Do Equids Live longer than Grazing Bovids?

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ABSTRACT

A large part of the diversity of longevity and actuarial senescence (i.e. the progressive decline of survival probabilities with age) across vertebrates can be related to body size, phylogeny and the species' position on the slow-fast continuum of life histories. However, differences in mortality patterns between ecologically similar species, such as bovids and equids, remain poorly understood. Equids are commonly understood to outlive bovid species relative to their body mass, despite very similar feeding niches. Comparing survival patterns of 13 bovid and 10 equid sub-species, our findings confirm that equids outlive bovid species, with a higher adult survival rate and a delayed onset of senescence for equids, but no difference of rate of actuarial senescence. These differences are associated with a slower generation time and longer inter-birth interval, due to a longer gestation period, for equids compared to bovids. ==Finally, our results suggest that all biological times (i.e. all life history traits expressed in time units) have evolved synchronously in bovids, whereas in equids gestation time and inter-birth interval either were never in synchrony with, or have slowed down relative to other biological times.== Our findings suggest the existence of different selection pressures, or different constraints, on specific time-related traits between these two mammalian orders.

Keywords: actuarial senescence; biological times; demography; pace of life; slow-fast continuum

Running head: Equids *vs* bovids' actuarial senescence

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INTRODUCTION

Actuarial senescence, defined as the progressive decrease of survival with increasing age, is a ubiquitous process across the tree of life (Nussey et al. 2013; Jones et al. 2014). Striking differences in actuarial senescence and lifespan have been found in related species, such as the naked mole rat (*Heterocephalus glaber*) which lives nine times longer than similar-sized rodents (Buffenstein 2008; Ruby et al. 2018). Such differences across phylogenetically related species or across species sharing the same lifestyle remain poorly understood and are currently attracting much interest (Gorbunova et al. 2014; Healy et al. 2014). However, little work has been done, so far, to understand variation in senescence between distantly related species that have converged into closely similar niches.

Here we compare patterns of actuarial senescence (hereafter 'senescence') between taxa from two orders of mammals, equids (Perissodactyl) and grazing bovids (Artiodactyl), which are large herbivores whose evolution separated 55 million years ago (Janis 1976). Many of the grazing species, among the equids and bovids, have evolved in parallel in similar environments since the Miocene (Janis 1976). These two groups of herbivores display evolutionary convergence in key morphological characters, such as elongated limbs and hypsodonty (i.e. the height of the molar teeth), and occupy similar feeding niches despite having different digestive systems (Janis 1976). Moreover, it is commonly assumed that horses live longer than cattle. For instance, in the AnAge database (Tacutu et al. 2012), the maximum lifespan recorded for the seven species of extant equids ranges from 30.1 years for kiang (*Equus kiang*) to 57 years for domestic horse (*E. caballus*), while for grazing bovids the maximum longevity recorded is 36.1 years for the lowland anoa (*Bubalus depressicornis*).

Among bovids, grazers live longer and senesce later and more slowly than do browsers, both in the wild (Gaillard et al. 2008) and in captive populations (Lemaître et al. 2013; Tidière et al. 2015). This difference is even more marked in captivity, probably because the

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food provided in zoos is more suitable for grazers than for browsers (Müller et al. 2010, 2011; Lemaître et al. 2013; Tidière et al. 2015). The extant equids are typically grazers (Schulz and Kaiser 2013), while bovids comprise species ranging over a continuum of dietary niches from grazers to browsers (Hofmann 1989; Gordon and Prins 2008); therefore, we only used data from grazers among the bovids to perform a valid comparison of longevity and senescence patterns across these groups. The use of captive populations allows patterns of longevity and senescence of the two orders to be studied independently of environmental variation, which is likely to be a key driver of mortality patterns (Gaillard et al. 1993). In captivity, animals are protected against starvation and predation, and competition for resources is minimal or absent. Using a dataset of 15 species (comprising 23 species or subspecies; 13 bovids and 10 equids) living in captivity, we found strong support for longer longevity in equids than in bovids after taking into account allometric relationships. This difference is associated with higher adult survival and delayed onsets of senescence for equids, but there is no difference between the two orders in the rate of actuarial senescence.

