Sex-specific body mass ageing trajectories in adult Asian elephants

3 Lucas D. Lalande[1,2,3,a] (ORCID iD: 0000-0001-9319-8033),

4 Virpi Lummaa[1,a] (ORCID iD: 0000-0002-2128-7587),

5 Htoo H. Aung[4],

6 Win Htut[4],

7 U. Kyaw Nyein[4],

8 Vérane Berger[1,a,*] (ORCID iD: 0000-0002-2153-0719),

9 Michael Briga[1,a,*] (ORCID iD: 0000-0003-3160-0407)

10 [1] Department of Biology, University of Turku, Turku, Finland;

11 [2] Université Bourgogne Franche-Comté, Dijon, France;

12 [3] Present address: Université de Lyon, Université Lyon 1, UMR CNRS 5558, Villeurbanne
13 CEDEX, France;

14 [4] Myanma Timber Enterprise, Ministry of Natural Resources and Environmental
15 Conservation, West Gyogone Forest Compound, Yangon, Myanmar;

16 [*] Equal contribution of these authors

17 [a] Corresponding authors: L. D. Lalande: lucas.lalande@univ-lyon1.fr, V. Lummaa:
18 virpi.lummaa@gmail.com, V. Berger: verane.berger@orange.fr, M. Briga:
19 michbriga@gmail.com

Abstract

In species with marked sexual dimorphism and where one sex undergoes stronger intrasexual competition, that sex is expected to age earlier or quicker. Here, we utilise a unique, longitudinal dataset of a semi-captive population of Asian elephants (*Elephas maximus*), a species with marked male-biased intrasexual competition, with males being larger and living shorter, and test the hypothesis that males show earlier and/or faster body mass ageing than females. We show sex-specific body mass ageing trajectories: adult males gained weight up to the age of 48 years old, followed by a decrease in body mass until natural death. In contrast, adult females gained body mass with age until a body mass decline in the last year of life. Our study shows that sex-specific life-histories shape ageing patterns, consistent with the predictions of the classical theory of ageing.

Introduction

36 Ageing – a decline in organismal functioning with age (Monaghan et al., 2008) – has

37 been observed in many species (Jones et al., 2014). However, the onset and rates of

38 ageing differ both between (Jones et al., 2014) and within species (Nussey et al.,

39 2007) and between sexes (Clutton-Brock & Isvaran, 2007; Lemaître et al., 2020;

40 Tidière et al., 2015). A main challenge in ageing research is to quantify and explain

41 such differences in the onset and rates of ageing (Rando & Wyss-Coray, 2021).

42 In species with sex-specific intrasexual competition, classical theory of ageing

43 predicts that the sex with the highest intrasexual competition has a shorter lifespan

44 and an earlier onset and/or higher rate of ageing (Williams, 1957). The rationale is

45 that high intrasexual selection often results in one sex showing conspicuous displays

46 or aggressive intrasexual behaviours, leading to increased mortality and a *live fast,*

47 *die young* pace of life (Bonduriansky et al., 2008; Clutton-Brock & Isvaran, 2007;

48 Maklakov & Lummaa, 2013). For that sex, antagonistically pleiotropic genes or

49 deleterious mutations are not counter selected due to a weakened force of selection

50 in late-life (Williams, 1957). Accordingly, in polygynous species with male-biased

51 intrasexual competition, males often die earlier (Lemaître et al., 2020) and age earlier

52 or faster than females (Beirne et al., 2015; Clutton-Brock & Isvaran, 2007; Douhard et

53 al., 2017; Nussey et al., 2009; Tidière et al., 2015). However, recent conceptual

54 developments have shown that this association can be disrupted. This can occur for

55 example because of condition-dependent extrinsic mortality selecting particularly

56 high-performing individuals in the population (Chen & Maklakov, 2014) or

57 canalisation (*i.e.* the more a trait contributes to fitness, the less it should deviate from

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58   optimal trait value, with respect to environmental variation (Flatt, 2005)), thereby

59   contradicting the theoretically expected earlier or faster ageing in males. The extent

60   to which such phenomena occur in nature remains unknown.

61   Here, we used a unique long-term dataset to describe sex-specific body mass ageing

62   trajectories in a nutritionally unsupplemented semi-captive timber population of Asian

63   elephants (*Elephas maximus*) living in their natural environment in Myanmar. Body

64   mass is of interest in the study of ageing because it is positively associated with key

65   life-history traits such as reproduction and lifespan in many non-human species

66   (Briga et al., 2019; Gaillard et al., 2000; Hämäläinen et al., 2014; Pelletier et al.,

67   2007). Therefore, the study of body mass ageing fits into the evolutionary framework

68   of ageing. Accordingly, in Asian elephants, seasonal variation in body mass was

69   positively associated with survival the following month (*e.g.* low body mass was

70   associated with low survival during dry season) (Mumby, Mar, Thitaram, et al., 2015).

