Using semi-captive Asian elephants to examine population dynamics in long-lived mammals

by

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For Naomi

Abstract

Amidst the global biodiversity crisis, understanding the processes that underpin population decline in a changing environment is crucial to develop effective conservation management strategies. External drivers of population decline such as human disturbance and climate change have an immediate influence on population vital rates such as survival and reproduction, which has implications for population dynamics. However, anthropogenic activity may also have long-lasting demographic consequences for wildlife populations, influencing vital rates for several years and affecting demographic structure. Long-lasting demographic effects may be particularly important in long-lived species that experience years or decades of environmental variation, but long-term demographic data is needed to pick apart the drivers of population dynamics. Here, I explore the drivers of population dynamics in semi-captive Asian elephants using a long-term, individual-based demographic dataset collected between 1951-2014 from timber camps in Myanmar. First, in chapter 2 I demonstrate that capture from the wild reduced lifetime reproductive success in female elephants, and that the negative effects of wild-capture lasted for over a decade and affected survival in subsequent generations. In chapter 3, I further explore the role of wild-capture for population dynamics and find that the sustainability of this semi-captive population was dependent on capture from the wild for decades. Furthermore, long-term projections suggest that without wild-capture, there may be transient population declines lasting for over half a century. Wild-capture influenced the age-structure of the population, and in chapter 4 I investigate the contribution of population age-structure to short-term population growth rates. Age-structure varied substantially across the study period and was a critical driver of transient population dynamics in this disturbed population. Finally, to assess other potential drivers of population dynamics, in chapter 5 I tested whether the past climate influenced vital rates in semi-captive elephants under contrasting mechanisms of delayed climate effects and find little evidence for delayed climate effects at this temporal scale. I highlight that the negative effects of human activity on wildlife populations can last for decades, and the important role of transient population dynamics in long-lived species. These results provide novel insight into the impact of human disturbance on population dynamics in a long-lived species.

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Statement of intellectual contribution

The work in this thesis would not have been possible without the intellectual contributions of several collaborators. All data chapters are presented as manuscripts for publication, with journal information given at the start of each chapter. All photographs are my own. Major contributions are listed here, and additional contributions are noted in the acknowledgement sections at the end of each data chapter.

Chapter 2: ML, JJ and VL conceived and designed the paper. WH contributed to data collection. JJ and ML performed the analyses. ML, JJ and VL wrote the paper. All authors read and approved the final manuscript.

Chapter 3: KUM and WH collected the data. JJ, DZC and VL designed the study. JJ carried out analysis with support from DZC and VL. JJ wrote the manuscript, with contributions from VL and DZC. All authors approved the manuscript for publication.

Chapter 4: KUM and WH collected the data. JJ, DZC and VL designed the study. JJ carried out analysis with support from DZC and VL. JJ wrote the manuscript, with contributions from DZC and VL. All authors approved the manuscript for publication.

Chapter 5: The study was designed by JJ, VL, DZC, RC and BH, with support from WH. JJ carried out demographic analyses, with support from DZC, RC, VL and BH. RC performed climate data processing, with assistance from JJ. JJ wrote the manuscript, with comments from DZC, RC, VL and BH. All authors provided feedback and approved the manuscript for publication.

Declaration

This thesis contains original work and does not contain material previously published or written by other persons, except where due reference has been made in the text. The contribution of collaborators to the conceptualisation, data collection, statistical analysis, authorship, and editing of this thesis has been clearly stated. This thesis content results from work I have undertaken since starting my research higher degree and includes no work submitted to qualify for any other degree or diploma in any university or other institution. I have clearly stated which parts of the thesis have been submitted for scientific publication and have obtained the required permissions to include this work. I acknowledge that copyright of the thesis content resides with the copyright holder(s) of that material.

Contents

Chapter 1

General introduction

1.1 The population dynamics of long-lived species in a changing world

Human population increase is directly responsible for widespread declines in global biodiversity, and current rates of extinction suggest that we have entered a sixth, anthropogenically induced mass extinction (Butchart et al. 2010, Barnosky et al. 2011, Tittensor et al. 2014, Ceballos et al. 2015). Over 1 million species of plants and animals are threatened with extinction based on the recent Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) report (Díaz et al. 2019). The living planet index, documenting declines in vertebrate populations globally, indicates that 60% of populations were lost between 1970-2014 (Grooten and Almond (Eds) 2018). Alarmingly, global biodiversity is declining despite the continued expansion of the global protected area network and increased investment into environmental protection (Butchart et al. 2010, Tittensor et al. 2014). Aside from the societal changes needed to reduce the drivers of population decline, the effectiveness and efficiency of conservation strategies must be improved to prevent future declines (Rands et al. 2010). Therefore, it is vital that we understand the processes underpinning population decline and population dynamics amid environmental change, to mitigate against future declines (Caughley 1994).

