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Changes in age-structure over four decades were a key determinant of population growth rate in a long-lived mammal

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Abstract

1. A changing environment directly influences birth and mortality rates, and thus population growth rates. However, population growth rates in the short term are also influenced by population age-structure. Despite its importance, the contribution of age-structure to population growth rates has rarely been explored empirically in wildlife populations with long-term demographic data.
2. Here we assessed how changes in age-structure influenced short-term population dynamics in a semi-captive population of Asian elephants *Elephas maximus*.
3. We addressed this question using a demographic dataset of female Asian elephants from timber camps in Myanmar spanning 45 years (1970–2014). First, we explored temporal variation in age-structure. Then, using annual matrix population models, we used a retrospective approach to assess the contributions of age-structure and vital rates to short-term population growth rates with respect to the average environment.
4. Age-structure was highly variable over the study period, with large proportions of juveniles in the years 1970 and 1985, and made a substantial contribution to annual population growth rate deviations. High adult birth rates between 1970 and 1980 would have resulted in large positive population growth rates, but these were prevented by a low proportion of reproductive-aged females.
5. We highlight that an understanding of both age-specific vital rates and age-structure is needed to assess short-term population dynamics. Furthermore, this example from a human-managed system suggests that the importance of age-structure may be accentuated in populations experiencing human disturbance where age-structure is unstable, such as those in captivity or for endangered species. Ultimately, changes to the environment drive population dynamics by influencing birth and mortality rates, but understanding demographic structure is crucial for assessing population growth.

KEYWORDS
Asian elephants, demography, matrix population models, population dynamics, transient dynamics

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Dylan Z. Childs and Virpi Lummaa hold joint contribution and shared authorship.

1 | INTRODUCTION

Population growth rates are valuable indicators of a population's trajectory, informing us about how they may respond to changes in their environment. Age- or stage-specific birth and mortality rates are the fundamental components used to calculate population growth rates, and accounting for age-specific variation in birth and mortality is vital when quantifying population dynamics (Caswell, 2001; Colchero et al., 2019). However, population growth rates in the short term are not only determined by birth and mortality, but by demographic structure, or the number of individuals at different ages and of each sex. A change in demographic structure may, for example, lead to a population that lacks a sufficient number of reproductive-aged individuals, limiting population growth in the short term. Changes in demographic structure may even result in rapid population decline (Le Galliard, Fitze, Ferriere, & Clobert, 2005). As age-specific birth and mortality rates, or 'vital rates', are directly impacted by the environment (Pardo, Barbraud, Authier, & Weimerskirch, 2013; Stearns, 1992; Weimerskirch, 2018), past environmental perturbations to these rates may result in changes to age-structure, which eventually lead to persistent differences in population size relative to a population at stable age-structure (Koons, Holmes, & Grand, 2007). Indeed, in a constantly changing environment we observe large fluctuations in the demographic structure of populations through time alongside changes in population size (Ezard et al., 2010; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000; Moss, 2001; Trimble, Ferreira, & Aarde, 2009). Thus, with variation in demographic structure we expect variation in population dynamics, even with constant survival and reproduction (Coulson et al., 2001), and there is a need to explore how age-structure influences population growth in addition to variation in birth and mortality rates.

Studies assessing population growth rates have typically focused on long-term, stable population dynamics, which are not reliant upon population age-structure. However, transient dynamics, or short-term population dynamics arising from non-stable age-structure, have been shown to be a crucial driver of population dynamics in many populations (Ellis & Crone, 2013; Ezard et al., 2010; McDonald, Stott, Townley, & Hodgson, 2016; Stott, Townley, & Hodgson, 2011). For both animals and plants, transient dynamics are particularly pronounced in long-lived organisms with 'slow' life histories, which typically display short-term population dynamics with a larger amplitude (Gamelon et al., 2014; Stott et al., 2010). Furthermore, the role of short-term population dynamics is likely to be inflated in populations that have been disturbed. One example is species that are hunted such as bighorn sheep (*Ovis canadensis*), for which increased harvest rates that target mature individuals with bigger horns result in a younger age-structure (Schindler, Festa-Bianchet, Hogg, & Pelletier, 2017). Therefore, it is important to consider short-term population dynamics in species that are endangered, captively managed, experience poaching/harvest and are vulnerable to rapid environmental change (Gaoue, 2016; Jackson, Childs, Mar, Htut, & Lummaa, 2019).

Decomposing the effects of environmental processes on population growth is a key goal in population ecology, and retrospective analyses such as life-table response experiments provide a framework for separating the drivers of population growth rates (Caswell, 1989; Maldonado-Chaparro, Blumstein, Armitage, & Childs, 2018). This approach has been applied to investigate how invasive species influence population dynamics (Kalisz, Spigler, & Horvitz, 2014; Williams & Crone, 2006). Furthermore, the life-table response experiment framework has also recently been applied to decompose population growth rates into contributions from vital rates and population structure (Koons, Iles, Schaub, & Caswell, 2016). However, there are many direct and indirect interactions between vital rates and population structure (e.g. Coulson et al., 2001; Weimerskirch, 2018), and thus assessing their contributions empirically is a challenge. Extreme environmental conditions such as drought can increase age-specific mortality rates for vulnerable age-classes (Foley, Pettorelli, & Foley, 2008), which causes a shift to age-structure. Conversely, high densities of individuals at specific age-classes could result in density-dependent effects such as competition for resources, thereby increasing mortality rates (Coulson et al., 2001). One promising alternative is to investigate the contributions of age-structure and vital rates to short-term population dynamics, but few studies have applied our understanding of transient dynamics empirically to quantify the role of age-structure.

