

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

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Sex-specific life-histories are thought to shape sex-specific ageing patterns. 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 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.

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

## 1 Introduction

2 Ageing – a decline in organismal functioning with age [1] – has been observed in  
3 many species [2]. However, the onset and rates of ageing differ both between [2] and  
4 within species [3] and between sexes [4]. A main challenge in ageing research is to  
5 quantify and explain differences in onset and rates of ageing [5].

6 In species with sex-specific intrasexual competition, classic theory predicts that the  
7 sex with the highest intrasexual competition has a shorter lifespan and an earlier  
8 onset and/or higher rate of ageing [6]. The rationale is that high intrasexual selection  
9 often results in one sex showing conspicuous displays or aggressive intrasexual  
10 behaviours, leading to increased mortality and a *live fast, die young* pace of life [6–8].  
11 Accordingly, in polygynous species with male-biased intrasexual competitions, males  
12 often die earlier [9] and age earlier or faster than females [4,8,10–12]. However,  
13 recent conceptual developments have shown that this association can be disrupted.  
14 This can occur for example because of condition-dependent extrinsic mortality  
15 selecting particularly high-performing individuals in the population [13] or canalisation  
16 (*i.e.* the more a trait contributes to fitness, the less it should deviate from optimal trait  
17 value, with respect to environmental variation [14]), thereby contradicting the  
18 theoretically expected earlier or faster ageing in males. The extent to which such  
19 phenomena occur in nature remains unknown.

20 Here, we used a unique long-term dataset to describe the sex-specific body mass  
21 ageing trajectories in a nutritionally unsupplemented semi-captive timber population  
22 of Asian elephants (*Elephas maximus*) living in their natural environment in Myanmar.  
23 Body mass is of interest in the study of ageing because it is positively associated with  
24 key life-history traits such as reproduction and lifespan in many non-human species  
25 [15]. Accordingly, Asian elephants show seasonal variation in body mass associated  
26 with survival even within a one-month delay (*e.g.* low body weight and survival during  
27 dry season) [16].

28 However, we know almost nothing of body mass ageing in elephants despite the  
29 interest in studying ageing in such a long-lived, social and sexually dimorphic non-  
30 human species. While females live in kin groups, adult males often roam solitary  
31 through the forest, undergo a more intense intrasexual competition for dominance

32 and mating [17] and hence are bigger, heavier [18], and shorter-lived than females  
33 (respective median lifespans: 30.8 and 44.7 years) [19]. Based on this male-biased  
34 intrasexual competition and shorter lifespan, and following the classic theory of  
35 ageing, we expected males to display earlier and/or faster body mass ageing than  
36 females [6,7].

## 37 **Material and methods**

### 38 **Study population**

39 We studied the world's largest semi-captive Asian elephant population, including  
40 around 3,000 individually-marked elephants owned by the government-run Myanma  
41 Timber Enterprise (MTE) [20]. These elephants are distributed across Myanmar in  
42 forest camps and used as riding, transport and drafting animals. Males and females  
43 follow the same government set limitations on workload, taming and retirement, with  
44 the exception of pregnant females and during early motherhood (details in SI1). Their  
45 birth, death, pedigree details, and morphological measurements have been recorded  
46 for almost a century by local veterinarians. Elephants work during the day and  
47 socialise, mate and forage freely in forests at night [21,22]. Consequently, their  
48 access to resources, reproduction, and social behaviour resemble that of wild  
49 elephants.

### 50 **Data collection and selection**

51 We extracted 1,901 body masses of 347 elephants with known sex, year of birth  
52 ('YOB'), alive or dead status, origin (captive-born or wild-caught) and measurement  
53 season (hot: Feb-May, monsoon: Jun-Sep, cold: Oct-Jan [16]) from 325 working  
54 localities ('township') monitored on average every 1.5 years between 1968-2018.  
55 When body mass measurements were not available, we estimated body masses  
56 using height to the shoulder and chest girth (n=1,985 measurements on 342  
57 individuals, method in Supplementary Information 1 (SI1)). In Asian elephants, chest  
58 girth reflects changes in mass in addition to the fixed effect of structural size during  
59 adulthood (details in SI2). In total, we obtained a median of 4.0  
60 measurements/individual [2.5-97.5<sup>th</sup> percentiles: 1.0-36.4], followed for a median  
61 period of 2.8 years [2.5-97.5<sup>th</sup>: 0.0-36.6] on 493 elephants (n=3,886).