Demographic studies that investigate population dynamics in a changing environment provide valuable insight into the causes of population declines and can illuminate key strategies for conservation management. For example, in killer whales (*Orcinus orca*) survival and fecundity data from populations across the species range was combined with plastic pollution data, which reduces calf survival and immune function and is predicted to cause widespread population declines (Desforges et al. 2018). The foundation of population dynamics is demographic data (Caswell 2001). First, demographic data enable us to construct life-tables and begin to understand the factors that influence vital rates such as survival, reproduction (e.g. Catchpole et al. 2000, Moss 2001, Mumby et al. 2013, Genovart et al. 2016), and migration (e.g. Dolman and Sutherland 1995, Visser et al. 2009). Then, vital rates such as survival and reproduction across the life-cycle of a species can be used to parameterise population models and describe population dynamics (Crouse et al. 1987, Caswell 2001). However, the accuracy and utility of population models is dependent on the quality of demographic data (Harcourt 1995, Coulson et al.

2001b). Using of detailed demographic data to understand population dynamics is therefore crucial to understand population declines.

One key consideration in the study of population dynamics is the variability of populations both spatially and through time (Gaillard et al. 2000, Hastings et al. 2011). Because vital rates are ultimately influenced by changing external abiotic and biotic factors, temporal changes in the environment results in variation in demographic rates through time (Gaillard et al. 2000, 2003, Coulson et al. 2001a). Furthermore, populations are often structured demographically, with different life-history stages that exhibit differences in vital rates. Different life-history stages respond differently to the environment, which causes changes to the demographic structure of populations through time, contributing to population growth (Coulson et al. 2001a, Weimerskirch 2018). Central to addressing this variation is the use of detailed, long-term demographic datasets, which monitor populations through a changing environment and across the lifecycle. Long-term studies that are individual-based not only significantly improve our understanding of population dynamics, but contribute more to policy (Clutton-Brock and Sheldon 2010, Hughes et al. 2017). Incorporating variability in vital rates through time and within populations enables us to investigate the drivers of population dynamics, and there is a need for more long-term, individual-based studies to improve our understanding of population decline.

Temporal changes in vital rates and differences between ages (or life-history stages) may be particularly important in long-lived species. Long-lived species can generally be defined as organisms with lifespans of several years or decades, which typically display “slow” life-history characteristics, but patterns of mortality and reproduction across lifespan vary for both long- and short-lived species (Jones et al. 2014). Importantly, long-lived species experience several years of environmental variation, which has the potential to influence population dynamics. Indeed, in long-lived species such as African elephants, wandering albatross and Soay sheep, there is annual variability in mortality, reproduction and population structure over several decades in relation to the environment (Coulson et al. 2001a, Moss 2001, Weimerskirch 2018). However, relating long-term changes in vital rates to population dynamics in long-lived species is more of a challenge because of the requirement of extensive long-term demographic data. Long-lived species may actually be buffered against annual variability in vital rates;

a comparative analysis of 36 animal and plant species found that compared to long-lived species, population growth rates in shorter-lived organisms were more negatively affected by variability in vital rates (Morris et al. 2008). Further study is needed to pick apart the factors underpinning temporal variation in vital rates for long-lived species and how this relates to population dynamics. Nevertheless, long-lived species have been identified as vulnerable to population declines, not least because they are disproportionately targeted by poaching and hunting (Cardillo et al. 2005, Kuussaari et al. 2009). Furthermore, while long-lived species may be less responsive on average to environmental perturbations, when populations are disturbed through drivers such as poaching, recovery can take decades (Turkalo et al. 2016).

Differences in vital rates at different ages/stages or between the sexes can also have a big influence on population dynamics in long-lived species (e.g. Coulson et al. 2001a, Weimerskirch 2018, Paniw et al. 2019). Both age-specific (Pardo et al. 2013) and sex-specific (Clutton-Brock et al. 2002) differences in vital rates are common in long-lived species. Furthermore, accounting for age-specific vital rates improves the reliability of population growth rate estimates in structured population models (Colchero et al. 2019). For long-lived mammals, generally population growth rates are most sensitive to changes in adult female survival and reproduction (Eberhardt 2002, Faust et al. 2006, Paniw et al. 2019). In meerkats (*Suricata suricatta*), a climate-induced reduction in adult fecundity in the breeding season, mediated by reductions in body mass, increased the risk of extinction (Paniw et al. 2019). Thus, understanding how vital rates at different ages/stages respond to external drivers such as human disturbance or climate changes in long-lived species is critical to understanding population decline (Gaillard et al. 2000, Colchero et al. 2019). Furthermore, the responses of different life-history stages to the environment not only influences vital rates, but also demographic structure, or the number of individuals at each age/stage and of each sex (Coulson et al. 2001a). Sex-ratio in particular has received attention as a driver of population dynamics (Clutton-Brock et al. 2002, Le Galliard et al. 2005). However, the role of age-structure in population dynamics has not been explored extensively in long-lived species.