A major axis of variation in longevity and senescence across species is included in the slow-fast continuum of the life histories (Stearns 1983). Indeed, variation in life history traits among species is structured along a continuum of biological times that contrasts species with short longevity, early reproduction, high annual fecundity, and early onset and/or fast rates of senescence (at the continuum's fast end), with species with long longevity, delayed reproduction, low annual fecundity, and late onset and/or slow rates of senescence (at its slow end, e.g. Gaillard et al. 1989; Ricklefs 1998, 2010; Jones et al. 2008; Bronikowski and Vleck 2010). We, therefore, assessed whether observed differences of longevity between bovids and equids simply correspond to a different ranking over the slow-fast continuum as measured by the generation time (Gaillard et al. 2005). Two plausible, but different, demographic scenarios were tested: (1) all biological times or (2) only certain biological times are slower in equids

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84 than in bovids, leading to a difference in the pace of life (as represented by longer generation

85 times in equids). Causes of the differences could be selection pressures for a slower pace of

86 life in equids, or for a faster pace of life in bovids, with potentially different selection pres-

87 sures and constraints acting on the different components of generation time. Evolutionary

88 processes behind the differences in extant equids and bovids are discussed.

89 **METHODS**

90 **Datasets**

91 The life tables of the zoo populations were compiled from the Species360 database, which

92 contains data since 1817 from more than 1,000 member institutions in over 90 countries

93 worldwide. Information on sex, dates of birth and death is available for each individual.

94 Assuming that the total number of individuals living in zoos for a given species corresponds

95 to a worldwide meta-population, we computed population parameters for species living in

96 captivity. We constructed life tables available for females of equid and grazing bovid species

97 for which the exact dates of birth and death are known. We considered all dead and living

98 females but, to avoid any overestimation of the species' longevity due to some individuals

99 never being recorded as dead, we removed individuals still alive in January 2014 with an age

100 more than 125% older than the maximum age at death reported in AnAge, as longevity can be

101 longer in zoos today than 20 years ago due to the improvement of captive conditions (e.g.

102 Wich et al. 2009 for orang-utan, *Pongo* sp.). To ensure that the inclusion of all cohorts did not

103 bias the results, the same analyses were done with cohorts for which all individuals are dead,

104 defined as cohorts for which all females were already dead in January 2014. For some species,

105 wild-type and domestic populations are kept in zoos (e.g. *Bos javanicus*). For these species,

106 only the wild-type taxa were retained in the analyses. We obtained a final dataset of 23 taxa

107 including 13 grazing bovids and 10 equids (Fig. S1).

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Survival and actuarial senescence metrics

For each species, five different, and complementary, metrics were used to assess senescence patterns: maximum age at death, longevity, average adult survival rate, age at the onset of senescence and rate of senescence. The maximum age at death was determined as the maximum age at death observed in the database (Table S1). For the four other metrics, we built the capture history of each female and obtained age-specific survival estimates using the CMR (capture-mark-recapture) software E-SURGE (Choquet et al. 2009) (see appendix S1 for more details). From these age-specific survival estimates, we calculated the proportion of individuals alive at each age (l_x, with $l_0 = 1$) and longevity was measured as the age at which 90% of individuals from the initial cohort were dead (age x at which $l_x = 0.1$) (Table S1). This avoids spurious estimates due to different sample sizes or exceptionally long lives of a few individuals (Moorad et al. 2012).

To assess actuarial senescence, we fitted different age-dependent models from birth onwards: constant survival, two age-classes, full age-dependence, and several Gompertz models with different onsets of actuarial senescence (see appendix S1 for more details). To select the best survival model, we used a model selection procedure based on the Akaike Information Criterion (AIC, Burnham and Anderson 2002). For each species, we retained the model with the lowest AIC (Table S2). For 10 of the 13 bovids and 9 of the 10 equids, a Gompertz model provided a better fit than either the constant or the two-age class model, and was more parsimonious than the full age-dependent model (Table S2). The age at which survival begins to decline, corresponding to the age at the onset of senescence (Péron et al. 2010), varied among taxa (Table S1). In addition, from the selected Gompertz model, we measured both adult survival rate as the mean annual survival estimated between 1 year of age and the onset of senescence (Table S1) and rate of senescence as the exponential rate of mortality increase with age (Table S1). On a logit scale, age variation in survival was,

