

# Sex-specific body mass ageing trajectories in adult Asian elephants

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Sex-specific life-histories are thought to shape senescence patterns differently for males and females. In species with marked sexual dimorphism and where one sex is undergoing stronger intrasexual competition, it is expected that this sex ages earlier or quicker. Here, we utilise a unique, longitudinal dataset of a semi-captive population of Asian elephants (*Elephas maximus*) to describe the body mass ageing trajectories in this species with marked sexual dimorphism in size and lifespan, with males being larger and living shorter. Our results show sex-specific ageing trajectories: males gained weight throughout their life, at a diminishing rate until natural death. In contrast, adult female body mass did not change significantly with age until an abrupt decline during the last year of life. Our study shows that sex-specific life-histories shape ageing patterns contrary to those predicted by classical theory and expands the previously described diversity of ageing dynamics.

**Keywords:** senescence, ageing, sex-differences, terminal decline, *Elephas maximus*, long-term data

## 28 Introduction

29 Senescence – a gradual age-specific decline in contribution to fitness [1] – has been observed  
30 across species [2]. However, the onset and rates of senescence differ both between [2] and  
31 within species [3] and between sexes [4]. A main challenge in senescence research is to quantify  
32 and explain these differences in onset and rates [e.g. 5].

33 In species with sex-specific intrasexual competition, theory predicts that the sex with the  
34 highest intrasexual competition should have the shorter lifespan and show an earlier onset  
35 and/or higher rate of senescence [6]. The rationale is that high intrasexual selection often results  
36 in one sex showing conspicuous displays or aggressive intrasexual behaviours, leading to  
37 increased mortality and a *live fast, die young* pace of life [6–8]. Accordingly, in polygynous  
38 species where intrasexual competition is higher for males, males often die earlier (15.7% earlier  
39 in mammals [9]) and senesce earlier or faster than females [4,8,10–12]. However, recent  
40 conceptual developments have shown that this classic association can be disrupted, for example  
41 because of condition-dependent extrinsic mortality [9] or canalisation (*i.e.* the more a trait  
42 contributes to fitness, the less it should deviate from optimal trait value, with respect to  
43 environmental variations [14]), thereby contradicting the theoretically expected earlier or faster  
44 ageing in males. The extent to which such phenomena occur in nature remains unknown.

45 Here, we took advantage of a unique long-term dataset to describe the sex-specific body mass  
46 ageing trajectories of an unsupplemented semi-captive population of Asian elephants (*Elephas*  
47 *maximus*) living in natural conditions in Myanmar. Body mass is of interest in the study of  
48 senescence because it is positively associated with key life-history traits such as reproduction  
49 and lifespan in many non-human species [15]. Accordingly, Asian elephants show seasonal  
50 variation in body mass which is positively associated with subsequent survival [16].

51 However, we know almost nothing on body mass ageing in this species despite the interest of  
52 studying ageing on such a long-lived, social and sexually dimorphic non-human species. While  
53 females live in kin groups, adult males roam solitary through the forest [17], undergo a more  
54 intense intrasexual competition for dominance and mating [17] and are therefore bigger, heavier  
55 [18], and shorter-lived (median lifespan: 30.8 years) than females (44.7 years) [19]. Based on  
56 this male-biased intrasexual competition and shorter lifespan, we expected males to display  
57 earlier and/or faster body mass ageing than females [6,7,20].

58

## 59 Material and methods

### 60 Study population

61 The unsupplemented study population is the world's largest semi-captive Asian elephant  
62 population, including around 3,000 individually-marked elephants owned by the government-  
63 run Myanmar Timber Enterprise (MTE) [21]. These elephants are distributed across Myanmar  
64 in forest camps and used as riding, transport and drafting animals. Their birth, death and  
65 pedigree details, and morphological measurements have been recorded for almost a century by  
66 local veterinarians in elephant-specific logbooks. Elephants work during the day and socialise,  
67 mate and forage freely in forests at night (see [22,23] for further details). Consequently, their  
68 life-history and lifespan closely resemble that of wild elephants [19].

69

## 70 Data collection and selection

71 We extracted 1,975 body masses of 347 elephants with known sex, year of birth ('YOB'), alive  
72 or dead status, origin (captive-born or wild-caught) and measurement season (hot: Feb-May,  
73 monsoon: Jun-Sep, cold: Oct-Jan [16]) from the 325 working localities ('township') monitored  
74 on average every 1.5 years between 1968-2018. When body mass measurements were not  
75 available, we estimated body masses using height to the shoulder and chest girth ( $n = 2,098$ ,  $r$   
76  $= 0.89$ , method described in table S1). We obtained a median of 4.0 measurements/individual  
77 [2.5-97.5<sup>th</sup> percentiles: 1.0-38.7], followed for a median of 2.8 years [2.5-97.5<sup>th</sup>: 0.0-37.3] for a  
78 total of 493 elephants ( $n = 4,073$ ).

