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1 **Do equids live longer than grazing bovids?**

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14 **ABSTRACT**

15 A large part of the diversity of longevity and actuarial senescence (i.e. the progressive decline
16 of survival probabilities with age) across vertebrates can be related to body size, phylogeny
17 and the species' position on the slow-fast continuum of life histories. However, differences in
18 mortality patterns between ecologically similar species, such as bovids and equids, remain
19 poorly understood. Equids are commonly understood to outlive bovid species relative to their
20 body mass, despite very similar feeding niches. Comparing survival patterns of 13 bovid and
21 10 equid sub-species, our findings confirm that equids outlive bovid species, with a higher
22 adult survival rate and a delayed onset of senescence for equids, but no difference of rate of
23 actuarial senescence. These differences are associated with a slower generation time and
24 longer inter-birth interval, due to a longer gestation period, for equids compared to bovids.
25 Finally, our results suggest that all biological times (i.e. all life history traits expressed in time
26 units) have evolved synchronously in bovids, whereas in equids gestation time and inter-birth
27 interval either were never in synchrony with, or have slowed down relative to other biological
28 times. Our findings suggest the existence of different selection pressures, or different
29 constraints, on specific time-related traits between these two mammalian orders.

30 **Keywords:** actuarial senescence; biological times; demography; pace of life; slow-fast con-
31 tinuum

32 **Running head:** Equids vs bovids' actuarial senescence

33 **Word count:** 5734 words

34 INTRODUCTION

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

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

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

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

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

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).

108 **Survival and actuarial senescence metrics**

109 For each species, five different, and complementary, metrics were used to assess senescence
110 patterns: maximum age at death, longevity, average adult survival rate, age at the onset of
111 senescence and rate of senescence. The maximum age at death was determined as the
112 maximum age at death observed in the database (Table S1). For the four other metrics, we
113 built the capture history of each female and obtained age-specific survival estimates using the
114 CMR (capture-mark-recapture) software E-SURGE (Choquet et al. 2009) (see appendix S1
115 for more details). From these age-specific survival estimates, we calculated the proportion of
116 individuals alive at each age (l_x , with $l_0=1$) and longevity was measured as the age at which
117 90% of individuals from the initial cohort were dead (age x at which $l_x=0.1$) (Table S1). This
118 avoids spurious estimates due to different sample sizes or exceptionally long lives of a few
119 individuals (Moorad et al. 2012).

120 To assess actuarial senescence, we fitted different age-dependent models from birth
121 onwards: constant survival, two age-classes, full age-dependence, and several Gompertz
122 models with different onsets of actuarial senescence (see appendix S1 for more details). To
123 select the best survival model, we used a model selection procedure based on the Akaike
124 Information Criterion (AIC, Burnham and Anderson 2002). For each species, we retained the
125 model with the lowest AIC (Table S2). For 10 of the 13 bovids and 9 of the 10 equids, a
126 Gompertz model provided a better fit than either the constant or the two-age class model, and
127 was more parsimonious than the full age-dependent model (Table S2). The age at which
128 survival begins to decline, corresponding to the age at the onset of senescence (Péron et al.
129 2010), varied among taxa (Table S1). In addition, from the selected Gompertz model, we
130 measured both adult survival rate as the mean annual survival estimated between 1 year of age
131 and the onset of senescence (Table S1) and rate of senescence as the exponential rate of
132 mortality increase with age (Table S1). On a logit scale, age variation in survival was,

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.

138 **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).

148 **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

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 \pm 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

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

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**

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; $t = 4.69$; $df = 10.678$; $p\text{-value} < 0.001$, 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

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

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 (Claus 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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454 **Table 1.** Parameter estimates from the linear models of the relationship between survival (i.e.
 455 maximum age at death, longevity, and adult survival rate) or actuarial senescence (i.e. onset
 456 and rate of senescence) metrics and the mean female adult body mass among 23 taxa of large
 457 herbivores belonging to two orders of mammals.

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

458

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

462

463 **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.