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133   therefore, constrained to be linear from the age at the onset of senescence onwards (Gaillard

134   et al. 2004). For four species (*Connochaetes taurinus albojubatus*, *Kobus kob leche*, *Syncerus*

135   *caffer* and *Equus quagga boehmi*), the full age-dependent model had a lower AIC than any

136   Gompertz model. For these four taxa, only the maximal age at death and longevity were

137   analyzed.

Mean values for the traits of adult females in each taxon

139   Mean body mass (BMa, in kg) for adult females was extracted from the literature (Table S3)

140   to correct for allometric constraints. When available, body mass measures from wild

141   populations were preferred.

142   The pace of life of a given taxon was measured as the generation time using the

143   method described in Gaillard et al. (2005) (see appendix S1 for more details). As life history

144   traits with a currency of time, we considered gestation length (GL, in days), age at first

145   parturition (AFP, in days), and the inter-birth interval (IBI, in days) to test the potential

146   difference of life history strategy between equids and bovids (Table S3). Values for GL, AFP,

147   and IBI were extracted from the literature (Table S3).

Analyses

149   We first tested the differences in survival and actuarial senescence metrics between bovids

150   and equids, accounting for body mass, because large species live longer and senesce later and

151   more slowly than small species (e.g. Jones et al. 2008; Ricklefs 2010; Lemaître et al. 2014;

152   Tidière et al. 2015). Dependent variables included maximum age at death, longevity, adult

153   survival rate, onset of senescence and rate of senescence. The full models included body mass

154   and order (as factor) as independent variables.

155   In a second step, we tested whether the differences in survival and actuarial

156   senescence metrics between bovids and equids parallel a difference in life history strategy. For

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157 each trait corresponding to a biological time included in the study (i.e. generation time,

158 gestation length, inter-birth interval and age at first parturition), the full models included body

159 mass and order (as factor) as independent variables.

160   In a third step, we ran a normed Principal Component Analysis (PCA, package '*ade4*',

161 (Dray and Dufour 2007) for bovids (N=5 taxa) and equids (N=7 taxa) separately, with

162 generation time, longevity, age at first parturition, gestation length and inter-birth interval as

163 biological times. Under scenario 1, all biological times in both equids and bovids should

164 contribute equally to the overall time scale (i.e. equi-correlation sensu Morrison 1967), which

165 corresponds to the slow-fast continuum (Gaillard et al. 2016). In contrast, under scenario 2,

166 equi-correlation should not be observed, meaning that the overall time scale is driven more

167 strongly by some specific biological times and less by others.

168   Analyses were not corrected for phylogenetic relatedness beyond the inclusion of

169 order as a factor because the number of species was rather small and did not allow estimating

170 reliably the phylogenetic inertia. All traits were log-transformed to improve the normality of

171 the distributions, except order (entered as a factor) and adult survival rate that was logit-

172 transformed. Analyses were performed using the linear model (lm) in R version 2.14.0 (R

173 Development Core Team 2016) and parameter estimates are given ± SE and/or 95%

174 confidence intervals.

175   The datasets generated during and/or analysed during the current study are available in

176 the supplementary data. However, the raw longevity dataset used to compute the survival and

177 senescence metrics are available upon request and with permission of Species360.

178 **RESULTS**

179 **Differences in survival and actuarial senescence parameters**

180 As expected, all survival metrics (i.e. maximum age at death, longevity and adult survival

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181 rate) increased with adult body mass (Tables 1 and S4, Fig. 1). Moreover, for a given body

182 mass, equids had a maximum age at death 6.9 years (95%CI [3.9; 10.0], Table 1, Fig. 1A)

183 longer and a longevity 5.5 years (95%CI [2.4; 8.6], Table 1, Fig. 1B) longer than bovids.

