Sex-specific body mass ageing trajectories in adult Asian elephants

Lucas D. Lalande[1,2,3,a], Virpi Lummaa[1,a], Htoo H. Aung[4], Win Htut[4], U. Kyaw Nyein[4],
Vérane Berger[1,a,*], Michael Briga[1,a,*]

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

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

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

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

[*] Equal contribution of these authors

[a] Corresponding authors: L. D. Lalande: lucas.lalande@univ-lyon1.fr, V. Lummaa:
virpi.lummaa@gmail.com, V. Berger: verber@utu.fi, M. Briga: michbriga@gmail.com

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

Introduction

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

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

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

However, we know almost nothing about how body mass changes with age in elephants despite the interest in studying ageing in such a long-lived, social and sexually dimorphic non-human species. While females live in kin groups, adult males often roam solitary, undergo a more intense intrasexual competition for dominance and mating [17] and hence are bigger, heavier [18], and shorter-lived than females (respective median lifespans: 30.8 and 44.7 years) [19]. Based on this male-biased intrasexual competition and shorter lifespan, and following the classic theory of ageing, we expected males to display earlier and/or faster body mass ageing than females [6,7].

Material and methods

Study population

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

Data collection and selection

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

Our analyses focused on age- and sex-specific variation in adult body mass from age 18 onwards, omitting the phase of height growth [18]. Study elephants were aged 18-72 years (mean=39.3) and born 1941-1999. Age and cohort information were comparable between sexes, with 171 males (n=1,316) born 1954-1999 and aged 18-64 years (mean=37.4), and 322 females (n=2,570) born 1941-1999 and aged 18-72 years (mean=40.2). Two influential observations measured at age 18 and 23 were removed for one male because of particularly low Δage (Cook's distance=0.61 and 0.25, mean of 0.001 on all males). Other observations for this male, all after age 50, were included.

Statistical analyses

We investigated the age- and sex-specific variation in body mass in R version 4.0.3 [23], using the log-transformed body mass as a dependent variable with a normal error distribution. We first tested whether there were sex-specific ageing trajectories (table S2) and then compared the sex-specific ageing trajectories using linear mixed models with the function 'lmer' (package 'lme4' [24]) and identified best-fitting models using model selection with the function 'dredge' (package 'MuMIn' [25]). The retained model had the lowest AICc and all models leading to other conclusions worsened model fit with >4ΔAICc (see SI3). Visual inspection of model residuals confirmed that these fulfilled all assumptions of distribution and homogeneity without any influential data points or outliers.

Within- vs. between-individual change

In all models, we accounted for non-independence of data due to repeated measurements from the same individual by including elephant identity ('ID') as a random intercept. Here we are interested in within-individual changes in body mass. Because population composition can change with age (*e.g.* selective disappearance), body mass changes at the population level can result from both between-individual and within-individual changes. To capture the within-individual trajectory, we followed the approach developed in [26] and decomposed the age variable in the models into *i)* a term 'age-at-last-measurement' (henceforth 'age-last') capturing the between-individual changes with age and *ii)* a 'Δage' term (age at measurement minus the individual's mean age for all measurements) capturing the within-individual changes with age. We mean-centered and standardised Δage so that *i)* individuals measured once all get a Δage=0 so contribute to the variance of the Δage intercept but not to its slope and *ii)* to avoid collinearity and to have comparable variance for Δage and Δage^2.

Testing ageing trajectories

We tested several within-individual ageing trajectories of increasing complexity (linear, quadratic, threshold, terminal models, figure S1) and selected the model with the lowest AICc. For threshold models (figure S1C), we followed the approaches previously developed in [4,27]. Briefly, we first identified the best-fitting threshold age in a series of models, varying the threshold in the 'Δage' term between -35 to 22 years with intervals of 1Δage (=4.4 and 4.5 years for males and females respectively) and estimated the threshold and its confidence intervals using ±4ΔAIC age range. Then we compared the best-fitting threshold model with the other ageing trajectories. Sometimes, declines in trait value appear shortly before death (terminal decline). We coded a 'terminal' change (figure S1D) as a binomial factor for whether an individual died during the year following the measurement. We used a one-year-window to avoid seasonal covariation in weight, but note that other time-windows gave consistent conclusions (figure S2). Because terminal changes can occur with each ageing trajectory, we tested their combinations. We also performed analyses using cubic smoothing splines, leading to consistent conclusions (results not shown).

Accounting for seasonal and spatial variation in body mass

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

Results

At the measurements' starting age of 18 years, males were on average 294kg heavier than females, weighing respectively 2,601kg [95%CI: 2,472-2,738] and 2,307 kg [95%CI: 2,259-2,355] and this difference was statistically significant.