One key issue when assessing the impact of demographic structure on population dynamics is that individuals may live for several years or even decades, making long-term studies crucial (Clutton-Brock & Sheldon, 2010). Ideally, demographic data on individuals spanning several generations are available to quantify vital rates and age-structure within a population (Coulson et al., 2001; Moss, 2001; Robinson, Mar, & Lummaa, 2012; Weimerskirch, 2018). Long-term studies are of particular importance for long-lived species where changes in the environment and subsequent effects on age-structure may last for several decades or generations. Long-lived species with growth rates near replacement may be slow to recover from anthropogenic disturbance, and exhibit delayed responses to changes in the environment (Jackson et al., 2019; Kuussaari et al., 2009; Lahdenperä, Jackson, Htut, & Lummaa, 2019; Moss, 2001; Mumby et al., 2015; Turkalo, Wrege, & Wittemyer, 2016). Therefore, age-structure may be particularly important for short-term population growth rates in long-lived species, because past perturbations in the environment can disturb age-structure for many years before stable dynamics are reached.

Here we aim to assess how age-structure influences short-term population dynamics in a long-lived mammal. Deviation away from a stable age-structure has been shown to drive short-term population dynamics (Ellis & Crone, 2013; Koons et al., 2016), but rarely has this concept been applied empirically to animal populations using long-term demographic data. To address this, we used an extensive multigenerational demographic studbook ($N = 2,223$) of captive-born female Asian elephants *Elephas maximus* from Myanmar, from 1970 to 2014. This long-term, individual-based dataset enables us to accurately capture variation in age-structure and individual life histories over several decades (Chapman, Jackson, Htut, Lummaa, & Lahdenperä, 2019), with which we can estimate vital rates and population growth rates (Jackson et al., 2019). First, we explore changes in population age-structure through time. Then, by capturing short-term, transient population dynamics in each year with matrix population models, we used a retrospective approach to assess the contributions of age-structure and vital rates to deviations in annual population growth rates, with respect to the average environment.

2 | MATERIALS AND METHODS

2.1 | Study population

Asian elephants have a substantial ex situ population of approximately 16,000 individuals globally (Sukumar, 2006; Sukumar & Santiapillai, 1996). Most captive elephants are held in range states (e.g. India, Myanmar and Thailand) and used as working animals, either for use in the timber industry, tourism or for ceremonial purposes. The Union of Myanmar has the largest working population of over 5,000 individuals (Sukumar, 2006; Toke Gale, 1971). Our study population is comprised of over 2,700 state-owned working timber elephants across Myanmar, which are used in the logging industry. Importantly, although timber elephants in Myanmar are captively managed and may be influenced by work-related stress, we define them as semi-captive. They have mortality and fecundity patterns comparable to natural populations (Clubb et al., 2009), with an onset of reproduction at the age of 13 and a peak age of reproduction at 19 (Hayward, Mar, Lahdenperä, & Lummaa, 2014). Furthermore, they have extended rest periods during the hot season (February–June) and at night, forage naturally in the forest without extensive supplementation, wean calves and reproduce naturally without human management, and are not culled. Timber elephants have been managed in Myanmar for centuries, and both wild-caught and captive-born individuals breed in captivity, but the current population was initially established mostly through the capture of wild individuals before 1994 (Jackson et al., 2019; Uga, 2000). In 2014, approximately 75% of the population was born in captivity. The state-owned timber elephants included in our study are all registered and managed centrally by the Myanma Timber Enterprise (MTE), and thus keeping systems and workload regulations are consistent across the country (Mar, 2007). We used a demographic dataset compiled from individual elephant logbooks and annual MTE reports.

All registered elephants have data on the following: identification number and name, birth origin (captive-born or wild-caught), date and place of birth (estimated for wild-caught individuals, see Lahdenperä, Mar, Courtiol, & Lummaa, 2018), mother's identification number and name, year and place of capture (if wild-captured), year or age of taming, identities of all calves sired (if female), date of death or last known date alive and cause of death (Lynsdale, Mumby, Hayward, Mar, & Lummaa, 2017). We restricted the initial demographic studbook for several reasons. First, we used female-only data for assessing fluctuations in age-structure and population growth because we could not reliably quantify age-specific reproduction in males. Using female-only data was also appropriate for the current study as reproduction was likely not limited by the number of males, and females also mated with wild individuals during rest periods. Second, we only used data from captive-born females, to reduce the confounding effects of capture from the wild on age-structure and population growth, and to prevent the need to incorporate immigration into our analyses (Jackson et al., 2019; Lahdenperä et al., 2018). Third, only sparse demographic records were available before the 1950s. Thus, we only included females that were born after 1940 (all but two individuals), reaching peak reproductive age (20–30 years old) in the 1960s. Finally, we removed any females with contradictory death/departure/birth information (5% of data). The final studbook contained 2,568 captive-born females, ranging in birth year from 1941 to 2014, and this data were used in all subsequent analyses.

2.2 | Temporal variation in population age-structure

We first explored long-term changes in population age-structure across the study period, which may influence population dynamics. We calculated the observed age-structure of the population as the proportion of females in each 5-year age-class between the ages of 0 and 50 (e.g. 0–4, 5–9, 10–14) in each year between 1970 and 2014. We used 5-year age-classes to maintain a sufficient sample size for each age-class in each year to visualize general patterns of changes to age-structure. Age-structure was only calculated from 1970 onwards because before this point only very few captive-born individuals were present in the population (<459, and none above the age of 29). In addition, we included only population growth measures from 1970 to 2014, again to account for smaller sample sizes and a lack of old-aged individuals. All analyses were carried out using R version 3.6.2 (R Core Team, 2019). For full details see Supporting Information Section B and data supporting the manuscript in Jackson, Mar, Htut, Childs, and Lummaa (2020; https://doi.org/10.5061/dryad.m905qftwx).