71   Moreover, male Asian elephants benefit from being heavy during intrasexual

72   competition for dominance and mating (Sukumar, 2003).

73   However, we know almost nothing about body mass ageing in elephants despite the

74   interest in studying ageing in such a long-lived, social and sexually dimorphic non-

75   human species. While females live in kin groups, adult males often roam solitarily,

76   undergo a more intense intrasexual competition for dominance and mating (Sukumar,

77   2003) and hence are bigger, heavier (Mumby, Chapman, et al., 2015), more

78   aggressive and less sociable (Seltmann et al., 2019) and shorter-lived than females

79   (respective median lifespans in this population: 30.8 and 44.7 years) (Lahdenperä et

80   al., 2018). Based on this male-biased intrasexual competition and shorter lifespan,

81   and following the classical theory of ageing (Williams, 1957), we tested the prediction

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82 that males experience an earlier and/or faster body mass loss than

83 females (Bonduriansky et al., 2008; Maklakov & Lummaa, 2013).

Material and methods

Study population

86   We studied the world's largest semi-captive Asian elephant population

87 consisting of around 3,000 individually-marked elephants owned by the government-

88 run Myanma Timber Enterprise (MTE) (Leimgruber et al., 2008). Their birth, death,

89 maternal-lineage pedigree, and morphological measurements have been recorded

90 for almost a century by local veterinarians. These elephants are distributed across

91 Myanmar in forest camps and used as riding, transport and drafting animals.

92 Elephants work during the day and, at night, they socialise, mate and forage freely,

93 unsupervised in forests (Oo, 2010; Zaw, 1997). There are no husbandry procedures

94 and timber elephants are never culled. Calves born in captivity are cared for and

95 nursed by their biological mother and allomothers (Lahdenperä et al., 2016; Lynch et

96 al., 2019). Therefore, breeding rates are natural with no reproductive management.

97 Moreover, there is minimal food provisioning, but elephants benefit from veterinary

98 care that consists of treatment of simple injuries and monitoring of working

99 conditions.

100 Both males and females are used in the workforce, and each working group of six

101 elephants is composed of both sexes. Males and females follow the same

102 government set limitations on taming age, working and retirement age, working-days

103 per year, hours of work per day and tonnage pulled annually apply to both sexes,

104 although it is possible that males might be used for somewhat different working tasks

105   at times (*e.g.* when use of tusks is required; only males can possess long tusks in

106   Asian elephants). Pregnant females are given a rest period from mid-pregnancy

107   (around 11 months into gestation) until the calf is 1-year-old (Toke Gale, 1974), while

108   they and their calf are being monitored by their mahouts (individual caretakers and

109   riders) throughout this period. Following this break, mothers are used for light work

110   but are kept with calves at heel and able to suckle on demand until the calf is four or

111   five years old (Oo, 2010) at which point calves are assigned a rider, name, logbook

112   and registration number. After the training period, elephants are used for light work

113   duties until the age of 17, when they enter the full workforce until retirement around

114   age 50. The MTE maintains their care and logbooks until death.

115   **Data collection and selection**

116   Our analyses focused on age- and sex-specific variation in adult body mass

117   from age 18 onwards, in order to omit the phase during which elephants grow in

118   height (Mumby, Chapman, et al., 2015) and to focus only on adult body mass age-

119   specific variations. We compiled a total of 3,886 body masses on 493 individuals

120   (2,570 body masses on 322 females, and 1,316 body masses on 171 males). These

121   data came from two sources: (i) body masses were either measured on elephants on

122   the field or (ii) estimated using height to the shoulder and chest girth (method in

123   Supplementary Information 1). For the first source, we extracted 1,901 body masses

124   of 347 elephants (1,297 measurements on 230 females, and 604 measurements on

125   117 males) and for the second source we estimated 1,985 body masses on 342

126   individuals (1,273 estimations on 226 females, and 712 estimations on 116 males - a

127   same individual can have both measured and estimated body masses). For all

128   elephants of the 325 working localities ('township') sampled, sex, year of birth

129   ('YOB'), alive or dead status at the moment of the study, origin (captive-born or wild-

130   caught) and measurement season (hot: Feb-May, monsoon: Jun-Sep, cold: Oct-Jan

131   (Mumby, Mar, Thitaram, et al., 2015)) were known. The alive or dead status was

132   used to test for potential terminal decline. Among the 493 individuals considered, 5

133   males (63 observations) and 18 females (185 observations) were known to be dead.