62 Our analyses focused on age- and sex-specific variation in adult body mass from age  
63 18 onwards, omitting the phase during which elephants grow in height [18]. Study  
64 elephants were aged 18-72 years (mean=39.3) and born 1941-1999. Age and cohort  
65 information were consistent between the sexes, with 171 males (n=1,316) born 1954-  
66 1999 and aged 18-64 years (mean=37.4), and 322 females (n=2,570) born 1941-  
67 1999 and aged 18-72 years (mean=40.2). Two influential data points were removed:  
68 one male measured once at 18 and 23 and repeatedly after 50 years old, resulting in  
69 two particularly low  $\Delta$ age.

## 70 **Statistical analyses**

71 We investigated the age- and sex-specific variation in body mass in R version 4.0.2  
72 [23], using the log-transformed body mass as a dependent variable with a normal  
73 error distribution. We first tested whether there were sex-specific ageing trajectories  
74 (table S2) and then compared the sex-specific ageing trajectories using linear mixed  
75 models with the function 'lmer' (package 'lme4' [24]) and identified best fitting models  
76 using model selection with the function 'dredge' (package 'MuMIn' [25]). The retained  
77 model had the lowest AICc. If several models fitted within 4 AICc, we chose the  
78 simplest (details in SI3). Visual inspection of model residuals confirmed that these  
79 fulfilled all assumptions of distribution and homogeneity without any influential data  
80 points or outliers.

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

82 In all models, we accounted for non-independence of data due to repeated  
83 measurements from the same individual by including elephant identity ('ID') as a  
84 random intercept. Here we are interested in within-individual changes in body mass.  
85 Because population composition can change with age (e.g. selective disappearance),  
86 body mass changes at the population level can result from both between-individual  
87 and within-individual changes. To capture the within-individual trajectory, we followed  
88 the approach developed in [26] and decomposed the age variable in the models into  
89 *i*) a term 'age-at-last-measurement' (henceforth 'age-last') capturing the between-  
90 individual changes with age and *ii*) a ' $\Delta$ age' term (age at measurement minus the  
91 individual's mean age for all measurements) capturing the within-individual changes  
92 with age. We mean-centered and standardised  $\Delta$ age so that *i*) individuals measured

93 once all get a  $\Delta$ age of 0 so contribute to the variance of the  $\Delta$ age intercept but not to  
94 its slope and *ii*) to avoid collinearity of and have comparable variance for  $\Delta$ age and  
95  $\Delta$ age<sup>2</sup>.

#### 96 *Testing ageing trajectories*

97 We tested several within-individual ageing trajectories of increasing complexity  
98 (linear, quadratic, threshold, terminal models, figure S1) and selected the model with  
99 the lowest AICc. For threshold models (figure S1C), we followed the approaches  
100 previously developed in [4,27]. Briefly, we first identified the best fitting threshold age  
101 in a series of models, varying the threshold in the ' $\Delta$ age' term between -35 to 22  
102 years with intervals of 1 $\Delta$ age (=4.4 and 4.5 years for males and females respectively)  
103 and estimated the threshold and its confidence intervals using  $\pm 4 \Delta$ AIC age range.  
104 Then we compared the best fitting threshold model with the other ageing trajectories.  
105 Sometimes declines in trait value appear shortly before death (terminal decline). We  
106 coded a 'terminal' change (figure S1D) as a binomial factor for whether an individual  
107 died during the year following the measurement. We used a one-year-window to  
108 avoid seasonal covariation in weight, but note that other time-windows gave  
109 consistent conclusions (figure S2). Because terminal changes can occur with each  
110 ageing trajectory, we tested their combinations.

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

112 As body mass variation can be influenced by seasonal, spatial and within-individual  
113 factors, we accounted for whether body mass values were measured or estimated,  
114 individuals were alive or dead, captive- or wild-born, and the measurement season in  
115 the selected models (table S3). For females, 'ID' and 'township' were included as  
116 random intercepts, but 'YOB' was removed because of insufficient power to estimate  
117 its variance [28]. For males, only ID was included for the same reasons. Note that for  
118 females, models with and without 'township' yielded consistent conclusions.