184 Equids also had a higher adult survival (+ 0.018, 95%CI [0.002; 0.035], Table 1, Fig. 1C) than

185 bovids. Order was the only factor included in the selected model to explain variation observed

186 in the onset of actuarial senescence (Table S4): equids began to senesce 5.89 years (95%CI

187 [2.33; 9.44], Table 1) later than bovids, irrespective of body mass (Fig. S2). Finally, observed

188 variation in the rate of senescence was explained only by the age at the onset of senescence

189 (Table S4), with the rate of senescence increasing when the onset was late (Table 1, Fig. S3).

190 However, the model also including body mass was competitive (Δ AIC = -1.31, Table S4) that

191 for a given onset of senescence, the rate of senescence tended to decrease with increasing

192 body mass (β=-0.342±0.196). There was no detectable difference between bovids and equids

193 in the rates of senescence in any of the models.

194   Using only extinct cohorts in the dataset results were similar to those obtained with all

195 individuals (Tables S5-S7): the order factor was included in the selected models for all

196 survival metrics, which indicates that equids outlived bovids and had higher adult survival.

197 For senescence metrics, the selected models did not include body mass or the order factor.

198 However, for the onset of senescence, the AIC of the model with order as a factor was only

199 0.51 AIC units lower than the selected model with equids senescing 4.21±1.57 years later than

200 bovids. Finally, the rate of senescence was only influenced by the onset of senescence.

201 **Differences in life history traits**

202 As expected, irrespective of the order, the four biological times were positively correlated to

203 adult body mass (Table 2 and S8, Fig. S4). Bovids had shorter generation times (by 2.31

204 years, Fig. S4A), shorter gestation lengths (by 89.2 days, Fig. S4B) and shorter inter-birth

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205　intervals (by 157.3 days, Fig. S4C) than equids. On the other hand, no detectable difference of

206　age at first parturition was found between equids and bovids (Fig. S4D, Tables 2 and S8).

207　**Evolutionary pathways**

208　In absence of species-specific selection pressure on a particular trait, generation time is

209　expected to be isometrically related to other biological times such as longevity, age at first

210　reproduction, inter-birth interval and gestation length. The generation time thus constitutes an

211　integrative measure of the time scale at which the life cycle of a given species is completed

212　(Gaillard et al. 2005; Staerk et al. 2019). Here, we assessed whether equids displayed longer

213　generation times either, as a part of a generally slower pace of life compared to bovids, in

214　which case all biological times should be isometrically associated, or whether the two groups

215　differed in only one particular biological time such as gestation length, which would lead to

216　longer generation times in equids than bovids. We found that all five of the biological times

217　contributed almost equally to the bovids' pace of life, although the gestation length was

218　slightly less tightly associated with other time-related traits (Table S9, Fig. 2A). Moreover, the

219　generation time was equivalent to the PC1 (Fig. 2A), which means that generation time

220　provides an overall measure of the pace of life in bovids. On the other hand, the picture was

221　markedly different for equids. Age at first parturition, instead of generation time (Fig. 2B),

222　was the closest to PC1 and was independent of inter-birth interval and gestation length (Table

223　S9). Longevity was negatively associated with the overall time scale (Table S9, Fig. 2B).

224　These findings demonstrate that, while bovids closely match the biological time syndrome

225　hypothesis, the variation among biological times was uncoupled in equids. This suggests the

226　existence of different selection pressures, or different constraints, on specific time-related

227　traits between the families.

228　**DISCUSSION**

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229   Our findings confirm that, for a given body mass, equids live longer than bovids, whatever the

230   metric used (maximum age at death or longevity). This difference in longevity between

231   bovids and equids is associated with both higher survival and a delay in the onset of actuarial

232   senescence in equids, but there is no difference in the rates of actuarial senescence. This is

233   consistent with several recent studies highlighting that the onset of senescence has to be

234   considered when analyzing senescence, and is more responsive than the rate of senescence

235   (Péron et al. 2010; Hammers et al. 2013; Gamelon et al. 2014; Tidière et al. 2015), although

236   the latter is still preferentially used in comparative analyses (e.g. Jones et al. 2008; Ricklefs

237   2010). Moreover, the analyses of covariation among biological times in bovid and equid taxa

238   indicate that a synchronization of all biological times evolved in bovids, whereas biological

239   times were uncoupled in equids. This could be the result of a specific selection for longer

240   gestation lengths in equids, a physiological constraint that prevents the evolution of shorter

241   gestation lengths in equids, a stronger selection for a faster pace of life in bovids, or a

242   combination of any of these factors.