134   We had measurements during the last year of life for 2 males (7 observations) and 10

135   females (54 observations). Study elephants were aged 18 – 72 years (mean = 39.3)

136   and born 1941 – 1999. Age and cohort information were comparable between sexes,

137   with 171 males (n = 1,316) born 1954 – 1999 and aged 18 – 64 years (mean = 37.4),

138   and 322 females (n = 2,570) born 1941 – 1999 and aged 18 – 72 years (mean =

139   40.2).

140   Most elephants of this semi-captive population get at least occasionally

141   measured for height and chest girth, with no selection with respect to their age, sex

142   or condition. Body mass is measured only in camps provided with measurement

143   scales (mainly in regions with the highest concentrations of elephants and the best

144   accessibility). All elephants within the reach of those camps get weighed, again

145   without any bias regarding their age, sex or condition. The logbooks containing these

146   measurements have thus far been translated from Burmese to English mainly from

147   the Sagaing region for logistic reasons, but again without any bias or pre-selection of

148   certain individuals.

149   In total, we obtained a median of 4.0 measurements/individual (2.5 – 97.5th

150   percentiles: [1.0; 36.4], followed during a median period of 2.8 years (2.5 – 97.5th:

151   [0.0; 36.6] on 493 elephants (n = 3,886). Two influential observations measured at

152   age 18 and 23 were removed for one male because of particularly low Δage (Cook's

153   distance = 0.61 and 0.25, mean of 0.001 on all males). Other observations for this

154   male, all after age 50, were included.

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155 **Statistical analyses**

156 　　We investigated the age- and sex-specific variation in body mass in R version

157 4.1.1 (R Core Team, 2021), using the body mass (log-transformed to reach normality

158 of the variable and because of the allometric relationship between body mass and

159 size) as a dependent variable with a normal error distribution. First, we tested in a

160 single model, whether there were sex-specific ageing trajectories using an interaction

161 term (Table S2). Given that this interaction was statistically significant, we compared

162 the sex-specific ageing trajectories for both sexes separately. We did these analyses

163 using both general additive mixed models (GAMMs) with cubic regression splines

164 (but note that other spline functions gave similar conclusions as those shown here)

165 and general linear mixed models (GLMMs) with respectively the functions 'gamm' of

166 the package 'mgcv' (v. 1.8-36, Wood, 2011) and the function 'lmer' of the package

167 'lme4' (v. 1.1-27.1, Bates et al., 2015)). GAMMs allow more flexible ageing

168 trajectories than GLMMs, but the more constrained ageing trajectories in GLMMs

169 allow a less descriptive identification of differences in ageing trajectories (Fig. S1)

170 and both approaches gave consistent conclusions (see results section). We identified

171 the best fitting models using the model selection approach based on the second

172 order Akaike Information Criterion (AICc) as implemented in the package 'MuMIn' (v.

173 1.43.17, Bartoń, 2021). In brief, the best fitting model has the lowest AICc value, with

174 other models within 4 ΔAICc being plausible and models becoming increasingly

175 equivocal up to 14 ΔAICc, after which they become implausible (Burnham et al.,

176 2011). Visual inspection of model residuals confirmed that these fulfilled all

177 assumptions of distribution and homogeneity without any influential data points or

178 outliers (see above).

179 *Within- vs. between-individual change*

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180   In all models, we accounted for non-independence of data due to repeated

181   measurements from the same individual by including elephant identity ('ID') as a

182   random intercept. The composition of the population can change with age for

183   example due to selective disappearance of certain (*e.g.* lighter or heavier) individuals,

184   which can affect the age trajectory. In order to alleviate as much as possible this

185   problem in such a long-lived species, we decomposed body mass changes with age

186   into between- and within-individual changes following the approach developed by van

187   de Pol & Verhulst, (2006) and van de Pol & Wright, (2009) using two terms: *i)* the age

188   at last measurement for each individual, which captures the between-individual

189   variations and *ii)* a 'Δage' term (age at measurement minus the individual's mean age

190   for all measurements) capturing the within-individual changes with age. We mean-

191   centered and standardised 'Δage' so that *i)* individuals measured once all get a Δage

192   = 0 and hence contribute to the variance of the Δage intercept but not to its slope and

193   *ii)* to avoid collinearity and to have comparable variance for Δage and Δage² (Bolker,

194   2008; Zuur et al., 2009). Among the 493 individuals of our dataset, 105 individuals

195   had only one measurement. We included these individuals by giving them Δage = 0

196   (*i.e.* mean-centered) so they do not contribute to the coefficient but do contribute to

197   the variance along the Y axis on Δage = 0, diminishing the likelihood of a false

198   positive, and ii) do contribute to the coefficient of the age at last measurement term,

199   thereby avoiding a bias in the dataset from selecting only the longer-lived or most

200   monitored individuals.