The demographic structure of populations influences short-term or transient population dynamics (Ezard et al. 2010). Traditionally, in structured population models, a key indicator for use in population management has been the long-term population growth rate, λ, which captures equilibrium/asymptotic dynamics under a stable stage-structure (Caswell 2001). However, in reality stage structure fluctuates over the short term in natural populations, leading to short-term, non-equilibrium transient dynamics (Koons et al. 2005, Ezard et al. 2010, Stott et al. 2011). For populations with identical stage-specific vital rates and excluding density dependence, differences in stage-structure result in different long-term trajectories, a process formalised as population inertia (Koons et al. 2007). Importantly, comparative evidence suggests that long-lived species are expected to have stronger, higher amplitude transient dynamics (Stott et al. 2010, Gamelon et al. 2014), and so changes in age- or stage-structure are likely to have a large impact on short-term population growth. A study by Koons et al. (2016) developed a framework to assess the contribution of stage-structure to variance in short-term population growth rates, but found that in simulations of a simple two-stage lifecycle, the contribution of demographic structure was actually greatest when survival was low i.e. in short-lived species. However, how observed changes in demographic structure contribute to short-term population dynamics in long-lived species is largely unknown and needs to be addressed using long-term data.

Several other factors call for careful consideration when assessing population dynamics in long-lived species. The first is the timescale of demographic processes, which may be several decades. For example, in forest elephants population recovery from poaching was predicted to take several decades due to slow life-history traits and population replacement times, and so conservation management must be adapted to timescales that are relevant to the life-history of target species (Turkalo et al. 2016). Second, the environment early in life can have an influence on individual performance and fitness across lifespan. Natal habitat quality (van de Pol et al. 2006), resource competition (Nussey et al. 2007), climatic conditions (Lee et al. 2013, Herfindal et al. 2015), and stress (Mumby et al. 2015) have all been demonstrated to have long-term effects on survival, reproduction, overall fitness and ageing rates in long-lived species. As a result, there may be strong cohort effects in long-lived species where current vital rates depend on past conditions, with potential effects on future population dynamics (Gaillard et al. 2003, Hastings et al. 2011).

1.2 Long-lasting drivers of population dynamics

Anthropogenic activity is directly responsible for innumerable population declines through the key drivers of land use (or sea use) change, direct exploitation, climate change, pollution and invasive species (Butchart et al. 2010, Steffen et al. 2011, Díaz et al. 2019). These drivers pose an immediate threat to mortality, for example in hunting, and cause population declines. However, direct human exploitation/activity and human-induced climate change, which I focus on here, may also have long-term (potentially unintended) effects on demography and population dynamics, particularly in long-lived species. Direct human actions such as poaching and hunting have long been known to pose significant threats to biodiversity, and in particular to large-bodied megafauna, which are selectively targeted for meat or ornamental purposes (Brook and Bowman 2004, Rosen and Smith 2010). Alongside these negative effects, there are also long-lasting demographic effects caused by the selective harvest of individuals in a population, which may influence sex-ratio, age-structure and social structure (Ginsberg and Milner-Gulland 1994, Milner et al. 2007, Schindler et al. 2017). In brown bears, even with regulated hunting, which targets large bodied adults, increased hunting pressure was associated with broad changes to life-history, including declines in life-expectancy and reproductive value across ages (Bischof et al. 2018).

Long-lasting demographic effects not only apply when animals are poached or hunted, but also in conservation management strategies. Translocations for example can directly influence the demographic structure of relocated populations and influence subsequent intraspecific competition (Brett 1998), but may also have an influence on population growth and demographic structure when habitat preferences are ignored (Lea et al. 2016). For African elephants (*Loxodonta africana*) in Addo national park, South Africa, to reduce collisions with trains and farmers shooting elephants, a fence was erected around the protected area in 1954, but this had an immediate effect on the survival of males and a long-term negative impact on social behaviour (Whitehouse and Kerley 2002). The management of populations in altered or captive environments (Redford et al. 2011) also largely has a negative impact on demography and population dynamics. Of mammalian zoo populations, only half were breeding to replacement rate, and many are founded from a small number of individuals, and thus there is the potential for inbreeding and strong demographic stochasticity effects (Lees and Wilcken 2009, Redford et al. 2011). Ultimately, understanding the long-term impacts of human disturbances on demography, both when conservation is the primary goal and when animals are targeted by threats such as poaching, will enable us to mitigate against population declines.