79 Our analyses focused on age- and sex-specific variation in adult body mass from age 18  
80 onwards, omitting the phase during which elephants grow in height [18]. The study elephants  
81 were aged 18-72 years (mean = 39.3) and born 1941-1999. Age and cohort information were  
82 consistent between the sexes, with 171 males ( $n = 1,378$ ) born 1954-1999 and aged 18-64 years  
83 (mean = 37.2), and 322 females ( $n = 2,695$ ) born 1941-1999 and aged 18-72 years (mean =  
84 40.4).

85

## 86 Statistical analyses

87 All analyses were performed on R version 4.0.2 [24]. We investigated the age- and sex-specific  
88 variation in body mass, using the log-transformed body mass as a dependent variable with a  
89 normal error distribution. We first tested whether there were sex-specific ageing trajectories  
90 (table S2) and then compared the ageing trajectories for both sexes separately using general  
91 linear mixed models with the function 'lmer' (package 'lme4' [25]) and identified the models  
92 that best fitted the data using model selection with the function 'dredge' (package 'MuMIn'  
93 [26]). Better-fitting models are indicated by their lower AICc, models  $<4 \Delta AICc$  are plausible  
94 and models become increasingly equivocal up to  $14 \Delta AICc$ , after which they become

95 implausible [27]. Visual inspection of model residuals confirmed that these fulfilled all  
96 assumptions of distribution and homogeneity without any influential data points or outliers.

97

#### 98 *Within- vs. between-individual change*

99 In all models, we accounted for non-independence of data due to repeated measurements from  
100 the same individual by including elephant identity ('ID') as a random intercept. Here we are  
101 interested in within-individual changes in body mass. Because population composition can  
102 change with age (*e.g.* selective disappearance), body mass changes at the population level can  
103 result from both between-individual and within-individual changes [28]. To capture the within-  
104 individual trajectory, we decomposed the age variable in the models into *i*) a 'mean age' term  
105 (mean age for all the measurements of the same individual) capturing the between-individual  
106 changes with age and *ii*) a ' $\Delta$ age' term (age at measurement minus the individual's mean age)  
107 capturing the within-individual changes with age, following the approach developed in [28].  
108 We mean-centered and standardized all age terms.

109

#### 110 *Testing ageing trajectories*

111 We tested a number of within-individual ageing trajectories of increasing complexity (linear,  
112 quadratic, threshold models, figure S1). To determine whether changes in body mass started at  
113 a certain threshold age (figure S1C), we followed the approaches previously developed in [4,29].  
114 Briefly, we tested a series of models varying the threshold in the ' $\Delta$ age' term between -36 to 22  
115 years with intervals of 1  $\Delta$ age (= 3.4 years for males and 4.5 years for females). We identified  
116 the best fitting threshold model based on the AICc and its confidence intervals using  $\pm 4 \Delta$ AIC  
117 age range. Ageing is sometimes better described using the time before death (terminal decline).  
118 A 'terminal' change (figure S1D) is captured by a binomial factor for whether an individual  
119 died during the year following the measurement. To avoid dealing with seasonally-driven  
120 terminal effects, we used a terminal decline window of one year prior to death. Note that other  
121 time windows gave consistent conclusions (Results section, figure S2). We tested the terminal  
122 decline in combination with each ageing trajectories.

123

#### 124 *Accounting for seasonal and spatial variation in body mass*

125 As body mass variation can be influenced by seasonal, spatial and within-individual factors, we  
126 accounted for whether body mass values were measured or estimated, individuals were alive or  
127 dead, captive- or wild-born, and the measurement season in the selected models for both sexes  
128 (table S3). For females, ID and township were included as random intercepts, but YOB was

129 removed because of insufficient power to estimate its variance [30]. For males, ID and YOB  
130 were included and ‘township’ excluded for the same reasons. Note that for models with only  
131 ID as random intercept, results yielded consistent conclusions. Repeating the analyses adding  
132 log(height) as a covariate to correct for the allometric relationship between height and body  
133 mass gave consistent conclusions (table S4, S5 and S6).

134

## 135 Results

136 Elephants weighed 1,334-4,582 kg (mean = 2,631.3). Males weighed 1,334-4,582 kg (mean =  
137 3,024.3) and were on average 593.9 kg heavier than females which weighed 1,458-4,181 kg  
138 (mean = 2,430.4). This difference was statistically significant ( $\Delta\text{AICc} = -257.0$ , table S2).