2.3 | Parameterizing an age-structured model

We parameterized annual age-structured matrix population models using predicted age-specific per capita vital rates. We refer to the component of population growth that can be attributed to variation in the age-specific vital rates as the 'environmental contribution'. We encoded raw demographic rates as an annual time series, spanning each year of a female's life from birth/capture to death/censoring (last known alive date) between 1940 and 2014, where mortality and birth rates were recorded as binary response variables, with 1 indicating a birth or death in a given observation year. The time-series dataset contained 44,842 year-age observations from the 2,568 females. We smoothed birth and mortality rates from raw demographic data using a generalized additive mixed effects modelling (GAMM) approach, implemented using the *gam* function in the MGCV package

(Wood, 2011). The variance in raw demographic data was smoothed using GAMMs because the sample size in many age-year combinations was too small to directly estimate the corresponding vital rates.

We modelled the probability of birth/mortality as a function of age and year using GAMMs fitted with binomial error structures and a logit link function. The interacting effects of age and year were captured with a full tensor product smoothing term (Wood, 2006) with a basis dimension of 25 to prevent undersmoothing of the raw data. Birth and mortality models also accounted for spatial variation in vital rates by incorporating an effect of regional division in Myanmar (grouped to make sample sizes more comparable, see S1 in Supporting Information Section A), penalized with a ridge penalty (Wood, 2008). We assessed the distributional assumptions of the models using simulated residual diagnostic tools from the DHARMa package of R, testing for under/overdispersion and uniformity in simulated residuals from 1,000 simulations (Hartig, 2018). To incorporate the parameter uncertainty of vital rate predictions into subsequent analyses on population growth rates, we used posterior simulation of the birth and mortality models. We calculated 1,000 sets of predicted values from the posterior mean and covariance matrix of the model. Posterior simulation was selected ahead of other bootstrapping techniques to prevent the risk of under-smoothing.

We then used the predicted birth and mortality rates for captive-born females and the age-structure in each year to construct annual matrix projection models for the population between 1970 and 2014, using 71 annual age-classes (0–70 years old):

$$\boldsymbol{n}_{t+1} = \boldsymbol{A}_t \boldsymbol{n}_t, \tag{1}$$

where $\boldsymbol{n}_t$ is a population vector giving the starting age-structure of the population (number of individuals in each age-class) in year t, and $\boldsymbol{A}_t$ is a Leslie matrix containing predicted age-specific survival and fertility values for captive-born females, and captures the environmental component (i.e. the component that is directly influenced by the environment in each year) of population growth, in year t. The Leslie matrix $\boldsymbol{A}_t$ is given by

$$\boldsymbol{A}_t = \boldsymbol{P}_t + \boldsymbol{F}_t, \tag{2}$$

where $\boldsymbol{P}_t$ is the matrix of survival and $\boldsymbol{F}_t$ is the matrix of fertility in year t. Here we parameterized $\boldsymbol{P}_t$ using the mean probabilities of survival for each age class in each year, $\boldsymbol{p}_t$, given by, $\boldsymbol{p}_t = 1 - \boldsymbol{\mu}_t$, where $\boldsymbol{\mu}_t$ is a vector of the mean predicted probabilities of mortality for each age-class in year t. We parameterized $\boldsymbol{F}_t$ using the mean predicted fertilities for each age in each year, $\boldsymbol{b}_t$, given by $\boldsymbol{b}_t = \boldsymbol{p}_t \boldsymbol{f}_t$, where reproduction is conditional on survival and $\boldsymbol{f}_t$ is a vector of the mean predicted probabilities of birth for each age-class in year t. Because of the small sample size for old-aged individuals early in the study, predicted values were only calculated for age-year combinations with five or more individuals in the raw demographic data. For age-year combinations with less than five individuals, the earliest year with more than five individuals was used in the place of year for predictions. From annual population projection models, we calculated the short-term population growth rate, λ, in year t, given by

$$\lambda\left(\boldsymbol{A}_t, \boldsymbol{n}_t\right) = \frac{\left\|\boldsymbol{n}_{t+1}\right\|}{\left\|\boldsymbol{n}_t\right\|} = \frac{\left\|\boldsymbol{A}_t \boldsymbol{n}_t\right\|}{\left\|\boldsymbol{n}_t\right\|}, \tag{3}$$

where $\|\ \|$ denotes the sum of (absolute value) entries in a vector. The short-term population dynamics described by $\lambda(\boldsymbol{A}_t,\boldsymbol{n}_t)$ capture realized annual population growth rates instead of stable population dynamics (Ezard et al., 2010), from past demographic data. Here $\lambda(\boldsymbol{A}_t,\boldsymbol{n}_t)$ in each year of the study is a function of the two processes, $\boldsymbol{A}_t$ and $\boldsymbol{n}_t$ presented in Equation 1. Short-term population growth rates and annual matrix population models were used in subsequent analyses on age-structure.

2.4 | Partitioning the effect of age-structure variation on population growth rate

To investigate how much variation in population growth rate could be attributed to variation in age-structure across the study period, we used a retrospective approach to partition the deviations in annual realized population growth rate $\lambda(\boldsymbol{A}_t,\boldsymbol{n}_t)$ into contributions from the environmental component (projection matrix), $\boldsymbol{A}_t$, and the age-structure component, $\boldsymbol{n}_t$ (See Supporting Information Section B for further details). The goal of this approach was to assess how the age-structure and environmental components in each year affected annual population growth rates relative to the average conditions across the study period. Thus, in addition to the annual realized population growth rates captured in Equation 3, we also constructed population models to capture the average environment, and to incorporate the observed age-structure and environmental components separately. Population growth rates from 1970 to 2014 in each scenario were also calculated incorporating parameter uncertainty over 1,000 iterations, and confidence intervals in population growth rates were calculated at the 90% confidence level.