Human-induced climate change also poses both immediate and long-term pressures on demography and population dynamics. Climate change is predicted to cause widespread extinctions, and many species have already been negatively impacted by a changing climate (Thomas et al. 2004, Pacifici et al. 2017). Variation in life-history traits within and between taxa may also be a key predictor of how species or populations respond to climate change (Fay et al. 2015, Cayuela et al. 2017). In long-lived species, it is predicted that populations are actually buffered against temporal variation in vital rates observed with variability in the climate (Morris et al. 2008). However, several studies have found immediate climate effects on demography, where climate influences body condition and thus individual performance and survival/reproduction (Foley et al. 2008, Cook et al. 2013, Peeters et al. 2017). A changing climate may also have delayed or long-term effects on demography in long-lived species; harsh climate conditions early in life have been linked with reduced fitness later in life (Nussey et al. 2007, Herfindal et al. 2015). There has been relatively little exploration of the impact of climate on vital rates across lifespan in long-lived species, and the mechanism by which climate conditions have delayed impacts on vital rates and fitness is largely unknown, despite recent increases in global temperatures.

The relatively recent increase in the availability of long-term, individual-based datasets monitoring wildlife populations has led to important insights into demography and population dynamics amidst environmental change and human population increase. However, the number of study systems using long-term datasets is still relatively small (Clutton-Brock and Sheldon 2010). Without such datasets, our understanding of the long-term impacts of a changing environment on population dynamics remain limited, especially in long-lived species, which show such marked variation across the lifecycle and lasting responses to human disturbance. Here, I present a novel study system for the investigation of demography and population dynamics in a long-lived species; semi-captive Asian elephants (*Elephas maximus*) used in the timber industry in Myanmar.

1.3 Semi-captive Asian elephants as a model system

The Asian elephant, *Elephas maximus*, is one of three extant species of Proboscidea alongside the two African species' in the genus *Loxodonta* (Roca et al. 2008). Asian elephants are among the world's longest living mammals, with a maximum lifespan of approximately 80 years and a generation time of 20-25 years, and display life-history traits typical of traditional 'k-selected' species (Choudhury et al. 2008, Lahdenperä et al. 2014). The onset of reproduction for females typically begins at the age of 12-13, with an average age at first reproduction of 19.8, which coincides with the peak age of reproduction at the age of 19 (Fig. 1.1a; Hayward et al. 2014, Lahdenperä et al. 2014). At peak reproductive ages between 19-25, approximately 15% of females are reproductive each year, and across lifespan the mean interbirth interval is 5.99 years (Fig. 1.1a; Hayward et al. 2014). The social structure and mating system of Asian elephants is matriarchal, and maternal and female kinship bonds are crucial for reproduction, with calves receiving extensive maternal care until the weaning age of 4-5 (Lahdenperä et al. 2016, Lynch et al. 2019). Mortality patterns in Asian elephants follow the "bathtub" curve, and as with reproduction overall annual mortality rates are low (Fig. 1.1b). Initially, juveniles (ages 0-4) have high annual mortality rates, which decline rapidly until the age of ~10, at which point annual mortality rates are low (<1%), but increase exponentially at the age of 30 (Fig. 1.1b; Lahdenperä et al. 2018). Males typically display higher age-specific mortality rates across lifespan.

The most recent estimate of the total population of wild Asian elephants from Sukumar (2003) found between 41,410 and 52,345 individuals, and other studies have found between 30,000 and 50,000 individuals since 1978 (Olivier 1978, Sukumar 1989, 2003, Santiapillai and Jackson 1990, Sukumar and Santiapillai 1996, Kemf and Santiapillai 2000). Before widespread human-induced decline, Asian elephants were present throughout Asia, from the Tigris-Euphrates valley in what is now the Middle