201   *Testing ageing trajectories*

202   We tested several within-individual ageing trajectories, first using GAMMs,

203   which can provide curvilinear relationships and allow to describe trends, and using

204   GLMMs, able to detect breaking points if necessary, by testing linear, quadratic,

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205 threshold and terminal models (Fig. S1) and we selected the ageing trajectory with

206 the lowest AICc. For GAMMs, we identified the age at which maxima occurred based

207 on the first-order derivative (= 0) using the function 'fderiv' of the package 'gratia' (v.

208 0.6.0, Simpson & Singmann, 2021). For threshold models (Fig. S1C), we followed the

209 approaches previously developed in Briga et al., (2019) and Douhard et al., (2017).

210 In brief, we first identified the best-fitting threshold age in a series of models, varying

211 the threshold in the 'Δage' term between -35 to 22 years with intervals of one Δage (1

212 mean-centered Δage = 4.4 and 4.5 years for males and females respectively) and

213 estimated the threshold and its confidence intervals using ± 4 ΔAIC age range. Then

214 we compared the best-fitting threshold model with the other ageing trajectories.

215 Sometimes, declines in trait value appear shortly before death (terminal decline). We

216 coded a 'terminal' change (Fig. S1D) as a binomial factor for whether an individual

217 died during the year following the measurement. We used a one-year-window to

218 avoid a possible seasonal covariation in weight and because it was the best fitting

219 time-window, but note that models with other time-windows gave consistent

220 conclusions (Fig. S3).

221 *Accounting for temporal and spatial variation in body mass*

222   As body mass variation can be influenced by seasonal, spatial and within-

223 individual factors, we tested whether body mass values were affected by (i)

224 measured or estimated, (ii) individuals were alive or dead, (iii) captive- or wild-born

225 and (iv) the measurement season. To this end we used a model selection approach,

226 performing a dredge on the best-fitting ageing trajectories for each sex to test for

227 confounding factors (Table S3). In our models, we included as random intercepts

228 individual identity to account for the repeated measurement of the same individual.

229 We also included 'township' to account for the spatial clustering of individuals across

230   Myanmar, although actually adding township worsened the model fit in most cases

231   (male GAMM: ΔAICc = +1.5, GLMM: ΔAICc = +1.8; female GAMM: ΔAICc = +0.6,

232   GLMM: ΔAICc = -21.2).

Results

234   At the measurements' starting age of 18 years, males were on average 235 kg

235   heavier than females, weighing respectively 2,541 kg [95%CI: 2,406; 2,683] and

236   2,306 kg [95%CI: 2,258; 2,355] and this difference was statistically significant (ΔAICc

237   = -122.6 in a GLMM with vs without sex as a fixed effect).

238   We identified the elephant's body mass ageing trajectories using general additive

239   mixed models (GAMMs) and general linear mixed models (GLMMs) and both

240   approaches gave consistent results. Both analyses showed that sexes have different

241   body mass ageing trajectories (interaction term, GAMM: ΔAICc = -65.7, Fig. S4,

242   Table S2; GLMM: ΔAICc = -47.0, Fig. 1, Table S2) and hence, we identified the

243   ageing trajectories for both sexes separately.

244   For males, both GAMMs and GLMMs indicated a body mass gain from age 18 years

245   until their late-forties or early fifties (GAMM maximum: 54 years [95%CI: 53; 56], Fig.

246   S5; GLMM maximum: 48.2 years [4 AICc CI: 47.1; 51.6], Fig. 1A), followed by a

247   decline until death (Fig. S4A, Fig. 1A, Table 1, Table S4). In GLMMs, this maximum

248   was shown through the best fit of a threshold model (ΔAICc = -30.4 compared to a

249   linear trajectory): males gained mass at a rate of 22 kg/year [95%CI: 19.4 23.7] or 1%

250   [95%CI: 0.9; 1.1] of males' mean body mass and then lost mass at a rate of 29

251   kg/year [95%CI: 14.9; 41.9] or 1.3% [95%CI: 0.7; 1.9] of males' mean body mass

252   (Fig. 1A, Table 2). Regarding the decline, neither GAMMs nor GLMMs showed

253   confident statistical support that it was terminal (*i.e.* determined by time before death

254   rather than age): in GAMMs, models with and without the terminal term were almost

255   equivalent (ΔAICc = -0.01, Table S4) and in GLMMs adding a terminal term

256   worsened the model fit (ΔAICc = +5.0, Table 1, Fig. S3A).

257   For females, both GAMMs and GLMMs indicated a body mass gain throughout their

258   lives until a terminal decline during their last year of life (Fig. S4B, Fig. 1B, Table 1,

259   Table S4). GLMMs indicated a mass gain of 9 kg/year [95%CI: 7.5; 10.4] or 0.35%

260   [95%CI: 0.3; 0.4] of females' mean body mass (ΔAICc = -6.7, Table 1, Table 2). Loss

261   of body mass occurred in the last year of life (GAMM: ΔAICc = -12.2, Table S4, Fig.