First, we constructed an average-environment projection model using the estimated mean projection matrix over the study period. The corresponding average-environment short-term population growth rate, $\lambda(\bar{\boldsymbol{A}},\bar{\boldsymbol{n}})$, is defined as

$$\lambda(\bar{\boldsymbol{A}},\bar{\boldsymbol{n}}) = \frac{\left\|\bar{\boldsymbol{A}}\bar{\boldsymbol{n}}\right\|}{\left\|\bar{\boldsymbol{n}}\right\|}, \tag{4}$$

where $\bar{\boldsymbol{A}}$ is the mean projection matrix across the study period, parameterized using mean age-specific predicted birth and survival rates between 1970 and 2014, and $\bar{\boldsymbol{n}}$ is the right eigenvector or stable age-structure vector corresponding to $\bar{\boldsymbol{A}}$. We refer to $\bar{\boldsymbol{n}}$ as the average-environment age-structure, and $\bar{\boldsymbol{n}}$ does not correspond to an observed average age-structure in the population. The use of a mean projection matrix across the study period as a reference may be confounded by the length of the study. To investigate the validity of our approach, we repeated subsequent analyses with a time-varying average-environment model, for which the mean projection matrix was calculated in each year using a sliding window approach with 12 years of demographic data before and after the observation year (i.e. 24 years or 1 generation length of demographic data per year).

Then, we constructed annual age-structured projection models that included the observed age-structure, $\boldsymbol{n}_t$, but held the mean projection matrix, $\overline{\boldsymbol{A}}$, from the average environment. These projections capture the contribution of age-structure to annual population growth rates. The corresponding short-term population growth rate for these models, $\lambda(\overline{\boldsymbol{A}}, \boldsymbol{n}_t)$, in year t with the mean projection matrix $\overline{\boldsymbol{A}}$ is defined as

$$\lambda(\overline{\boldsymbol{A}}, \boldsymbol{n}_t) = \frac{\left\| \overline{\boldsymbol{A}} \boldsymbol{n}_t \right\|}{\left\| \boldsymbol{n}_t \right\|}. \tag{5}$$

To capture the contribution of the environmental component on population growth rates, we constructed annual age-structured projection models that included the observed projection matrix, $\boldsymbol{A}_t$, but held the average-environment age-structure, $\overline{\boldsymbol{n}}$. The corresponding short-term population growth rate for these models, $\lambda(\boldsymbol{A}_t, \overline{\boldsymbol{n}})$, in year t with the average-environment age-structure $\overline{\boldsymbol{n}}$ is defined as

$$\lambda(\boldsymbol{A}_t, \overline{\boldsymbol{n}}) = \frac{\left\| \boldsymbol{A}_t \overline{\boldsymbol{n}} \right\|}{\left\| \overline{\boldsymbol{n}} \right\|}. \tag{6}$$

With the average environment model terms as a reference ($\overline{\boldsymbol{A}}$ and $\overline{\boldsymbol{n}}$), in each year we partitioned the effects of age-structure and environment on observed population growth rates. To partition age-structure effects in each year we used an analysis of variance (ANOVA). The coefficients or effect sizes of age-structure and environmental components in each year give the contribution to short-term population growth rates. ANOVAs were repeated and effects were calculated over 1,000 iterations using the population growth rates calculated from predicted vital rates incorporating parameter uncertainty. Confidence intervals for contributions were given at the 90% confidence limit. On comparing population growth rates incorporating $\boldsymbol{n}_t$ (Equation 5) to the average environment population growth rate (Equation 4), we estimated the effect of age-structure on population growth in each year. On comparing population growth rates incorporating $\boldsymbol{A}_t$ (Equation 6) to the average environment population growth rate, we estimated the effect of the environmental component on population growth in each year. Interactions between $\boldsymbol{A}_t$ and $\boldsymbol{n}_t$ were then estimated by comparing the observed population growth rate (Equation 3) to the average environment population growth rate. We write the annual natural log-transformed observed population growth rate $\ln \lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$ in year t as a linear function of the corresponding population growth rate in the average environment, $\ln \lambda(\overline{\boldsymbol{A}}, \overline{\boldsymbol{n}})$, an environment effect, $\Delta \boldsymbol{A}_t$, an age-structure effect $\Delta \boldsymbol{n}_t$ and an interaction effect $\Delta \boldsymbol{A}_t \times \Delta \boldsymbol{n}_t$, such that

$$\ln \lambda(\boldsymbol{A}_t, \boldsymbol{n}_t) = \ln \lambda(\overline{\boldsymbol{A}}, \overline{\boldsymbol{n}}) + \Delta \boldsymbol{A}_t + \Delta \boldsymbol{n}_t + \Delta \boldsymbol{A}_t \times \Delta \boldsymbol{n}_t, \tag{7}$$

where $\ln \lambda(\overline{\boldsymbol{A}}, \overline{\boldsymbol{n}})$ is the intercept. Therefore, to estimate these effects, we compared the population growth rate in each year using all pairwise combination of terms described in Equations 3–6. We performed the models with the natural log-transformed population growth rate because they placed more weight on the main effect terms ($\Delta \boldsymbol{A}_t$ and $\Delta \boldsymbol{n}_t$), which were more interpretable. The resulting design of the simulation experiment was a fully factorial ANOVA without replication for each year (i.e. $\overline{\boldsymbol{A}}$ vs. $\boldsymbol{A}_t$, and $\overline{\boldsymbol{n}}$ vs. $\boldsymbol{n}_t$; see Supporting Information Section B for details). The effects in Equation 7 indicate the independent and interactive contributions of $\boldsymbol{A}_t$ and $\boldsymbol{n}_t$ to $\ln \lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$ relative to the average environment, and are analogous to 'treatment contrasts' in an ANOVA.

