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

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15   Sex-specific life-histories are thought to shape senescence patterns differently for males and females.

16   In species with marked sexual dimorphism and where one sex is undergoing stronger intrasexual

17   competition, it is expected that this sex ages earlier or quicker. Here, we utilise a unique, longitudinal

18   dataset of a semi-captive population of Asian elephants (*Elephas maximus*) to describe the body mass

19   ageing trajectories in this species with marked sexual dimorphism in size and lifespan, with males being

20   larger and living shorter. Our results show sex-specific ageing trajectories: males gained weight

21   throughout their life, at a diminishing rate until natural death. In contrast, adult female body mass did

22   not change significantly with age until an abrupt decline during the last year of life. Our study shows

23   that sex-specific life-histories shape ageing patterns contrary to those predicted by classical theory and

24   expands the previously described diversity of ageing dynamics.

25

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

27   data

## 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, dye 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

## Material and methods

### Study population

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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 Myanma 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$^{th}$ percentiles: 1.0-38.7], followed for a median of 2.8 years [2.5-97.5$^{th}$: 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 ΔAICc are plausible

94    and models become increasingly equivocal up to 14 ΔAICc, after which they become

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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 'Δage' 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 'Δage' term between -36 to 22

115    years with intervals of 1 Δage (= 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 ±4 ΔAIC

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

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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).

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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 ($\Delta$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<$\Delta$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 ($\Delta$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, $\Delta$AICc = -2.8), followed by a terminal decline in body mass during the last year

149    of life ($\beta$ = -0.076$\pm$0.019, $\Delta$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 ($\Delta$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

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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 ($\beta_{males}$ = -0.009±0.027, $\beta_{females}$ = -

176    0.076±0.019) and, including a male terminal factor resulted in a 7.3 ΔAICc 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 calfhood [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

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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.
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## 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.
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## Data accessibility

211    The dataset supporting the conclusions of this article will be made publicly available upon
212    acceptance.
213

## 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

## Competing interests

222    We declare we have no competing interests.
223

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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.

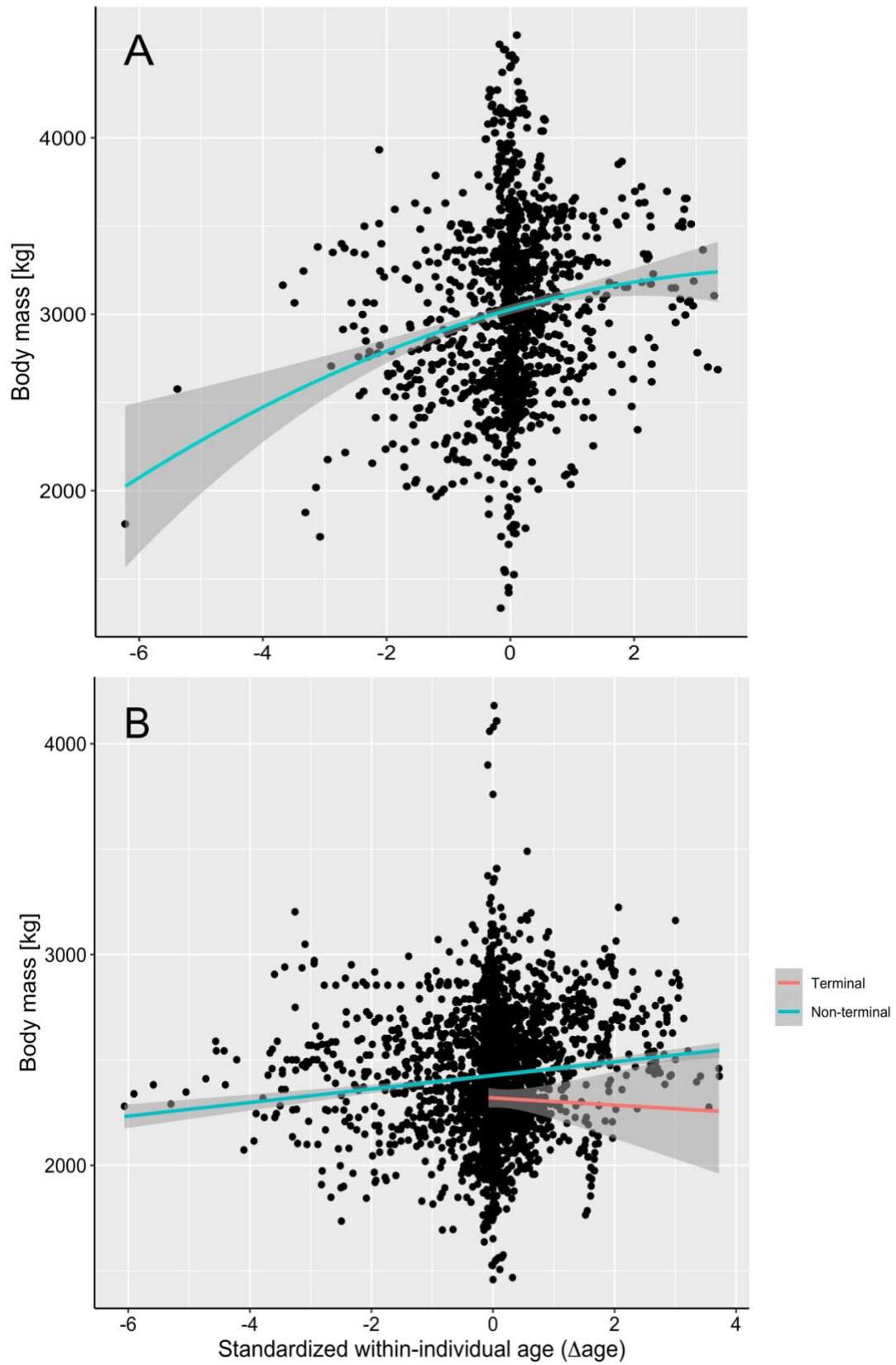| Model type | Model | k | Males | | Females | |
|---|---|---|---|---|---|---|
| | | | AICc | ΔAICc | AICc | ΔAICc |
| linear | $\log(bm) \sim \Delta age + mean\ age$ | 6 | -3,174.6 | 45.61 | -5,999.8 | 22.21 |
| +terminal | $\log(bm) \sim terminal + \Delta age + mean\ age$ | 7 | -3,167.5 | 52.67 | -6,010.4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

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## Figure Captions

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

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355                                    Figure 1