262   S4B; GLMM: ΔAICc = -4.9, Table 1, Fig. 1B, Fig. S3B) and consisted of 173 kg

263   [95%CI: 80; 263] or 6.8% [95%CI: 3.2; 10.4] of their mean body mass (Table 2). For

264   comparison, the extent of the terminal decline in males, if any, is just over half that in

265   females at 96 kg [95%CI: -19; 205] or 4.3% [95%CI: -0.9; 9.2] of males' mean body

266   mass (quantified in the aforementioned best-fitting threshold model). Note that for

267   females and for both GAMMs and GLMMs, the second best model confirms the linear

268   age trajectory, but excludes the terminal effect (GAMM: ΔAICc = +12.2, Table S4;

269   GLMM: ΔAICc = +4.9, Table 1). For males, the second best model (for GAMMs and

270   GLMMs) conserves the same threshold trajectory, but includes the terminal effect

271   (GAMM: ΔAICc = -0.01, Table S4; GLMM: ΔAICc = +5.0, Table 1, Fig. S3B). Model

272   averaging on ageing trajectories within 7 ΔAICc (Burnham et al., 2011) confirmed the

273   ageing trajectories found, *i.e.* a threshold trajectories for males with a significant

274   decline of body mass from 48 years old onwards (GLMM: β = -0.06 [95%CI: -0.09; -

275   0.03]) and a non-significant terminal decline (GLMM: β = -0.04 [95%CI: -0.10; 0.01],

276   GAMM: β = -0.04 [95%CI: -0.09; 0.01]). Similarly, model averaging performed on

277   models within 7 ΔAICc for females confirmed the ageing trajectory found, *i.e.* a body

278   mass gain throughout life (GLMM: β = 0.015 [95%CI: 0.01; 0.02]) with no significant

279   decline before the last year of life (GLMM: β = -0.07 [95%CI: -0.11; -0.03]). Also, we

280   found no effect of none of the temporal and spatial confounding variables tested
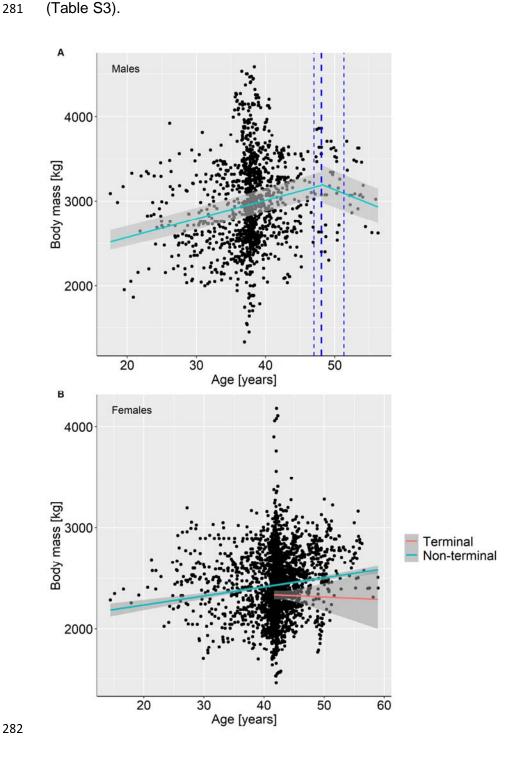
281   (Table S3).

282

283   **Figure 1.** Body mass ageing trajectories of (A) males (n = 1,316 measurements on
284   171 individuals) and (B) females (n = 2,570 measurements on 322 individuals) with
285   predictions of the best-fitting GLMMs (Table 1) with grey areas 95%CI. For males,
286   the thick dashed-line shows the threshold age at onset of the body mass decline (1.9
287   or 48.3 years) with thin dashed-lines the 4 ΔAICc-CI [46.6, 52.3]. For females,
288   measurements in the terminal year (red) are significantly lower (intercept) than
289   measurements at other ages (blue). Note 1: the terminal slope is for illustration
290   purposes only and was not statistically tested. Note 2: the original x-axis is Δage, but
291   for simplicity, we presented here x-axis as age. For the original figure, please see
292   Fig. S2.

293 **Table 1.** Best fitting body mass ageing trajectories (bold) for males and females, using GLMMs for each model ageing trajectories
294 ranked from the least to the most complex. AICc: second-order Akaike Information Criterion; ΔAICc: change in AICc relative to the
295 best fitting model; k: degrees of freedom.