Finally, to disentangle the influence of survival and birth rates on population growth rate deviations alongside the effect of age-structure, we further separated the effect of the environmental component ($\boldsymbol{A}_t$) into contributing effects from the annual probability of survival ($\boldsymbol{p}_t$) and probability of birth ($\boldsymbol{f}_t$), and their interaction with age-structure. We used the mean predicted birth probability as opposed to the mean predicted fertilities to avoid the confounding influence of survival on fertility (as fertility is conditional on survival), so birth and mortality effects could be addressed independently. We partitioned population growth rate deviations following the same ANOVA framework but calculating average-environment terms for survival and birth separately ($\overline{\boldsymbol{p}}$ and $\bar{f}$, respectively). Then, on comparing the population growth rate when including the observed survival and birth probabilities ($\boldsymbol{p}_t$ and $\boldsymbol{f}_t$, respectively) separately to the average environment terms, we could estimate the contribution of survival and birth to the observed population growth rate. Similarly, we write the annual natural log-transformed observed population growth rate, $\ln \lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$, in year t as a linear function of the corresponding population growth rate in the average environment, $\ln \lambda(\overline{\boldsymbol{A}}, \overline{\boldsymbol{n}})$, a survival effect $\Delta \boldsymbol{p}_t$, a birth effect $\Delta \boldsymbol{f}_t$, an age-structure effect $\Delta \boldsymbol{n}_t$ and interaction effects between survival/birth and age-structure, $\Delta \boldsymbol{p}_t \times \Delta \boldsymbol{n}_t$ and $\Delta \boldsymbol{f}_t \times \Delta \boldsymbol{n}_t$, such that

$$\ln \lambda(\boldsymbol{A}_t, \boldsymbol{n}_t) = \ln \lambda(\overline{\boldsymbol{A}}, \overline{\boldsymbol{n}}) + \Delta \boldsymbol{p}_t + \Delta \boldsymbol{f}_t + \Delta \boldsymbol{n}_t + \Delta \boldsymbol{p}_t \times \Delta \boldsymbol{n}_t + \Delta \boldsymbol{f}_t \times \Delta \boldsymbol{n}_t. \tag{8}$$

We estimated these effects using pairwise combinations of model terms; the design of the simulation experiment was a factorial ANOVA. However, this design was not fully factorial because we excluded the two-way interaction between $\Delta \boldsymbol{p}_t$ and $\Delta \boldsymbol{f}_t$ ($\Delta \boldsymbol{A}_t$ in Equation 7) and the three-way interaction between $\Delta \boldsymbol{p}_t$, $\Delta \boldsymbol{f}_t$ and $\Delta \boldsymbol{n}_t$ ($\Delta \boldsymbol{A}_t \times \Delta \boldsymbol{n}_t$ in Equation 7).

3 | RESULTS

3.1 | Fluctuations in age-structure over 45 years

There were large changes in the observed age-structure of the population across the study period, with the population biased towards a larger proportion of younger individuals early in the study period, and a more even distribution of ages (including older age-classes) after the year 2000 (Figure 1). Across the study period, 43% of individuals were under the age of 13, the onset of reproduction. However, the proportion of individuals older than 25 (after

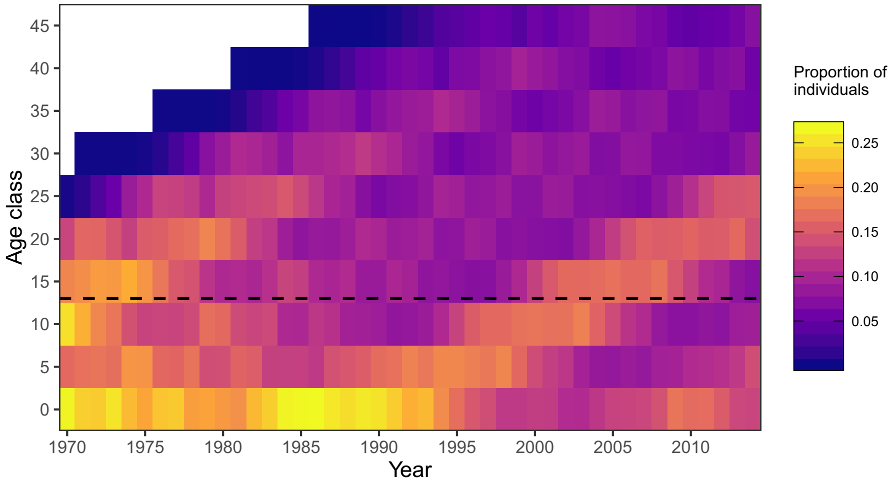

FIGURE 1 Changes in age-structure for captive-born female timber elephants between 1970 and 2014. A heatmap of the observed age-structure in each year for each 5-year age-class, with the colour denoting the proportion of individuals. The dashed line indicates the age of the onset of reproduction i.e. age 13

peak reproduction) increased across the study period (Figure 1). The variation in age-structure across the study period was particularly pronounced in young age-classes; the proportion of individuals between 0 and 4 ranged from 11% to 31% across the study period (Figure 1). As such, there were extended periods (~5 years) with markedly increased numbers of juveniles in the population, followed by an increase in the number of adults. These periods were observed in approx. 1970, 1985 and to a lesser extent in 2009 (Figure 1). There were relatively fewer individuals in older age-classes present in the study population between 1970 and 2014, with individuals over the age of 45 only present beyond 1986 (Figure 1). Together, these results suggest that there have been substantial changes in the demographic structure of the captive-born population over 45 years, particularly in younger individuals.