243   Tooth wear is an essential process in mammalian ageing (Skogland 1988; King et al.

244   2005), and there is evidence that tooth height is related to longevity within species (Veiberg et

245   al. 2007). The difference in longevity we reported may be explained by a difference in a key

246   morphological adaptation of grazers, hypsodonty. Comparison of estimates of hypsodonty

247   index for six bovid and seven equid taxa (see Table S3) showed that equids have hypsodonty

248   about 50% higher than bovids (difference = 2.49; t = 4.69; df = 10.678; p-value < 0.001, Fig.

249   S5). Dental anatomy could, therefore, provide a mechanical explanation for the greater

250   longevity of equids relative to similar-sized bovids, through a longer functional duration of

251   the chewing tooth-row. It has been suggested that wear rates should be less in ruminants,

252   because much of the chewing occurs during rumination, on material that has already been

253   washed of grit in the forestomach (Hatt et al. 2019). However, the limited information

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254 available has not yet demonstrated different rates of tooth wear between equids and bovids

255 (Damuth and Janis 2014). More data like that measured in red deer (*Cervus elaphus*) by

256 Péres-Barberia and Gordon (1998) are needed on tooth wear in free-ranging equids and

257 grazing bovids to conclude firmly whether the greater hypsodonty in equids plays a key role

258 in explaining their greater longevity.

259 The longer generation time of equids demonstrates that they have a slower pace of life

260 than similar-sized grazing bovids. This difference of pace of life is partly due to a difference

261 of inter-birth interval, itself caused in part by the longer gestation length of equids, and partly

262 to their higher adult survival, which also contributes to their slow pace of life. Two different

263 concepts exist for the occurrence of a slow pace of life. It could be the result of specific

264 selection pressures that facilitate its evolution as a specific adaptation to resource-limited

265 niches. Alternatively, species characterized by a slower pace of life might be displaced by

266 species with a faster pace of life except in resource-poor niches (Vermeij 1994). There are

267 differences in susceptibility to resource constraints between bovids and equids: the abundance

268 of wildebeest (i.e. a grazing bovid) is much more affected by food resources than zebras (a

269 similar-sized equid) (Grange and Duncan 2006). Whether longer gestation periods evolved

270 in equids from a common ancestor of the two groups, perhaps a Condylarth (Rose 1996),

271 which had shorter gestation periods, or whether a generally slower pace of life is a

272 characteristic of the equid lineage, cannot be determined from our study, since the

273 common ancestor's life history is of course unknown.

274 Most bovid species have an inter-birth interval of less than one year (mean of 334.00

275 days, 95%CI [286.54;381.46]), which allows them to produce one litter per year. On the other

276 hand, equids display mean inter-birth intervals of about 1 year and 4 months (491.29 days,

277 95%CI [440.34;542.23]). The bovid life history strategy thus allows breeding seasonally to

278 match plant phenology, which is clearly an advantage in many grassland systems. Decreasing

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279 the gestation length may have been part of the bovid evolution towards seasonal breeding

280 (Zerbe et al. 2012), and the shorter generation times may have allowed bovids to increase

281 their demographic rates and abundances. This may give them an advantage in resource rich

282 environments where predation pressure is higher than in poor environments (Melis et al.

283 2013). Indeed, the faster pace of life allows higher population growth rates, leading to a better

284 demographic response to predation pressure (Grange et al. 2004). A shorter generation time

285 allows faster evolution and this may also have facilitated their species diversity. For instance,

286 the shorter gestation length in bovids compared to giraffids has been invoked to explain the

287 replacement of a diverse giraffid community with a diverse bovid one over evolutionary time

288 (Clauss and Rössner 2014).