139 At the measurements’ starting age of 18 years, the body mass difference between the sexes was  
140 reversed, with males weighing on average 478.5 kg less than females, respectively at 1,861.6  
141 kg [95%CI: 1,742.3-1,989.0] and 2,330.1 kg [95%CI: 2,288.6-2,372.3]. However, sexes  
142 displayed different body mass ageing trajectories ( $-78.5 < \Delta\text{AICc} < -75.0$ , figure 1, table 1 and  
143 S2). Males continuously gained weight but the rate of increase diminished with age, as shown  
144 by a quadratic within-individual body mass ageing trajectory ( $\Delta\text{AICc} = -45.6$  compared to a  
145 linear trajectory, figure 1A, table 1), with a maximum at the oldest age at measurement of 64  
146 years.

147 In contrast, females showed a linear within-individual increase in body mass with age ( $\beta =$   
148  $0.013 \pm 0.001$ ,  $\Delta\text{AICc} = -2.8$ ), followed by a terminal decline in body mass during the last year  
149 of life ( $\beta = -0.076 \pm 0.019$ ,  $\Delta\text{AICc} = -7.5$ , figure 1B and S2) of 184.8 kg [95%CI: 94.7-271.5]  
150 (7.3% [95%CI: 3.8-10.8] of the mean adult body mass). The equivalent model containing a  
151 terminal decline factor for males was not statistically significant ( $\Delta\text{AICc} = +7.3$ , table 1, figure  
152 S3) as the drop in body mass was smaller and overlapped with 0: 27.8 kg [95%CI: -134.0-  
153 181.1] or 0.9% [95%CI: -4.5-6.1].

154

## 155 Discussion

156 We tested for sex differences in body mass ageing trajectories of Asian elephants in which the  
157 sexes differ in size, life-history and lifespan. We found that males gained weight at a decreasing  
158 rate throughout their lifespan, while females showed no body mass ageing until a 7.3% decline  
159 during the last year of life. In Asian elephants, males are more aggressive than females [31],  
160 fight more for dominance and show higher rates of mortality at all ages than females [19]. In  
161 species with such male-biased intrasexual selection on mortality, classic theory predicts that

162 males should show an earlier onset or accelerated ageing [32]. Indeed, in several polygynous  
163 mammals, males had higher rates of body mass declines than females, and this difference was  
164 suggested to be due to their higher intra-sexual competition [8,11]. Our results are thus opposite  
165 to what expected from classic theory and we here discuss three possible mechanisms and  
166 implications of our study.

167 The lack of body mass decline in males of this highly polygynous species is unlikely to be due  
168 to a power issue. First, the median lifespan in males and females is 30.8 and 44.7 years  
169 respectively [19]. Our dataset included 114 males ( $n = 899$ ) and 108 females ( $n = 1,051$ ) beyond  
170 these ages. Second, the MTE retires elephants at the age of 53 years [33], when the elephant's  
171 physical condition is insufficient for timbering, and we included 15 males ( $n = 141$ ) and 57  
172 females ( $n = 601$ ) beyond that age. Third, we included 5 dead males ( $n = 65$ ) and 18 dead  
173 females ( $n = 185$ ) to detect for a terminal decline. Although the power was lower for males,  
174 power is unlikely to be an issue here because the coefficient for the terminal decline in males  
175 was more than 8 times smaller than that of females ( $\beta_{\text{males}} = -0.009 \pm 0.027$ ,  $\beta_{\text{females}} = -$   
176  $0.076 \pm 0.019$ ) and, including a male terminal factor resulted in a 7.3  $\Delta\text{AICc}$  increase relative to  
177 the model without decline. Hence, we do not believe the lack of body mass decline in males or  
178 the different ageing trajectories between sexes to be driven by the power of the data.