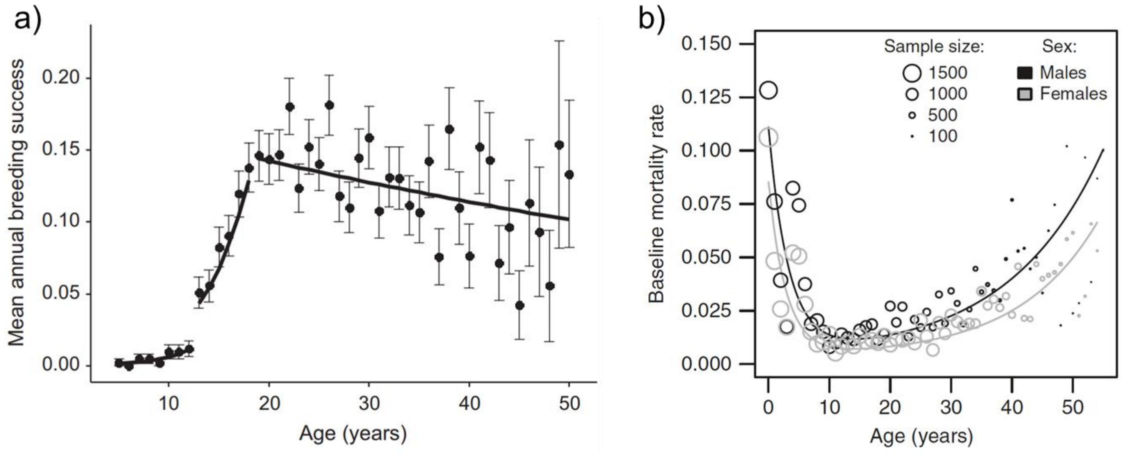

Figure 1.1 – Age-specific reproduction (a) and motality (b) in Asian elephants. a) Mean annual breeding success for female Asian elephants between ages 5-50, points are raw age-specific means with standard error bars, lines are model predicted values. Adapted from Hayward et al. 2014. b) Baseline age-specific mortality rate for male (black) and female (grey) Asian elephants from ages 0-55. Circles are raw mean age-specific mortality values, where the diameter indicates the sample size, lines are model averaged predicted values. Adapted from Lahdenperä et al. 2018.

East to most of South East Asia, India and southern China (Sukumar 1989). The wild population is likely to have been as large as 200,000 at the turn of the twentieth century (Sukumar and Santiapillai 1996). There are large uncertainties in these estimates (Blake and Hedges 2004), but even at the upper limit of current estimates approximately 75 % of the population has been lost in the last century. Furthermore, while it is likely that there has been a decline in this species for centuries, up to a 50 % loss has occurred in the past three generations (20-25 year generation time) (Sukumar 1989, Choudhury et al. 2008). Generally, Asian elephants occur within the forest-grassland ecotone, with a highly fragmented distribution across India and South East Asia (Figure 1.2; Sukumar 1989, Blake and Hedges 2004, Choudhury et al. 2008). The combination of large, recent population declines and a highly fragmented population has resulted in the Asian elephant being listed as endangered on the IUCN red list of threatened species (Choudhury et al. 2008).

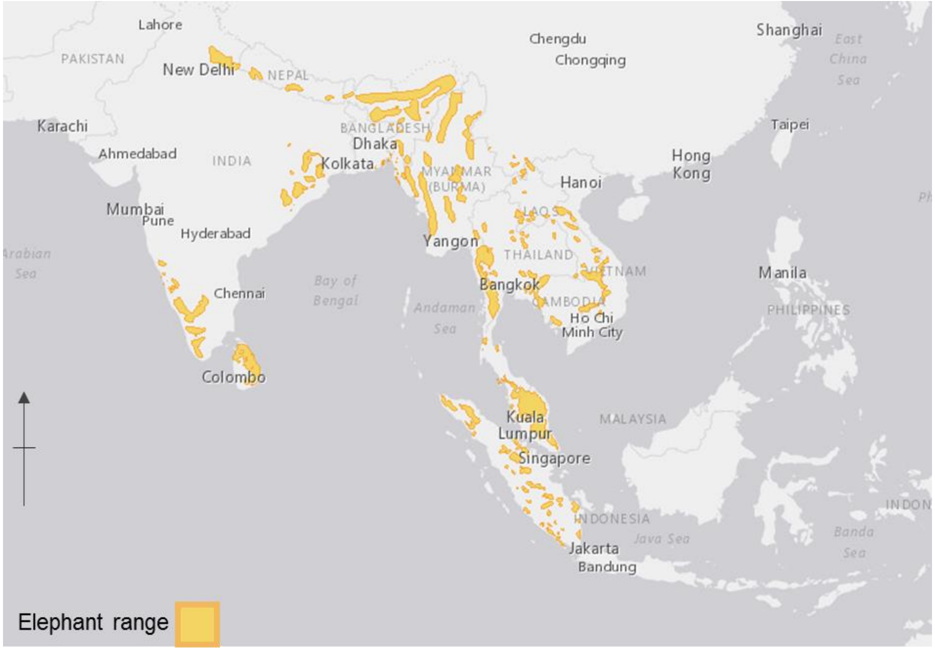

Figure 1.2 – The fragmented distribution of *Elephas maximus* across Asia, adapted from Choudhary et al. 2008.