3.2 | Age-structure is a key driver of short-term population growth rates

Generally, birth rates increased rapidly at the age of 12 until a reproductive peak between 18 and 24 years of age, and declined later in life, with few births recorded over the age of 55 (Figure S1). Mortality rates were higher in young and old individuals, particularly below 8 and above 45 years old, with lower mortality in individuals between 10 and 45 (Figure S1). For females between 19 and 45, the peak ages of reproduction and birth rates declined across the study period, and this was particularly due to high birth rates in the 1970s and 1980s in comparison to later years (Figures S1 and S2). There was no evidence of non-uniformity or overdispersion in the simulated model residuals of the birth and mortality models (Figure S3), indicating that the models met the distributional assumptions of the additive models. Across the study period, the observed log-transformed population growth rate ($\ln \lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$) in each year varied from −0.01 in 1991, to 0.01 between 2012 and 2014 (Figure 2a). Between 1985 and 2000, population growth rates were negative, but otherwise remained above replacement rate (i.e. $\ln \lambda(\boldsymbol{A}_t, \boldsymbol{n}_t) > 0$; Figure 2a).

The average-environment population growth rate was effectively 0, or at replacement rate (Figure 2a). Importantly, the observed population age-structure made substantial contributions to deviations in population growth rate, in addition to effects from the environmental component (Figure 2b). Between 1970 and 1985, population growth rates were higher when including the environmental contribution (but holding the average environment age-structure constant) relative to the average environment, with a mean contribution of 0.017 in 1970 (Figure 2b). If this positive contribution was constant and the age-structure was held at the average-environment, the population would double in size in under 42 years. However, the environmental contribution declined over the study period, becoming negative in 1985, then stabilizing and increasing after 2000 (Figure 2b).

Conversely, the contribution of age-structure to population growth rate devaitions increased across the study period (Figure 2b). There were negative contributions before 1978 when fewer old-aged individuals were present, with population growth rates including the observed age-structure being substantially lower than the average environment population growth rate. The mean contribution of the age-structure component in 1970 was −0.016, which if held constant would halve the population in under 43 years. Furthermore, the contributions of the age-structure component were of a similar magnitude to changes in the observed population growth rate (Figure 2). Importantly, the opposing contributions of age-structure and the environmental component highlight the combined role of age-structure and the environmental component as drivers of short-term population dynamics. The positive contribution of age-structure was greatest after 2002, where the population growth rate incorporating the observed age-structure (but holding the average environmental component constant) was ~0.01. However, before 1993, there was a period of ~8 years with small contributions to population growth rates relative to the average environment (Figure 2b). The importance of age-structure for population growth rates was also not dependent on the choice of average-environment conditions, with similar patterns observed when including a time-varying average environment model as a reference (Figure S4).

Finally, we separated the influence of the environmental component (projection matrix) into its two contributing processes, age-specific birth and survival probabilities. We conclude that the

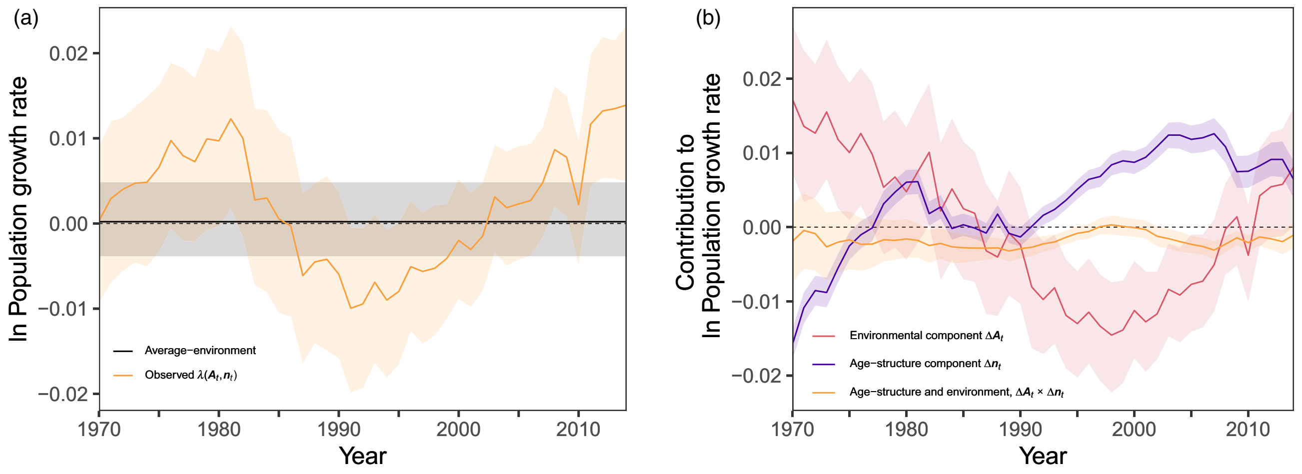

FIGURE 2 Age-structure is a key determinant of population growth rates. (a) The observed log transformed short-term population growth rate (yellow line, ln $\lambda(\boldsymbol{A}_t,\boldsymbol{n}_t)$ from Equation 3) between 1970 and 2014, relative to the average-environment short-term population growth rate (solid black line, ln $\lambda(\bar{\boldsymbol{A}},\bar{\boldsymbol{n}})$ from Equation 4). Lines are population growth rates with 90% confidence limits from posterior simulations. Dashed black line indicates a ln population growth rate of 0. (b) The contribution of the age-structure component (purple, $\Delta\boldsymbol{n}_t$) and environmental component (or age-specific vital rate component, pink, $\Delta\boldsymbol{A}_t$) to variation in annual log-transformed short-term population growth rates (ln $\lambda(\boldsymbol{A}_t,\boldsymbol{n}_t)$) between 1970 and 2014. The yellow line indicates non-additive contributions from both the age-structure and environmental components in a given year ($\Delta\boldsymbol{A}_t \times \Delta\boldsymbol{n}_t$). Lines are the mean contributions with 90% confidence limits from posterior simulation. The dashed black line indicates a contribution of 0. Contributions are relative to the average environment population growth rate, such that a negative contribution indicates that the population growth rate incorporating the observed age-structure or environmental component was lower than the average environment growth rate, and vice versa