179 The fact that the observed sex-specific body mass ageing trajectories were opposite to the  
180 classic predictions on sexual selection and ageing [32] raises questions regarding the underlying  
181 evolutionary mechanisms. Body mass in male elephants plays a predominant role in intrasexual  
182 competition [17], and therefore in the contribution to fitness, potentially causing the  
183 canalisation of males body mass, thereby preventing its decline [14]. Alternatively, condition-  
184 dependent mortality can filter weakest individuals and alter (sex-specific) within-individual  
185 ageing trajectories [34]. The rationale is that the disappearance of weaker males that would  
186 have declining body masses at older ages can result in a selection of males without body mass  
187 declines. Such condition-dependent mortality can occur at evolutionary timescales, but also at  
188 an individual timescale. For example, in Asian elephants, males experience higher mortality  
189 than females at all ages, including development and calthood [19], and parasite-associated  
190 mortality is higher for males than females at all ages [33]. In polygynous species, raising a male  
191 is costlier than raising a female and this could translate in a more pronounced condition-  
192 dependent mortality in males during early-life, as suggested in the wild boar (*Sus scrofa*) [35].  
193 Although canalisation and condition-dependent mortality are possible explanations for the  
194 absence of male-biased ageing in polygynous species [6], female-biased ageing is not supported  
195 in most of the current literature. Our finding that females experienced only a terminal body

196 mass decline is an interesting result. It emphasizes that the chronological age is rarely a perfect  
197 estimation of the biological age which can better describe the ‘true biological state’ of an  
198 organism [36]. The ‘terminal illness’ hypothesis refers to the age-independent decrease of a  
199 trait value, related to the imminent death of the individual [37] and such terminal effects were  
200 shown for example for body mass and sexual signals in mammals and birds [38]. Which traits  
201 or under which conditions to expect terminal declines remains yet unknown but our study  
202 highlights the importance of studying sex-specific differences in ageing and illustrates the need  
203 to improve our understanding of the mechanisms driving the diversity of ageing patterns in the  
204 wild.

205

## 206 **Ethics**

207 The study was performed with the permission from the Myanmar Ministry of Natural Resources  
208 and Environmental Conservation and following the University of Turku ethical guidelines.

209

## 210 **Data accessibility**

211 The dataset supporting the conclusions of this article will be made publicly available upon  
212 acceptance.

213

## 214 **Authors’ contributions**

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

220

## 221 **Competing interests**

222 We declare we have no competing interests.

223

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236

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339
- 340

341 **Table 1.** Selected models for males and females (bold). Model comparison describing the population body mass (bm) ageing trajectory. Models ranked from the  
 342 least to most complex. For each model type, first is presented the model and second its equivalent adding the terminal decline binary factor as a fixed variable  
 343 ('+terminal'). Models within 4ΔAICc in italic. AICc: Akaike Information Criteria; ΔAICc: relative AICc to the best model; k: degrees of freedom.

Model type	Model	k	Males		Females	
			AICc	ΔAICc	AICc	ΔAICc
linear	$\log(\text{bm}) \sim \Delta\text{age} + \text{mean age}$	6	-3,174.6	45.61	-5,999.8	22.21
+terminal	$\log(\text{bm}) \sim \text{terminal} + \Delta\text{age} + \text{mean age}$	7	-3,167.5	52.67	-6,010.4	11.58
mean age <sup>2</sup>	$\log(\text{bm}) \sim \Delta\text{age} + \text{mean age} + \text{mean age}^2$	7	-3,169.7	50.45	-6,014.6	7.46
<b>+terminal</b>	<b><math>\log(\text{bm}) \sim \text{terminal} + \Delta\text{age} + \text{mean age} + \text{mean age}^2</math></b>	<b>8</b>	-3,162.7	57.51	<b>-6,022.0</b>	<b>0.00</b>
<b>Δage<sup>2</sup></b>	<b><math>\log(\text{bm}) \sim \Delta\text{age} + \Delta\text{age}^2 + \text{mean age}</math></b>	<b>7</b>	<b>-3,220.2</b>	<b>0.00</b>	-5,985.1	36.94
+terminal	$\log(\text{bm}) \sim \text{terminal} + \Delta\text{age} + \Delta\text{age}^2 + \text{mean age}$	8	-3,212.9	7.29	-5,995.6	26.39
quadratic	$\log(\text{bm}) \sim \Delta\text{age} + \Delta\text{age}^2 + \text{mean age} + \text{mean age}^2$	8	-3,215.9	4.32	-5,999.9	22.10
+terminal	$\log(\text{bm}) \sim \text{terminal} + \Delta\text{age} + \Delta\text{age}^2 + \text{mean age} + \text{mean age}^2$	9	-3,208.6	11.60	-6,007.3	14.75
threshold	$\log(\text{bm}) \sim \Delta\text{age1} + \Delta\text{age2} + \text{mean age} + \text{mean age}^2$	9	-3,213.4	6.75	-6,012.6	9.44
<i>terminal</i>	<i><math>\log(\text{bm}) \sim \text{terminal} + \Delta\text{age1} + \Delta\text{age2} + \text{mean age} + \text{mean age}^2</math></i>	<i>10</i>	-3,206.1	14.08	-6,019.2	2.80