There are many difficulties associated with monitoring the populations of cryptic forest mammals (Carbone et al. 2001). For Asian elephants, it is recognised that wild population estimates are no more than an educated guess based mainly on expert opinion, and may not fully represented the actual number (Blake and Hedges 2004, Jathanna et al. 2015). More recently and at a smaller spatial scale, rigorous elephant occupancy studies have been carried out using systematic survey designs, and these reduce elements of bias in measures of density (Jathanna et al. 2015). This thorough approach must now be applied across the entire range of Asian elephants, but this will require a significant increase in external investment (Blake and Hedges 2004). As a result, we currently have a very poor understanding of population dynamics in the wild and almost no examples of individual-based demographic data (but see De Silva et al. 2013).

Along with many other endangered species, habitat loss and fragmentation are key drivers of population decline in wild Asian elephants (Sukumar 1989, Leimgruber et al. 2003). By the 1990s, only 51% of the elephant distribution coincided with unfragmented wild areas, but the largest populations were found in unfragmented landscapes (Leimgruber et al. 2003). Furthermore, very little of both unfragmented habitat and the elephants range as a whole occurred within protected areas (Leimgruber et al. 2003). Elephants require a large range with varied habitats in order to forage, and the development of interconnected, protected habitat networks that target large, unfragmented regions will be vital for sustaining this species in the future (Sukumar 1989, Santiapillai 1997, Leimgruber et al. 2003).

Several other threats to Asian elephant populations have been identified. Poaching poses a serious threat to Asian elephants, primarily for the trade of Ivory (Sukumar et al. 1998, WWF 2002, Hedges et al. 2005, Choudhury et al. 2008). As well as reducing the population directly, because of the sexual dimorphism of tusks in Asian elephants, removing only male individuals also influences the sex ratios of remnant populations (Sukumar et al. 1998, Hedges et al. 2005). Furthermore, live elephants are poached for illegal trade in the tourism industry, particularly in Thailand (Nijman 2014). Hunting was also a key threat to populations in the past, but little evidence has been found for elephant hunting in Asia more recently (Corlett 2007). Human-elephant conflict is common, particularly in communities that have suffered large-scale crop and property damage, and this threatens the persistence of populations locally (Zhang and Wang 2003). The role of climate change on Asian elephants has not been explored extensively, but a study by Mumby et al. (2013) found that monthly survival was affected by variation in temperature and precipitation, where survival was highest at intermediate temperatures and with high rainfall. In African elephants, drought conditions are also associated with high infant mortality (Foley et al. 2008). Amidst rapid climate change predicted in the coming decades, a better understanding of how Asian elephants will respond is crucial for conservation efforts.

In order to highlight the key pressures facing Asian elephants and develop more effective conservation strategies, a more detailed understanding of population dynamics, based upon long-term demographic data is needed. Although long-term, individual-based data is not present for Asian elephants as a whole, semi-captive elephants provide a unique opportunity to shed light on some of these issues. Humans have been inextricably linked to elephants in Asia for several millennia; hunter-gathers are assumed to have used elephants for meat and ivory as early as the late Pleistocene (Sukumar 1989, Shell 2019). Following agricultural development, elephants were captured, partially domesticated (4000-5000 BC), and eventually used for military purposes beginning around 1000 BC, and these practises continue today (Sukumar 1989, Lahiri-Choudhury 1991, Shell 2019). As a result, Asian elephants are relatively unique amongst endangered species, with substantial captive population of around 16,000 individuals globally, which is up to a third of the total population (Sukumar 2003). Only ~1000 captive elephants are held in zoos, and the vast majority are used as working animals for tourism, timber logging and ceremonial purposes in range countries such as Myanmar, India and Thailand (Sukumar 2006). Although the majority of captive elephants are primarily managed for economic purposes, conservation management must still be considered, and has now been incorporated in to local management plans in countries such as Myanmar (Win 2018).

The Union of Myanmar is home to the second largest wild population of Asian elephants after India with between 2,000 and 5,000 individuals (Sukumar 2003, Leimgruber et al. 2011). Furthermore, Myanmar has the largest area of unfragmented suitable habitat remaining for *E.maximus* (Leimgruber et al. 2003). In addition to the wild population, Myanmar has a captive working population of approximately 5,000 individuals, which is around a third of the total global captive population and a significant unit of conservation for Asian elephants globally (Sukumar 2003, 2006). The majority of the working elephants in Myanmar are semi-captive and used in the timber trade (Toke Gale 1971). Timber is the second largest export of Myanmar behind petroleum gas; in 2013 the timber trade in Myanmar was worth over $1.6 billion, and the export of rough wood constituted 9% of Myanmar's total exports (CIA 2013, Forest Trends 2014). As a result of the economic importance of timber for Myanmar, approximately 2,700 timber elephants are owned and managed by the state forestry commission, the Myanma Timber Enterprise (MTE), who have kept individual-based records for elephants in the population for over a century. Therefore, the study system of Myanmar's timber elephants provides an opportunity to explore long-term trends in demography and population dynamics for a long-lived species.

