i>Prionailurus bengalensis</i>	5,15			5,99	1	9,97	13	5		6,5	u	7,66	13	1,6
<i>Prionailurus rubiginosus</i>	1,5							4		5,35	u			6
<i>Profelis aurata</i>	11,75			9,18	3	15,49	3	7,25	3	10,09	3	11,27	3	1

62

63 **Supplementary Table 3** Samples for calculation of body mass regressions based on dental
64 parameters for Canidae. Listed are taxon, mean body mass (BM) [kg], tooth length [mm] (P3 inf, P4
65 inf, M1 inf), and abbreviation of regression (C-1 – C-3), n= sample size.

Taxon	BM	C-1		C-2		C-3	
		P3 inf	n	P4 inf	n	M1 inf	n
	[kg]	[mm]		[mm]		[mm]	
<i>Alopex lagopus</i>	3,685	7,35	5	8,1	5	12,72	5
<i>Canis adustus</i>	9,65	7,4	4	8,14	4	13,74	4
<i>Canis aureus</i>	8,15	8,95	5	10,05	5	18	5
<i>Canis latrans</i>	11,75	11,12	2	12,16	2	20,74	2
<i>Canis lupus arctos</i>	49	13,73	11	15,47	13	28,26	13
<i>Canis lupus dingo</i>	12,5	10,6	8	12,38	8	21,12	9
<i>Canis mesomelas</i>	9,25	8,51	8	9,95	7	16,56	5
<i>Canis simensis</i>	15,25	9,42	1	10,38	1	18,56	1
<i>Cerdocyon thous</i>	5,7	7,75	4	8,61	4	14,92	4
<i>Chrysocyon brachyurus</i>	25	11,58	5	12,92	5	21,52	5
<i>Cuon alpinus</i>	15	9,8	2	12	3	21,63	3
<i>Lycaon pictus</i>	27	11,57	6	13,19	7	24,52	7
<i>Speothos venaticus</i>	7,715	8,54	1	8,99	1	14,36	1
<i>Urocyon cinereoargenteus</i>	3,75	5,9	3	7,3	3	12,31	3
<i>Vulpes bengalensis</i>	2,5	6,34	1	7,13	1	10,71	1
<i>Vulpes zerda</i>	1,25	5,11	3	5,21	3	8,46	3

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67 **References**

68 Anyonge, W., 1993. Body mass in large extant and extinct carnivores. *J. Zool.* 231,
69 339–350.

70 Brongersma, L.D., 1935. Notes on some recent and fossil cats, chiefly from the
71 Malay Archipelago. Zool. Med. 18, 1–89.

72 Christiansen, P., Harris, J., M., 2005. Body size of *Smilodon* (Mammalia: Felidae). J.
73 Morphol. 266, 369–384.

74 Hemmer, H., 1971. Fossil Mammals of Java III: Zur Kenntnis der Evolution
75 Javanischer Kleinkatzen: *Prionailurus bengalensis koenigswaldi* sspn. und *Felis*
76 *chaus* ssp. aus dem Neolithikum von Sampung, Mittel-Java. Proc. Kon. Acad. Wet.,
77 Ser. B 74, 365–375.

78 Hemmer, H., 2001. Die Feliden aus dem Epivillafranchium von Untermassfeld, in:
79 Kahlke, R.-D. (Ed.), Das Pleistozän von Untermassfeld bei Meiningen (Thüringen) -
80 Teil 3. Dr. Rudolf Habelt GMBh, Bonn.

81 Hertler, C., Volmer, R., 2008. Assessing prey competition in fossil carnivore
82 communities - a scenario for prey competition and its evolutionary consequences for
83 tigers in Pleistocene Java. Palaeogeogr. Palaeoclimatol. Palaeoecol. 257, 67–80.

84 Hooijer, D.A., 1947. Pleistocene remains of *Panthera tigris* (LINNAEUS) subspecies
85 from Wanhsien, Szechwan, China, compared with fossil and recent tigers from other
86 localities. Am. Mus. Novit. 1346, 1–17.

87 Mazák, V., 1981. *Panthera tigris*. Mamm. Species, 1–8.

88 Mazlaghani, S.K., 2005. Funktionsmorphologische Untersuchungen pleistozäner
89 Pantherinae in der Sammlung "Von Koenigswald" (Südostasien), Fachbereich Biologie
90 und Informatik. Goethe-Universität, Frankfurt am Main.

91 Schmid, E., 1940. Variationsstatistische Untersuchungen am Gebiß pleistozäner und
92 rezenter Leoparden and anderer Feliden. Z. Säugetierkd. 15, 1–179.

93 Van Valkenburgh, B., 1990. Skeletal and dental predictors of body mass in
94 carnivores., in: Damuth, J., MacFadden, B.J. (Eds.), Body size in Mammalian

95 Paleobiology: Estimation and Biological Implications. Cambridge University Press,
96 Cambridge.