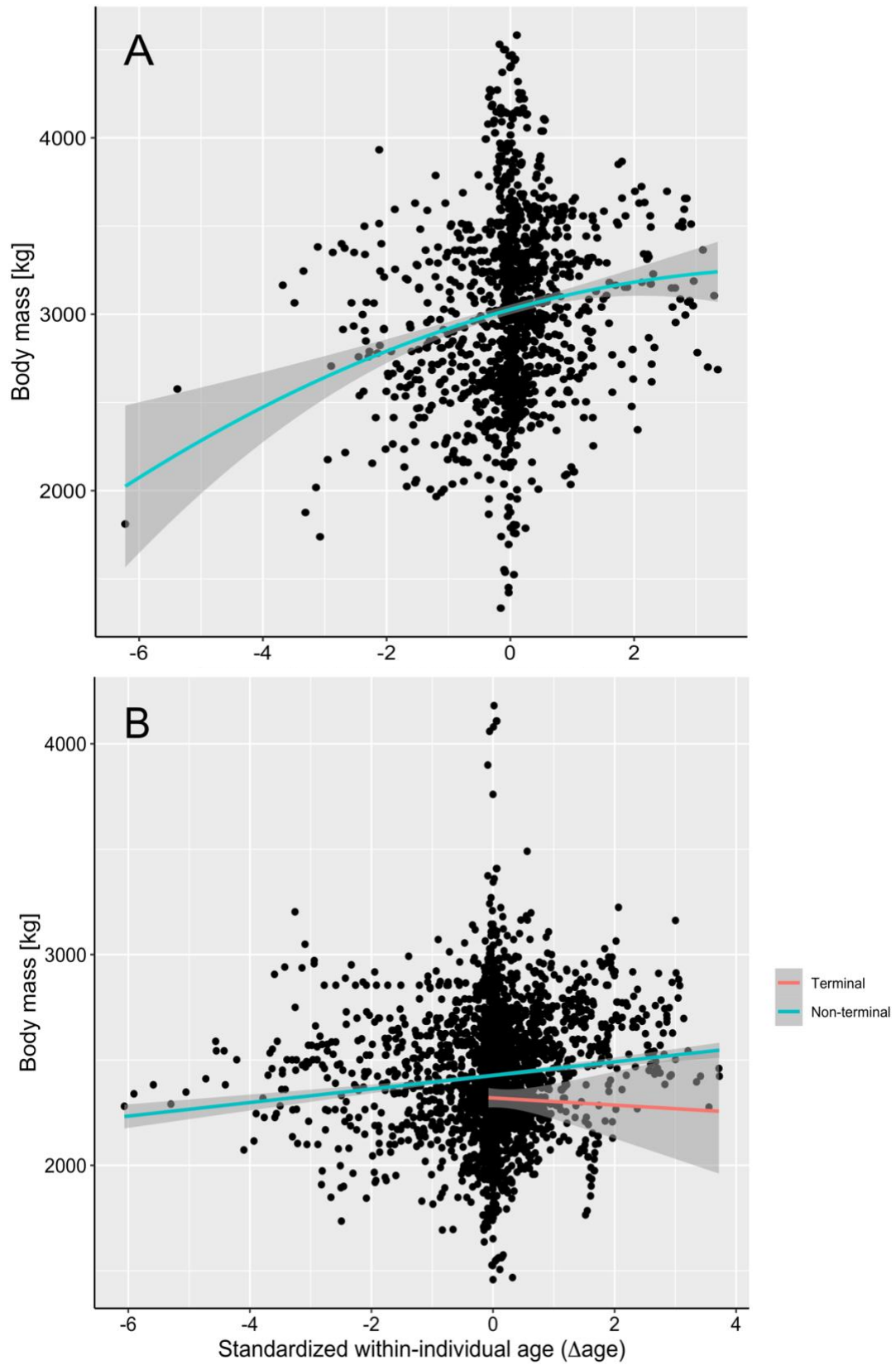
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345 **Figure Captions**

346

347 **Figure 1.** Body mass ageing trajectories for *a*) males (N=171, n=1,378) and *b*) females (N=322, n=2,695).  
348 Prediction of the models selected (table 1) with 95% confidence intervals. Evidence for a terminal  
349 decline in females body mass trajectory. The figure shows significantly lighter individuals during their  
350 last year of life (red) compared to the rest of life (blue).  $\Delta$ age: within-individual age;  $\Delta$ age=0: mean age  
351 of males (37.2 years) and females (40.4 years). 1  $\Delta$ age = 3.4 and 4.5 years for males and females  
352 respectively.

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354

355

Figure 1