Model type	Model	Males			Females		
		K	AICc	ΔAICc	k	AICc	ΔAICc
null	log(bm) ~ 1	4.0	-2,828.3	364.2	4.0	-5,442.9	160.7
linear	log(bm) ~ Δage + age-last	6.0	-3,162.0	30.4	6.0	-5,586.1	17.5
+terminal	log(bm) ~ Δage + age-last + terminal	7.0	-3,156.9	35.6	7.0	-5,592.3	11.3
age-last²	log(bm) ~ Δage + age-last + age-last²	7.0	-3,155.5	37.0	7.0	-5,598.7	4.9
+terminal	**log(bm) ~ Δage + age-last + age-last² + terminal**	8.0	-3,150.4	42.1	**8.0**	**-5,603.6**	**0.0**
Δage²	log(bm) ~ Δage + Δage² + age-last	7.0	-3,176.8	15.7	7.0	-5,571.6	32.0
+terminal	log(bm) ~ Δage + Δage² + age-last + terminal	8.0	-3,171.2	21.3	8.0	-5,577.9	25.7
quadratic	log(bm) ~ Δage + Δage² + age-last + age-last²	8.0	-3,170.1	22.3	8.0	-5,584.3	19.3
+terminal	log(bm) ~ Δage + Δage² + age-last + age-last² + terminal	9.0	-3,164.6	27.9	9.0	-5,589.3	14.3
threshold	**log(bm) ~ Δage1 + Δage2 + age-last**	**8.0**	**-3,192.5**	**0.0**	8.0	-5,580.5	23.1
+terminal	log(bm) ~ Δage1 + Δage2 + age-last + terminal	9.0	-3,187.5	5.0	9.0	-5,586.0	17.6
threshold (age-last²)	log(bm) ~ Δage1 + Δage2 + age-last + age-last²	9.0	-3,185.8	6.6	9.0	-5,592.6	11.0
terminal	log(bm) ~ Δage1 + Δage2 + age-last + age-last² + terminal	10.0	-3,180.9	11.6	10.0	-5,596.9	6.7

296

Table 2. Parameter estimates of linear mixed-effect models including individual body mass beyond 18 years of age as the response variable (in kg, log-transformed) for male and female Asian elephants. V: variance, SD: standard-deviation, SE: standard-error. Marginal and conditional R^2 give the variance explained by fixed effects, and both fixed and random effects, respectively.

Males			Females		
Random effects	**V**	**SD**	**Random effects**	**V**	**SD**
Individual identity	0.019	0.137	Individual identity	0.011	0.103
Township	0.0005	0.023	Township	0.003	0.056
Fixed effects	**Estimate**	**SE**	**Fixed effects**	**Estimate**	**SE**
Intercept	7.707	0.021	Intercept	7.840	0.019
Age at last measurement	0.087	0.012	Age at last measurement	0.025	0.007
Δage1	0.041	0.002	Age at last measurement²	-0.028	0.006
Δage2	-0.057	0.014	Δage	0.016	0.001
			Terminal (1)	-0.071	0.020
Marginal R²	0.24		**Marginal R²**	0.10	
Conditional R²	0.89		**Conditional R²**	0.77	

Discussion

We tested whether in a species with marked male-biased intrasexual competition, males showed an earlier and/or faster rate of body mass ageing than females. Both sexes gained mass during early adulthood. However, the onset of body mass ageing differed between both sexes: males began to lose mass from 48.3 years old onwards. In contrast, females lost body mass generally at an older age, namely in their last year of life. Compared to a previous study on growth curves of this population (Mumby, Chapman, et al., 2015), we are now using a larger dataset, including older and more numerous retired individuals. This allowed us to evidence body mass ageing in this species, which was not possible until now. Here we discuss

313   the implications of our results in the light of the classical theory of ageing (Williams,

314   1957) and of the management of Asian elephants.

315   We describe for the first time a sex-specific pattern of body mass ageing in this

316   species. Body mass ageing is often used in mammals as it may underpin actuarial

317   and reproductive ageing (Beirne et al., 2015; Bérubé et al., 1999; Nussey et al.,

318   2011). In our population, sex-specific mortality ageing has been already shown

319   (Lahdenperä et al., 2018) and males display higher mortality than females at all ages.

320   However, reproductive ageing has only been described in females of this population

321   due in part to the difficulty of recording paternity in male elephants (Hayward et al.,

322   2014; Mumby, Mar, Hayward, et al., 2015; Robinson et al., 2012). Our results provide

323   valuable insights on how body condition declines with age and offer another aspect

324   of the multifaceted ageing, often referred to as a mosaic (Walker & Herndon, 2010),

325   in this long-lived and highly social species.