Generally, the role of the MTE working elephants is to aid in the extraction of hard wood (primarily teak) from the forest (Toke Gale 1971, Zaw 1997). Elephants drag logs that have been felled, move timber with their foreheads or trunks and aid in clearing log jams that affect rivers and streams along extraction tracks (Toke Gale 1971). There is less human interference in the management of Myanmar's timber elephant population, which can formally be described as semi-captive, and provides a good example of a system that does not fit the binary *in-situ* vs. *ex-situ* definitions (Redford et al. 2011). First, log extraction is only carried out by healthy individuals between the ages of 18 and 53, and there are strict guidelines regarding the number of tonnes that can be extracted by a single elephant based on their age and condition. Pregnant females are also rested from halfway through pregnancy until the calf is one year old (after which they have a reduced workload until taming), and calves are cared for by their mother until the age of 4-5, at which point they are tamed and trained for working activities. Workload regulations are also consistent across the country. Second, timber elephants work for eight months of each year, usually from June to February, and have a rest season during the hottest time of the year. Third, MTE elephants are permitted to roam the surrounding forest outside of working hours i.e. in the hottest part of the day or at night, to forage and interact with other elephants. MTE elephants interact with wild elephants during rest periods, and many captive calves are thought to be sired by wild bulls. Fourth, MTE elephants receive only basic bi-monthly veterinary care, there is no reproductive management in the population and individuals are not culled. Finally, survival and reproduction rates in the MTE population are significantly larger than those in zoo populations (Clubb et al. 2008, 2009), and more comparable to vital rates in wild populations (De Silva et al. 2013).

To extract timber and manage the captive population effectively, the MTE has kept detailed records of the life-history and demography of individuals in the working population for over a century. More accurate and detailed life-history information has been documented for all individuals registered in the population after the 1950s. This information includes: Registration number, name of the elephant, birth origin (wild-caught or captive-born), date of birth (estimate if wild-caught), place of birth (estimate if wild-caught), mother's registration number (if known), mother's name (if known), method of capture (if wild-caught), year of capture (if wild-caught), place of capture (if wild-caught), date of death or last known date alive, and cause of death (Mar, 2007). Elephants are assigned an individual logbook to record their demographic information, and a rider (or mahout) who is responsible for the care and daily work/training of the elephant (Crawley et al. 2019). The presence of such detailed longitudinal data has greatly improved our understanding of the causes for variation in life-history and demography in Asian elephants (e.g. Mar et al. 2012, Mar 2013, Mumby et al. 2013, 2015, Crawley et al. 2017, Lynsdale et al. 2017). Recent findings have highlighted that the environment early in life can have long-term consequences for fitness (Mumby et al. 2015), and the long-term costs of capture for mortality (Lahdenperä et al. 2018). These results suggest that human disturbance has long-term consequences for demography in elephants, but how these changes relate to population dynamics is unknown.

Importantly, the working population in Myanmar has been supplemented through the capture of wild individuals for centuries (Toke Gale 1971). This process is carefully controlled by the Forestry department to minimise the negative impact on the wild population (Olivier 1978, Zaw 1997). Historically, Myanmar used three methods of wild-capture: 1) using large wooden stockades, which trap herds of wild elephants, 2) lassoing wild-elephants whilst riding on the back of specially trained working elephants and 3) immobilising individuals using tranquilizers (Lahdenperä et al. 2018). However, the stockade and lasso techniques were banned in 1985 by the authorities in Myanmar due to the harm they cause to elephants, after which capture was only carried out through immobilisation. Wild-capture itself was formally banned in 1994 when elephants were given formal conservation status in Myanmar (Uga 2000), but capture still continues at lower levels in cases of human-elephant conflict. The historical practise of wild-capture is an interesting case study for the study of population dynamics and demography with human disturbance. First, wild-capture directly reduced the number of wild elephants; from estimates of vital rates and capture rates of 100 elephants per year, the wild population was predicted to be extinct in 31 years and the captive population may also not be sustainable (Leimgruber et al. 2008). Therefore, an assessment of the contribution of wild-caught individuals to the working population and its future viability of the captive population is needed. Second, wild-capture reduces individual survival for over 10 years after capture (Lahdenperä et al. 2018), and so the long-term consequences of wild-capture for demography and population dynamics must explored further. Finally, the supplementation of the captive population with individuals from the wild may have had a large impact on the demographic structure of the population, and provide an opportunity to investigate short-term population dynamics in a human-disturbed system.