289   To conclude, equids live longer than grazing bovids of similar size. This is because

290 equids have higher survival, and their actuarial senescence begins at a later age. Equids also

291 have greater hypsodonty, which could be a key morphological adaptation allowing greater

292 longevity in equids, though more data are needed on wear rates in the wild to reach a firm

293 conclusion. Grazing bovids have a faster pace of life, with shorter gestation periods. The

294 shorter gestation periods of bovids may be associated with accelerated rates of intrauterine

295 growth (Baur 1977), although the morphological and physiological mechanisms involved

296 remain to be discovered. This scenario considers equids to be constrained by slower

297 intrauterine growth and a slower pace of life, which makes them mainly competitive in

298 environments with limited resources. Alternatively, a longer gestation length for equids may

299 be a specifically evolved adaptation to increased survival in these environments. The fast pace

300 of life in bovids may be a key to the rapid evolution of the bovids since the Miocene; today

301 they dominate communities of grazing animals, in species diversity and in abundance.

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Table 1. Parameter estimates from the linear models of the relationship between survival (i.e.

maximum age at death, longevity, and adult survival rate) or actuarial senescence (i.e. onset

and rate of senescence) metrics and the mean female adult body mass among 23 taxa of large

herbivores belonging to two orders of mammals.

		β	95% CI	t value	Adjusted-R^2
Maximum age at death	Intercept	2.496	2.033; 2.960	10.56	0.61
N= 23 taxa	Order (*Equidae*)	0.225	0.133; 0.318	4.79	
	Adult body mass	0.142	0.059; 0.225	3.34	
Longevity	Intercept	1.787	1.234; 2.341	6.33	0.63
N= 23 taxa	Order (*Equidae*)	0.225	0.115; 0.335	4.01	
	Adult body mass	0.228	0.129; 0.328	4.50	
Adult survival rate	Intercept	1.050	-0.224; 2.324	1.62	0.47
N= 19 taxa	Order (*Equidae*)	0.385	0.153; 0.617	3.25	
	Adult body mass	0.321	0.097; 0.544	2.81	
Onset of senescence	Intercept	2.056	1.845; 2.267	19.08	0.34
N= 19 taxa	Order (*Equidae*)	0.498	0.191; 0.804	3.18	
Rate of senescence	Intercept	-0.926	-2.123; 0.271	-1.52	0.31
N= 19 taxa	Onset	0.791	0.276; 1.305	3.01	

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459 **Table 2.** Parameter estimates from the linear models of the relationship between biological

460 times and the mean female adult body mass among 23 taxa of large herbivores belonging to

461 two orders of mammals.

		β	95% CI	t value	Adjusted-R^2
Generation time	Intercept	0.107	-0.668; 0.881	0.27	0.78
N= 12 taxa	Order (*Equidae*)	0.179	0.002; 0.356	1.98	
	Adult body mass	0.310	0.156; 0.464	3.95	
Gestation length	Intercept	4.844	4.542; 5.146	31.42	0.89
N= 15 taxa	Order (*Equidae*)	0.243	0.179; 0.307	7.44	
	Adult body mass	0.143	0.087; 0.200	4.99	
Inter-birth interval	Intercept	5.050	4.260; 5.840	12.53	0.72
N= 12 taxa	Order (*Equidae*)	0.295	0.115; 0.476	3.21	
	Adult body mass	0.150	-0.006; 0.307	1.88	
Age at first parturition	Intercept	5.582	4.670; 6.494	12.00	0.39
N= 14 taxa	Adult body mass	0.260	0.094; 0.426	3.07	

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Figure legends

464 **Figure 1.** Relationship between maximum age at death (A), longevity (B), or adult survival

465 (C) and taxon-specific body mass of adult females for 13 bovids (open dots) and 10 equids

466 (full dots). For a similar body mass, equids live longer and have a higher adult survival than

467 bovids.

468 **Figure 2.** Normed Principal Component Analyses performed on 5 biological times for 5 bovid

469 and 7 equid taxa separately. All biological times are positively correlated among bovids,

470 whereas for equids there is an uncoupling of biological times.