326   Asian elephants show male-biased intra-sexual competition, with males being more

327   aggressive (Seltmann et al., 2019), fighting more for dominance and showing higher

328   rates of mortality at all ages than females, including during early development, as

329   calves and during adulthood (Lahdenperä et al., 2018). In such species, classical

330   theory of ageing predicts that males should show an earlier onset or accelerated

331   ageing (Williams, 1957). Indeed, in several polygynous mammals, males display

332   earlier onset or higher rates of ageing than females, suggested to be due to their

333   stronger intrasexual competition (Clutton-Brock & Isvaran, 2007 but see also Camus

334   et al., 2012; Tower, 2006). For example, in European badgers (*Meles meles*, Beirne

335   et al., 2015) and Soay sheep (*Ovis aries*, Hayward et al., 2015), males systematically

336   showed stronger or earlier body mass ageing compared to females. Conversely, in

337   monogamous species, males and females' onsets and rates of ageing tend to be

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338   similar (Bronikowski et al., 2011; Clutton-Brock & Isvaran, 2007; Thorley et al., 2020).

339   Our results are consistent with those studies and with the prediction of the classical

340   theory of ageing. Moreover, our results are inconsistent with later alternatives that

341   suggest that the prediction of the classical theory of ageing can be disrupted by high

342   early-life condition-dependent mortality in males (Chen & Maklakov, 2014) or by

343   canalisation (Flatt, 2005).

344   However, as mentioned above, previous work on this population showed both

345   reproductive and survival age-related decline in females (Hayward et al., 2014;

346   Robinson et al., 2012). Hence, the ageing trajectories do not synchronise between

347   traits in females. Empirically, this heterogeneity of ageing patterns is more the rule

348   than the exception as found in other species (Briga & Verhulst, 2021; Hayward et al.,

349   2015; Walker & Herndon, 2010). In our population, this mismatch can be explained

350   by the fact that body mass is a poor predictor of reproductive success, number of

351   offspring produced or raised up to independence (5 years old), and that no

352   relationship between height and survival has been found in females (Crawley et al.,

353   2017). Our results that females do not show age-dependent body mass decline

354   combined with previous results are at odds with study on other vertebrates. Asian

355   elephants reproduce all year long (Brown, 2014), despite living in a seasonal

356   environment, meaning that females finance reproduction through energy stored

357   before reproduction. This is contrary to, say roe deer (*Capreolus capreolus*), an

358   income breeder financing reproduction concurrently to gestation as this ungulate

359   does not store reserves (Andersen et al., 2000). In the latter case, reproductive

360   success therefore depends on body condition and available resources, while in the

361   former case, elephants reproduce when they have stored sufficient resources to

362   finance gestation. This might in part explain the absence of relation between female

363   body mass ageing and reproductive senescence, contrary to males, benefiting more

364   from being heavy than females during intrasexual competition (Sukumar, 2003).

365   Our study is subject to a number of limitations when it comes down to identifying why

366   the sexes may differ in their ageing trajectories. First, it is possible that male

367   elephants in our timber elephant population are used more for tasks requiring

368   strength or tusks, thereby causing an earlier onset of body mass declines in males

369   than in females. However, both sexes fall under the same government-set workload,

370   care and retirement regulation, except for females' maternity leave. One substantial

371   difference between sexes is that parental care is concentrated on females, with for

372   example only females being given 'parental leave' following reproduction (Toke Gale,

373   1974). However, since maternity is energetically expensive and no more favourable

374   than timber working, this is unlikely to lead to the delayed onset of body mass

375   declines in females. An ideal test would be to analyse the effect of timber work and

376   maternity leave on body mass dynamics.

377   Second, elephants have a specific dentition that consists of molar teeth that

378   eventually wear down at the end of their lives, and pathologic malocclusions or lack

379   of molars can lead to weight loss and death by starvation. In sexually dimorphic

380   species of ungulates, males generally display smaller molar teeth size compared to

381   females, relatively to body size. This results in teeth wearing down faster and

382   depleting earlier for males than females (Carranza & Pérez□Barbería, 2007) with

383   potential consequences on male senescence compared to females. In Asian

384   elephants, although both sexes have the same molar dental anatomy, it is possible

385   that the earlier onset of body mass declines in males reflects sex-specific differences

386   in tooth wear. Indeed, in captive species, dental problems have been described well

387 before the last year of life (Gaillard et al., 2015) and, if there is sex-specific tooth

388 wear, this could be associated with the earlier onset of body mass ageing in males.

389 Third, male elephants have recurring periods of physiological "musth" throughout

390 their adult lives, which can temporarily but profoundly impact the body mass of

391 individual males (Eisenberg et al., 1971) thereby affecting the body mass ageing

392 trajectory. Unfortunately, recording morphological measurements is difficult during

393 the musth period during which males display highly aggressive behaviours, although

394 accounting for musth would improve future analyses.

395 Fourth, in our study, we did not find any evidence for body mass-based selective

396 disappearance, but, as it is often the case in long-lived species, the average

397 longitudinal individual monitoring is short relative to the lifespan of this species (*e.g.*

398 Global BMI Mortality Collaboration et al., 2016; Prospective Studies Collaboration,

399 2009), and hence we only have limited power to detect such association. It is

400 possible that there are sex-specific dynamics of selective disappearance, but whether

401 that is the case in Asian elephants remains to be shown. An analysis with more

402 longitudinal data would be useful to tackle this question.