## 119 **Results**

120 At the measurements' starting age of 18 years, males were on average 318 kg  
121 heavier than females, weighing respectively 2,625 kg [95%CI: 2,489-2,770] and  
122 2,307 kg [95%CI: 2,259-2,355] and this difference was statistically significant.

123 Sexes displayed different body mass ageing trajectories ( $\Delta\text{AICc} = -34.9$ , figure 1,  
124 table 1, figure S2). Males showed a threshold body mass trajectory ( $\Delta\text{AICc} = -21.7$   
125 compared to a linear trajectory). They gained weight from 18 till 48 years old ( $\Delta\text{age}$   
126 scaled = 1.9,  $\beta = 0.039 \pm 0.002$ ), after which body mass decreased linearly ( $\beta = -$   
127  $0.055 \pm 0.014$ , figure 1A). In contrast, females increased linearly in body mass with  
128 age ( $\beta = 0.016 \pm 0.001$ ,  $\Delta\text{AICc} = -6.7$ ), followed by a terminal decline during their last  
129 year of life ( $\beta = -0.071 \pm 0.019$ ,  $\Delta\text{AICc} = -4.8$ , figure 1B and S2) during which they lost  
130 173 kg [95%CI: 80-263] or 6.8% [95%CI: 3.2-10.4] of their mean body mass. Males  
131 showed no statistical support for a terminal decline, neither in their best fitting model  
132 nor in the equivalent model as for females ( $\Delta\text{AICc} = +6.9$ , table 1, figure S2A, 98 kg  
133 [95%CI: -22-212] or 4.2% [95%CI: -0.9-9.1]).

## 134 Discussion

135 We tested whether in a species with marked male-biased intrasexual competition,  
136 males showed an earlier and or faster rate of body mass ageing than females. Both  
137 sexes gained mass during early adulthood. However, males lost on average 39  
138 kg/year (1.3% of males mean weight) starting from the age of 48 years onwards. In  
139 contrast, females dropped in body mass much later, namely in their last years of life.  
140 Here we discuss the implications of our results in the light of evolutionary theories of  
141 ageing [29] and of the management of elephants.

142 Asian elephants show male-biased intra-sexual competition being more  
143 aggressive[30], fighting more for dominance and showing higher rates of mortality at  
144 all ages than females, including during development and calthood [19]. In such  
145 species, classic theory predicts that males should show an earlier onset or  
146 accelerated ageing [29]. Indeed, in several polygynous mammals, males display  
147 higher rates of body mass declines than females, suggested to be due to their higher  
148 intra-sexual competition [8,11]. Our results are consistent with those studies and with  
149 the prediction of the classic theory of ageing. Here, the prediction of the classic  
150 theory is not disrupted by high early-life condition-dependent mortality in males [13]  
151 or by canalisation [14].

152 Although male elephants in our timber elephant population may be used more for  
153 tasks requiring strength or tusks, generally both sexes fall under the same

154 government-set workload, care and retirement regulation. It is also noteworthy that  
155 the female body mass decline occurred largely after retirement age, suggesting work  
156 schedules are unlikely to drive the ageing patterns. One substantial difference  
157 between sexes is parental care concentrated on females, as only females are given  
158 ‘parental leave’ following reproduction [31]. However, since maternity is energetically  
159 expensive and no more favourable than timber working, this is unlikely to lead to  
160 delayed onset of body mass declines in females. An ideal test, would be to analyse  
161 the effect of timber work and maternity leave on body mass dynamics, but this is  
162 beyond the scope of this manuscript.

163 Body mass in male elephants plays a predominant role in intrasexual competition [17]  
164 hence contributing to fitness. It is not surprising to observe a steeper increase in male  
165 body mass than in females but in which it continues till older ages. For both sexes, it  
166 is possible that maximum body mass is set by constraints as indicated by the weight  
167 growth curves found earlier in this population [18]. One potential explanation for not  
168 finding such optimal body mass in females could be due to retirement (around 50 in  
169 both sexes), diminishing physical exercises and allowing more time for foraging.