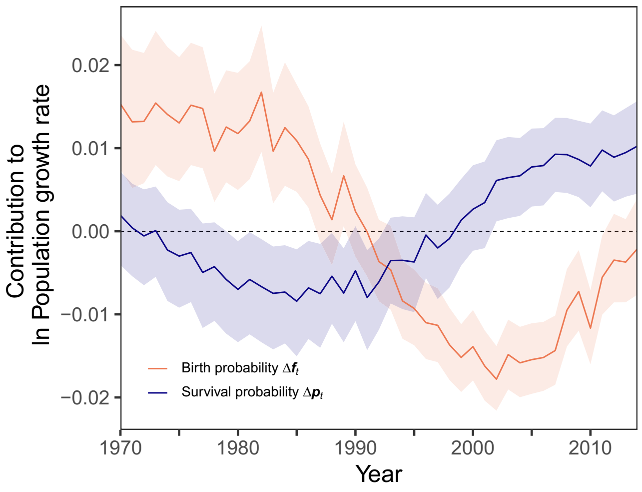

FIGURE 3 Age-specific birth probabilities are the key environmental component for population growth rates. The environmental component ($\Delta\boldsymbol{A}_t$) was partitioned into its components of predicted age-specific birth (orange, $\Delta\boldsymbol{f}_t$), and survival (blue, $\Delta\boldsymbol{f}_t$) probabilities to assess their contribution to log-transformed short-term population growth rates (ln $\lambda(\boldsymbol{A}_t,\boldsymbol{n}_t)$) in captive-born females between 1970 and 2014. Lines are contributions with 90% confidence limits from posterior simulation. Dashed black line indicates a contribution of 0

crucial environmental component governing population growth rates was age-specific birth probability, with positive contributions between 1970 and 1985, and declining contributions that stabilized later in the study period (Figure 3). Importantly, the contribution from age-specific birth probabilities mirrored the overall contribution from the environmental component and was also accompanied by the reduction in mean predicted adult birth rates (Figures 2b and 3; Figure S2). This suggests that the reduction in the contribution of the environmental component was due to the reduction in birth rates over the study. Age-specific survival probability made relatively smaller contributions to population growth rates between 1970 and 2000 but had positive contributions between 2000 and 2014 (Figure 3). Combined with negative contributions of age-structure early in the study period, this result suggests that despite larger observed birth rates having the potential to increase population growth rates in the 1970s and 1980s, age-structure was unstable, and observed population growth rates were lower.

4 | DISCUSSION

Many studies have investigated the drivers of population dynamics in long-lived species, with a particular focus on climate change, habitat loss and direct human drivers such as poaching and how these influence the vital rates that govern population decline (Boggs & Inouye, 2012; Flockhart, Pichancourt, Norris, & Martin, 2015; Jenouvrier et al., 2014; Lusseau & Lee, 2016; Moss, 2001). However, while the environmental component (vital rates) is crucial, a population's age-structure cannot be ignored when assessing population dynamics. Our results highlight the importance of age-structure as a driver of short-term population dynamics in long-lived species in addition to environmental contributions from vital rates. First, we observed large changes in population age-structure across the study. Then, using a retrospective approach, we found that there were substantial contributions from age-structure to annual population growth rates. These contributions were strongest in the 1970s, where a lack of reproductive-aged individuals counteracted high adult birth rates, preventing large observed population growth rates.

Temporal variation in age-specific vital rates (the 'environmental component') was still a key driver of population growth rate deviations between 1970 and 2014. At the beginning of the study, contributions from the environmental component would have caused the population to double in size in under 43 years, which was primarily driven by high birth rates. Furthermore, negative population growth rates between 1985 and 2000 were also associated with negative contributions from birth rates in the environmental component, and there were declines in predicted birth rates for prime-aged females (19–45). These results support previous findings of a decline in adult birth rates, which are the key demographic rates for population growth, between 1960 and 2014 (Jackson et al., 2019), but the reasons for this decline are less clear. Fecundity in long-lived mammals has generally been associated with environmental conditions such as climate or habitat availability, which affects body condition and thus a female's ability to provision for offspring (Cook et al., 2013; Coulson, Milner-Gulland, & Clutton-Brock, 2000; Parker, Barboza, & Gillingham, 2009). For example, adverse climatic conditions caused by drought in Kenya reduce birth rates in African elephants (Moss, 2001). In the current population, climate conditions have been linked to survival, which was highest at moderate temperatures and with increased rainfall (Mumby, Courtiol, Mar, & Lummaa, 2013). The decline in birth rates across the study period may also reflect declines in habitat availability with continued deforestation in the region (Leimgruber et al., 2005), but further study is needed to investigate the link between the environment and vital rates. Nevertheless, vital rates were critical for short-term population dynamics.