403 Fifth, for both sexes, it is possible that maximum body mass is set by physiological

404 and ecological constraints as indicated by the weight growth curves found earlier in

405 this population (Mumby, Chapman, et al., 2015). These constraints could be to some

406 extent sex-specific, although at this point, we can only speculate as to why these

407 constraints may drive sex-specific ageing trajectory. Finally, we found a maximum

408 body mass in males but not in females. This sex-specific differences could be driven

409 by the fact that male elephants benefit more than females from being heavy during

410 intrasexual competition (Sukumar, 2003).

19

411 Another factor to take into account is that retirement occurs at around 50 years in

412 both sexes, which likely diminishes physical exercise and allows more time for

413 foraging, thereby continuing the weight gain. The reduced intrasexual competition in

414 females relative to males, together with this retirement, could lead to the continued

415 mass gain of females. One way of disentangling the effect of senescence and

416 retirement on body mass trajectories would be to know whether muscle is lost over

417 fat. Unfortunately, we do not have the data to know this. However, it seems that

418 muscle function does not decrease with age in this semi-captive population in neither

419 sex (Reichert et al., 2022). On the contrary, fat storage as measured by levels of

420 circulating triglycerides remained constant up to adulthood, decreasing afterwards in

421 senior elephants (from retirement onwards) in both sexes (Reichert et al., 2022).

422 Also, all elephants officially retire at age 55, but most elephants enter pre-retirement

423 around the age of 50 because of decreased strength. These results, taken together

424 with the onset of body mass decline we found in males (*i.e.* 48 years old), suggest

425 that retired individuals lose fat in both sex rather than muscle and that body mass

426 ageing is rather a cause than a consequence of retirement in males. Nevertheless,

427 given that elephants in the wild do not experience timber labour and retirement, we

428 cannot exclude that the sex-specific body mass ageing trajectories could be different

429 in a wild (non-working) population of Asian elephants compared to those found in our

430 study.

431 We found that females experienced a terminal body mass decline in the last year of

432 life. Our data contain both males and females among the oldest ages (>50), hence

433 sex-specific terminal decline is unlikely to emerge from differences in lifespan. In

434 European badgers, a species in which females outlive males, both sexes displayed

435 terminal body mass declines (Beirne et al., 2015). It is possible that the sex-specific

20

436   terminal declines in our study resulted from differences in power, with 5 dead males

437   and 18 dead females. Indeed, for both males and females, the coefficient and effect

438   size of the terminal terms were negative, but the effect size in males remained about

439   half of that in females (Cohen's d_{males} = -0.045 [95%CI: -0.10; 0.01] = a decline of 96 kg

440   [95%CI: -19; 205], Cohen's $d_{females}$ = -0.071 [95%CI: -0.11; -0.03] = a decline of 173 kg

441   [95%CI: 80; 263]). Hence, it is possible that the sex-specific terminal effect is driven

442   by power issues and we look forward to testing that with several more years of

443   monitoring.

444   Terminal declines emphasise that the chronological age is rarely a perfect estimation

445   of the biological age which can better describe the 'true biological state' of an

446   organism (Klemera & Doubal, 2006). In that sense, terminal decline is a biomarker of

447   health and remaining lifespan. The 'terminal illness' hypothesis refers to the age-

448   independent decrease of a trait value, related to the imminent death of the individual

449   (Coulson & Fairweather, 2001). Such terminal effects were shown for example for

450   body mass in mammals (stronger in males than females in European badgers

451   (Beirne et al., 2015), in both sexes in Soay sheep (Hayward et al., 2015) and in male

452   but not female Alpine marmots (Tafani et al., 2013)) and for sexual signals in birds

453   (Simons et al., 2016). For which traits or under which conditions to expect terminal

454   declines remains yet poorly understood but our study highlights the importance of

455   studying sex-specific differences in ageing and illustrates the need to improve our

456   understanding of the mechanisms driving the diversity of ageing patterns in the wild.

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Conflict of interest

471 The authors have no conflict of interest to declare.

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Authors' contribution

477 HHA, WH and UKN performed field work and data collection. VL, VB and MB
478 designed the study and LL selected, extracted and translated data. LL carried out all
479 statistical analyses with contributions from VB and MB. LL wrote the manuscript and
480 all authors critically reviewed it. All authors approved the manuscript for publication
481 and agree to be held accountable for the content therein and approve the final
482 version of the manuscript.

Data accessibility

484 The datasets and codes supporting the conclusions of this article have been
485 uploaded on Dryad digital repository and will be made publicly available upon
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