170 We found that females experienced a terminal body mass decline in the last year of  
171 life. Our data contain both males and females among the oldest ages (>50), hence  
172 sex-specific terminal decline is unlikely to emerge from differences in lifespan.  
173 Similarly, in European badgers (*Meles meles*), a species in which females outlive  
174 males, both sexes displayed terminal body mass declines [11]. Here, sex-specific  
175 terminal decline could result from differences in power, with 5 dead males and 18  
176 dead females. However, the coefficient and effect size of the males’ terminal decline  
177 were about half of the females’ (Cohen’s  $d_{\text{males}} = -0.044$  [-0.10,0.01], Cohen’s  $d_{\text{females}}$   
178  $= -0.074$  [-0.11,-0.04] in addition to an increase of 6.9  $\Delta\text{AICc}$ ). Hence, the sex-  
179 specific terminal effect is unlikely driven by power issues, but we look forward to  
180 confirming that with several more years of monitoring.

181 Terminal declines emphasise that the chronological age is rarely a perfect estimation  
182 of the biological age which can better describe the ‘true biological state’ of an  
183 organism [32]. In that sense, terminal decline is a biomarker of health and remaining  
184 lifespan. The ‘terminal illness’ hypothesis refers to the age-independent decrease of  
185 a trait value, related to the imminent death of the individual [33] and such terminal

186 effects were shown for example for body mass and sexual signals in mammals and  
187 birds [11,34]. Our results highlight that such a biomarker can be subject to sexual  
188 selection. For which traits or under which conditions to expect terminal declines  
189 remains yet unknown but our study highlights the importance of studying sex-specific  
190 differences in ageing and illustrates the need to improve our understanding of the  
191 mechanisms driving the diversity of ageing patterns in the wild.

192 Data are accessible on Dryad [35].

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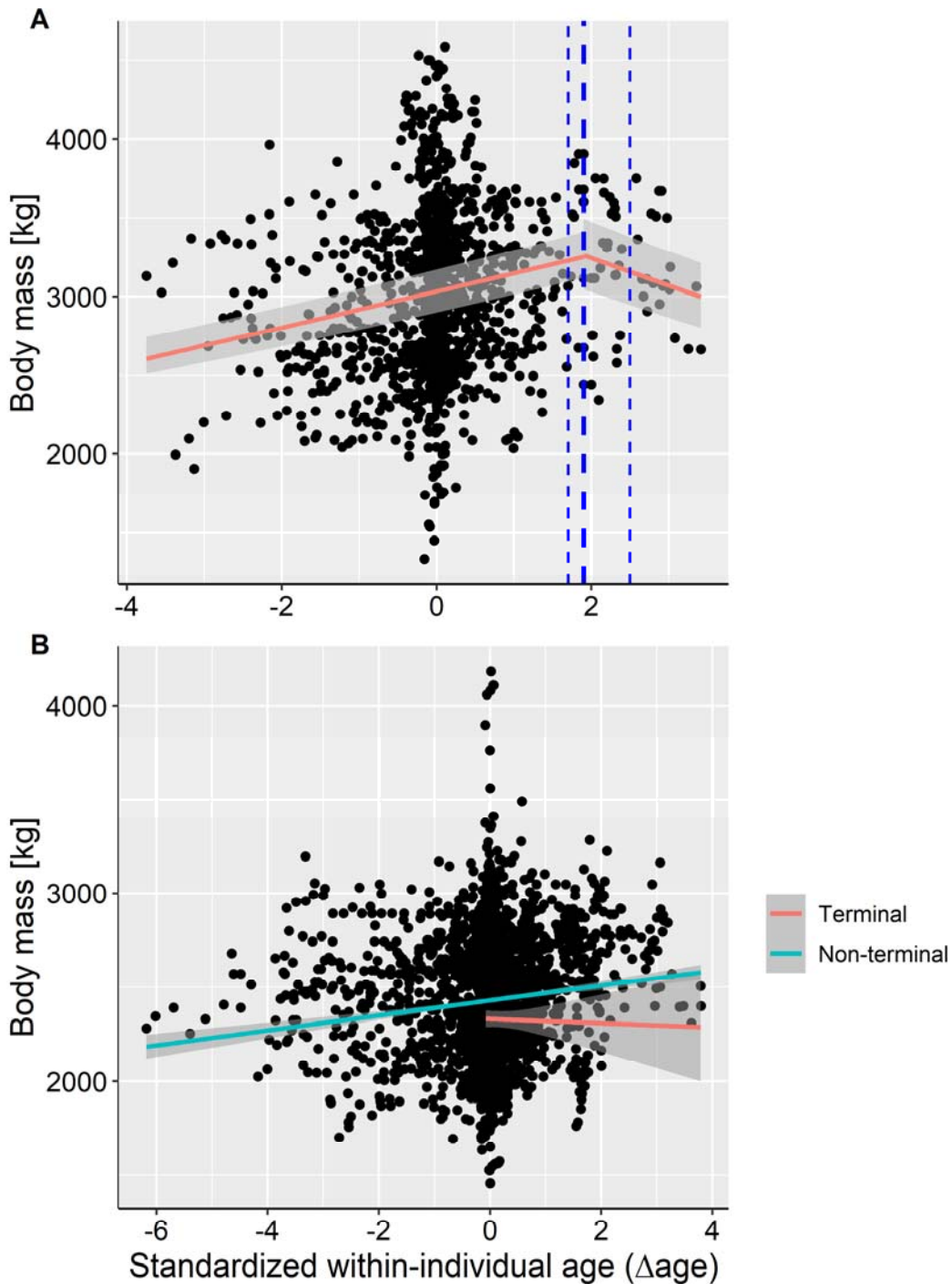
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296