Sexes displayed different body mass ageing trajectories (ΔAICc=-33.7, figure 1, table 1, table S2). Males showed a threshold body mass trajectory (ΔAICc=-27.2 compared to a linear trajectory). They gained weight from age 18 till 48 (Δage scaled=1.9, β=0.039±0.002), then lost weight linearly: on average 39kg/year (1.3% of males mean weight, β=-0.055±0.014, figure 1A). In contrast, females gained weight linearly with age (β=0.016±0.001, ΔAICc=-6.7), followed by a terminal decline during their last year of life (β=-0.071±0.019, ΔAICc=-4.8, figure 1B and S2) during which they lost 173kg [95%CI: 80-263] or 6.8% [95%CI: 3.2-10.4] of their mean body mass. Males showed no statistical support for a terminal decline, neither in their best-fitting model nor in the equivalent model as for females (ΔAICc=+4.9, table 1, figure S2A, 97kg [95%CI: -22-209] or 4.2% [95%CI: -1.0-9.1]).

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, males lost mass from 48 years old onwards. In contrast, females dropped in body mass much later, namely in their last years of life. Here we discuss the implications of our results in the light of theories of ageing [29] and of the management of elephants.

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

Although male elephants in our timber elephant population may be used more for tasks requiring strength or tusks, generally both sexes fall under the same government-set workload, care and retirement regulation. It is also noteworthy that the female body mass decline occurred largely after retirement age, suggesting work schedules are unlikely to drive the ageing patterns. One substantial difference between sexes is parental care concentrated on females, as only females are given ‘parental leave’ following reproduction [31]. However, since maternity is energetically expensive and no more favourable than timber working, this is unlikely to lead to delayed onset of body mass declines in females. An ideal test would be to analyse the effect of timber work and maternity leave on body mass dynamics, but this is beyond the scope of this manuscript. However, the possibility remains that in a wild (non-working) population of Asian elephants, sex-specific body mass trajectories with age are different from those found in our study.

For both sexes, it is possible that maximum body mass is set by constraints as indicated by the weight growth curves found earlier in this population [18]. At this point, we can only speculate as to why we found a maximum body mass in males but not in females. One possibility for the lack of a maximum in females is retirement (at around 50 years in both sexes), which likely diminishes physical exercise and allows more time for foraging, thereby continuing the weight gain. In contrast, male elephants reach a maximum body mass around the age of 48 possibly, because they benefit from being heavy during intrasexual competition [17].

We found that females experienced a terminal body mass decline in the last year of life. Our data contain both males and females among the oldest ages (>50), hence sex-specific terminal decline is unlikely to emerge from differences in lifespan. In European badgers (*Meles meles*), a species in which females outlive males, both sexes displayed terminal body mass declines [11]. It is possible that the sex-specific terminal declines in our study resulted from differences in power, with 5 dead males and 18 dead females. Indeed, for both males and females, the coefficient and effect size of the terminal terms were negative, but the effect size in males remained about half of that in females (Cohen’s d_{males}=-0.044 [-0.10,0.01], Cohen’s $d_{females}$=-0.074 [-0.11,-0.04]). Hence, it is possible that the sex-specific terminal effect is driven by power issues and we look forward to testing that with several more years of monitoring.

Terminal declines emphasise that the chronological age is rarely a perfect estimation of the biological age which can better describe the ‘true biological state’ of an organism [32]. In that sense, terminal decline is a biomarker of health and remaining lifespan. The ‘terminal illness’ hypothesis refers to the age-independent decrease of a trait value, related to the imminent death of the individual [33] and such terminal effects were shown for example for body mass and sexual signals in mammals and birds [11,34]. For which traits or under which conditions to expect terminal declines remains yet poorly understood but our study highlights the importance of studying sex-specific differences in ageing and illustrates the need to improve our understanding of the mechanisms driving the diversity of ageing patterns in the wild.

Data are available in the Dryad Digital Repository [35].

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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 the model and second its equivalent adding the terminal decline factor as a fixed variable (‘+terminal’). AICc: Akaike Information Criteria; ΔAICc: relative AICc to the best model; k: degrees of freedom.

Model type	Model	Males			Females		
		k	AICc	ΔAICc	k	AICc	ΔAICc
null	log(bm) ~ 1	3	-2,867.7	330.13	4	-5,443.3	160.43
linear	log(bm) ~ Δage + age-last	5	-3,170.7	27.15	6	-5,586.3	17.47
+terminal	log(bm) ~ terminal + Δage + age-last	6	-3,165.5	32.42	7	-5,592.4	11.29
age-last^2	log(bm) ~ Δage + age-last + age-last^2	6	-3,163.4	34.46	7	-5,598.9	4.84
+terminal	**log(bm) ~ terminal + Δage + age-last + age-last^2**	7	-3,158.2	39.72	**8**	**-5,603.7**	**0.00**
Δage^2	log(bm) ~ Δage + Δage^2 + age-last	6	-3,184.6	13.26	7	-5,571.7	32.01
+terminal	log(bm) ~ terminal + Δage + Δage^2 + age-last	7	-3,178.9	18.92	8	-5,578.1	25.67
quadratic	log(bm) ~ Δage + Δage^2 + age-last + age-last^2	7	-3,177.3	20.60	8	-5,584.5	19.26
+terminal	log(bm) ~ terminal + Δage + Δage^2 + age-last + age-last^2	8	-3,171.6	26.25	9	-5,589.5	14.25
threshold	**log(bm) ~ Δage1 + Δage2 + age-last**	**7**	**-3,197.9**	**0.00**	8	-5,580.7	23.08
+terminal	log(bm) ~ terminal + Δage1 + Δage2 + age-last	8	-3,193.0	4.92	9	-5,586.2	17.56
threshold (age-last^2)	log(bm) ~ Δage1 + Δage2 + age-last + age-last^2	8	-3,190.5	7.41	9	-5,592.7	11.01
terminal	log(bm) ~ terminal + Δage1 + Δage2 + age-last + age-last^2	9	-3,185.6	12.31	10	-5,597.0	6.73