Importantly, despite the positive contribution of birth rates to population growth rates early in the study period, observed population growth rates were moderate due to a negative contribution from population age-structure. In other words, high per-capita birth rates in the 1970s had the potential to cause large population increases, but the relative number of reproductive-aged females was small, and so population growth rates were moderate. If constant, the negative contribution of age-structure to population growth in 1970 would have resulted in the population to halve in less than two generations. Furthermore, population growth rates were negative between 1985 and 2000 as birth rates declined and the contribution from age-structure remained negative. After 2000, positive contributions from age-structure were dampened by negative environment effects. The magnitude of contributions from the age-structure component was also comparable to the magnitude of annual population growth rates. Thus, both an understanding of age-structure and environmental components (i.e. vital rates) is needed to assess short-term population dynamics.

Deviations away from a stable age-structure may be particularly important for the population dynamics of disturbed or fragmented populations. Indeed, in the current study we observed large changes in age-structure, with a greater proportion of individuals younger than 13 (the onset of reproduction; Hayward et al., 2014) between 1970 and 1990, and more reproductive-aged individuals between 1990 and 2014. We also observed short periods (around 1970, 1985 and 2009) with substantially higher numbers of juveniles. Practically for population management, fluctuations in age-structure may cause a surge in births when juvenile females reach maturity, and management may need to change to target the influx of young individuals in future. One potential explanation for this disruption to age-structure is an indirect long-term consequence of the capture of wild elephants in Myanmar. There was systematic capture from the wild in Myanmar until 1994, with approx. 3,000 individuals wild-captured between the 1950s and 1994, but after this point wild-capture occurred at lower rates (Lahdenperä et al., 2018; Mar, 2007; Uga, 2000). Wild-capture may have been particularly influential on age-structure because it targeted younger individuals (Lahdenperä et al., 2018). These initial imbalances in age-structure recovered over several decades as the population approached a more stable age-structure, resulting in positive contributions towards population growth rates.

The disturbance of demographic structure (altered age/stage-structure and sex-ratio) and its impact on population dynamics may have important implications for populations across the tree of life. In particular, short-term population dynamics arising from human disturbance through poaching, hunting, harvest and rapid environmental change may have important implications for endangered, invasive or agriculturally important species. In long-lived mammals, both hunting and poaching are generally focussed on specific age-sex classes in a population and can cause changes to demographic structure; older and large-bodied individuals with larger auxiliary structures (e.g. tusks) have a higher value to hunters and poachers (Bischof et al., 2018; Coltman et al., 2003). Of course, poaching and hunting have immediate effects on age-specific vital rates, with implications for population viability and extinction risk (Lusseau & Lee, 2016). However, they also have evolutionary implications by, for example, selecting for smaller bodied individuals with smaller auxiliary structures or disrupting social structure (Coltman et al., 2003; Gobush, Mutayoba, & Wasser, 2008; Jachmann, Berry, & Imae, 1995). Recent evidence from regulated hunting in brown bears also suggests that hunting pressure may be responsible for shifts in reproductive strategies, life expectancy and reproductive value (Bischof et al., 2018).

Beyond vertebrates, changes to stage structure are also crucial for population dynamics. In perennial plant species, transient dynamics contributed more to variation in observed population growth rates than vital rates alone (Ellis & Crone, 2013). Transient dynamics and stage-structure are also crucial for plant populations targeted by harvest, or in invasive species (McDonald et al., 2016). For example, in African dry zone Mahogany *Khaya senegalensis*, harvest had a strong impact on short-term dynamics relative to long-term growth rates, driven by changes to survival in early life stages (Gaoue, 2016). Transient dynamics in invasive plant species may also vary across populations in different ecological settings, and so understanding difference in stage-structure may improve management strategies (Horvitz, Denslow, Johnson, Gaoue, & Uowolo, 2018). Our results add to these studies across taxa, suggesting that the changes to population age-structure associated with human interference can influence short-term population dynamics in addition to vital rates.

Several recent studies have explored the prevalence of non-equilibrium dynamics in a broad range of taxa, leading to growing acceptance of the need to understand transient responses to environmental change (Gamelon et al., 2014; McDonald et al., 2016; Stott et al., 2010). Though a number of different methodological frameworks are available to assess such impacts (Ellis & Crone, 2013; Ezard et al., 2010; Koons et al., 2016), these have not typically distinguished between contributions to population growth from vital rate variation and (st)age-structure (Ozgul et al., 2010). However, Koons et al. (2016) recently developed a sensitivity-based approach to estimate the contribution from each unique demographic parameter and stage abundance. The approach used in the current study does not enable the same level of resolution because it only estimates the net contribution of stage-structure fluctuations. However, it avoids the need to calculate short-term growth sensitivities, which can be cumbersome for complex models, and can be applied without modification to alternative frameworks such as Integral Projection Models (Ellner, Childs, & Rees, 2016).

The long-term, multigenerational demographic studbook of timber elephants in Myanmar has provided novel empirical insights into the demographic drivers of population dynamics. In long-lived species such as Asian elephants, disturbances to the population may have a lasting effect on age-structure over several decades. Ultimately, understanding the interacting effects of demographic structure and environmental variation driving population growth rates will better equip ecologists in understanding population-level responses to environmental change.

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AUTHORS' CONTRIBUTIONS

K.U.M. and W.H. collected the data; J.J., D.Z.C. and V.L. designed the study; J.J. carried out analysis with support from D.Z.C. and V.L.; J.J. wrote the manuscript, with contributions from D.Z.C. and V.L. All authors approved the manuscript for publication.

DATA AVAILABILITY STATEMENT

Data and code supporting the manuscript are included in the Dryad Digital Repository https://doi.org/10.5061/dryad.m905qftwx (Jackson et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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