**Table 1.** Selected models for males and females (bold). Model comparison describing the population body mass (bm) ageing trajectory. Models ranked from the 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 ('+terminal'). AICc: Akaike Information Criteria;  $\Delta$ AICc: relative AICc to the best model; k: degrees of freedom.

Model type	Model	Males			Females		
		k	AICc	$\Delta$ AICc	k	AICc	$\Delta$ AICc
null	$\log(\text{bm}) \sim 1$	3	-2,867.7	322.8	4	-5,443.3	160.4
linear	$\log(\text{bm}) \sim \Delta\text{age} + \text{age-last}$	5	-3,170.7	21.74	6	-5,586.3	17.47
+terminal	$\log(\text{bm}) \sim \text{terminal} + \Delta\text{age} + \text{age-last}$	6	-3,165.5	27.01	7	-5,592.4	11.29
age-last <sup>2</sup>	$\log(\text{bm}) \sim \Delta\text{age} + \text{age-last} + \text{age-last}^2$	6	-3,163.4	29.05	7	-5,598.9	4.84
<b>+terminal</b>	<b><math>\log(\text{bm}) \sim \text{terminal} + \Delta\text{age} + \text{age-last} + \text{age-last}^2</math></b>	7	-3,158.2	34.31	<b>8</b>	<b>-5,603.7</b>	<b>0.00</b>
$\Delta\text{age}^2$	$\log(\text{bm}) \sim \Delta\text{age} + \Delta\text{age}^2 + \text{age-last}$	6	-3,184.6	7.85	7	-5,571.7	32.01
+terminal	$\log(\text{bm}) \sim \text{terminal} + \Delta\text{age} + \Delta\text{age}^2 + \text{age-last}$	7	-3,178.9	13.52	8	-5,578.1	25.67
quadratic	$\log(\text{bm}) \sim \Delta\text{age} + \Delta\text{age}^2 + \text{age-last} + \text{age-last}^2$	7	-3,177.3	15.19	8	-5,584.5	19.26
+terminal	$\log(\text{bm}) \sim \text{terminal} + \Delta\text{age} + \Delta\text{age}^2 + \text{age-last} + \text{age-last}^2$	8	-3,171.6	20.84	9	-5,589.5	14.25
<b>threshold</b>	<b><math>\log(\text{bm}) \sim \Delta\text{age1} + \Delta\text{age2} + \text{age-last} + \text{age-last}^2</math></b>	<b>8</b>	<b>-3,190.5</b>	<b>0.00</b>	9	-5,592.7	11.01
terminal	$\log(\text{bm}) \sim \text{terminal} + \Delta\text{age1} + \Delta\text{age2} + \text{age-last} + \text{age-last}^2$	9	-3,185.6	6.90	10	-5,597.0	6.73



**Figure 1.** Body mass ageing trajectories for (A) males ( $n=1,316$  measurements on 171 individuals) and (B) females ( $n=2,570$  measurements on 322 individuals). Prediction of the best fitting models (in table 1) with grey areas 95% CI. For males the thick dashed line shows the threshold age at onset of the body mass decline (1.9 or 48 years) with thin dashed-lines the 4  $\Delta$ AICc CI [47.1, 51.7]. For females,

measurements in the terminal year (red) are significantly lower than measurements at other ages (blue).  $\Delta$ age: within-individual age.