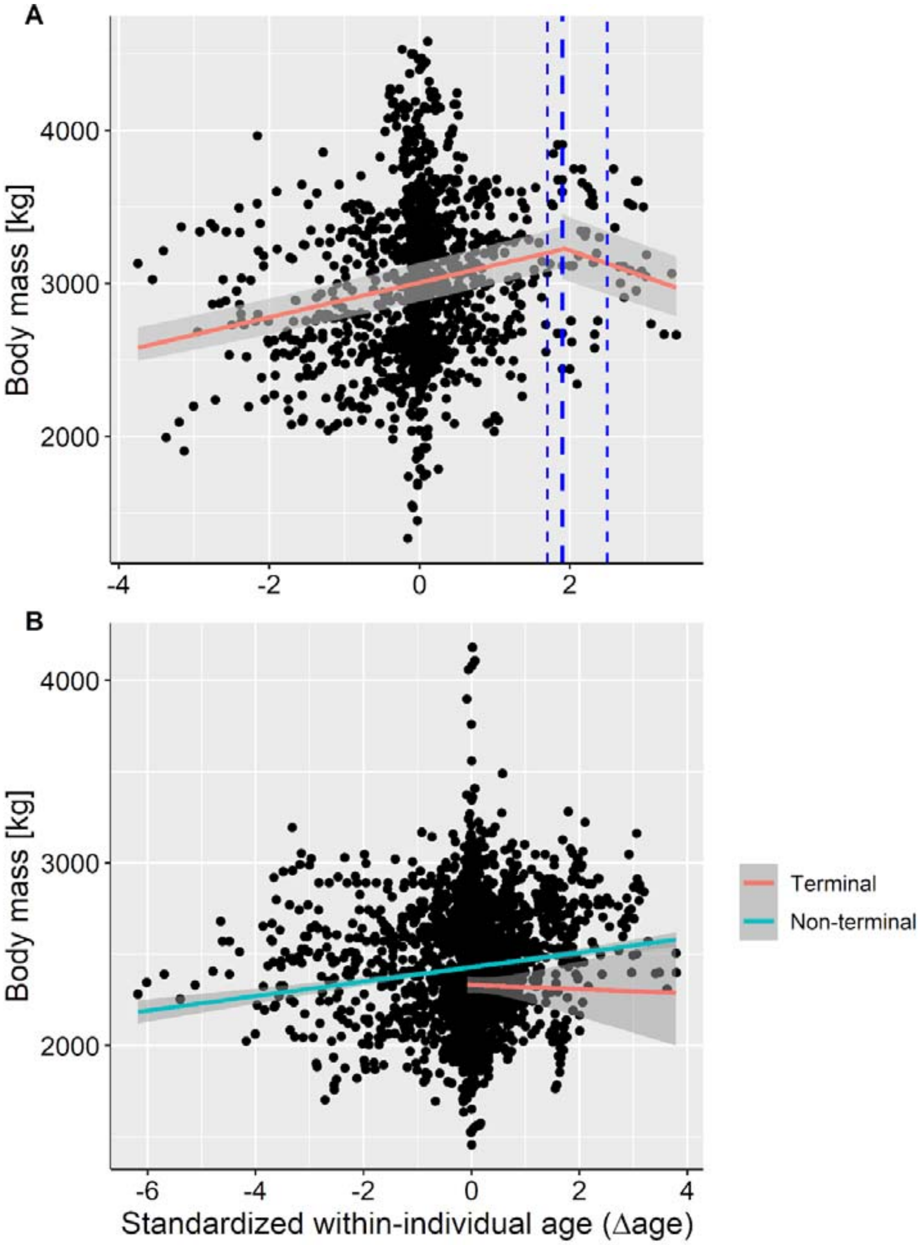

Figure 1. Body mass ageing trajectories. A) males (n=1,316 measurements on 171 individuals). B) females (n=2,570 measurements on 322 individuals). Prediction of the best-fitting models (table 1) with grey areas 95%CI. For males the thick dashed-line shows the threshold age at onset of the body mass decline (1.9 or 48 years) with thin dashed-lines the 4ΔAICc CI [47.1,51.7]. For females, measurements in the terminal year (red) are significantly lower than measurements at other ages (blue). Δage: within-individual age.