1.4 Thesis outline and aims

In this thesis, I present the case study of semi-captive Asian elephants from timber camps in Myanmar as a model system for understanding long-term trends in demography and population dynamics in a long-lived mammal. To achieve this, I use an exceptional long-term, individual-based demographic dataset spanning over half a century, collected from timber camps in Myanmar by the Myanma Timber Enterprise. My findings provide insight into the population dynamics of a long-lived species in a human-dominated system, and provide evidence to improve the conservation management of semi-captive Asian elephants, which are a significant unit of conservation.

First, in chapter 2 I explore the long-term consequences of capture from the wild on lifetime reproduction traits in semi-captive females. Extensive capture from the wild between the 1940s and the 1990s was used to supplement Myanmar's timber elephant population for timber extraction. However, capture from the wild has long-term consequences for mortality that last for over a decade (Lahdenperä et al. 2018), and the stress of capture is also predicted to influence reproduction. I tested the differences between captive-born and wild-caught females in a suite of lifetime reproductive traits, namely, lifetime reproduction probability, age-specific reproduction, age at first reproduction and the intergenerational effect on subsequent calf survival. Importantly, I explicitly investigated how the length of time in captivity and the age at capture influenced the potential negative effects of capture from the wild on reproduction.

Given that capture from the wild has long-term consequences for survival (Lahdenperä et al. 2018), and the direct negative influence on the wild population (Leimgruber et al. 2008), assessing population viability in the semi-captive population excluding capture from the wild is crucial for conservation management. In chapter 3, I address two key questions: i) how did variation in wild-capture between 1960 and 2014 contribute to observed annual population growth rates, and ii) now that systematic capture from the wild is banned, will the current population decline? To address this issue, I constructed an individual-based, stochastic population projection model to assess population viability using demographic data from years when capture was banned (1995-2014). Furthermore, I performed sensitivity analysis to highlight demographic targets for conservation management.

The semi-captive elephant population in Myanmar represents a human-disturbed population that has been supplemented for decades through wild-capture, which has the potential to influence demographic structure and short-term population dynamics. In chapter 4, I investigated how age-structure influenced short-term population dynamics in Asian elephants. First, I quantified the variation in population age-structure between 1970 and 2014. Then, by capturing short-term, transient population dynamics from annual matrix projection models, I decomposed variance in short-term population growth rates into contributions from age-structure and vital rates.

In chapter 5, I explore the impact of climate variation on vital rates in Asian elephants, which is another potentially crucial driver of population dynamics in a changing environment. While a changing climate has been shown to influence demography in long-lived species, the mechanisms of how climate impacts vital rates remains understudied. I tested delayed climate effects on juvenile mortality and peak-age reproduction under two contrasting biological models: *continuous* models where variation in vital rates depend on a direct cumulative effect of the past climate, and *risk window* models where climate in a critical seasonal window influenced subsequent annual vital rates.

Finally, in chapter 6 I present key conservation recommendations for semi-captive Asian elephants in Myanmar based on my findings for the Myanma Timber Enterprise.

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Chapter 2

Capture from the wild has long-term costs on reproductive success in Asian elephants

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2.1 Abstract

Capturing wild animals is common for conservation, economic, or research purposes. Understanding how capture itself affects lifetime fitness measures is often difficult because wild and captive populations live in very different environments and there is a need for long-term life-history data. Here we show how wild-capture influences reproduction in 2685 female Asian elephants (*Elephas maximus*) used in the timber industry in Myanmar. Wild-caught females demonstrated a consistent reduction in breeding success relative to captive-born females, with significantly lower lifetime reproduction probabilities, lower breeding probabilities at peak reproductive ages, and a later age of first reproduction. Furthermore, these negative effects lasted for over a decade, and there was a significant influence on the next generation: wild-caught females had calves with reduced survival to age 5. Our results suggest that wild-capture has long-term consequences for reproduction, which is important not only for elephants, but also for other species in captivity.

2.2 Introduction

Every year millions of animals, including many species of birds, reptiles and mammals, are captured from the wild for study and conservational purposes, or to be involved in the illegal wildlife trade (Mason et al. 2013). Wild-capture can have a negative impact on individual life-history, at least for some species, by reducing immediate or subsequent survival (e.g. Côté et al. 1998, Arnemo et al. 2006), fertility rates (e.g. Ramsay and Stirling 1986, Côté et al. 1998, Alibhai et al. 2001), or offspring survival (e.g. Côté et al. 1998). Generally, however, studies have focused on relatively short timescales, covering only a few months or years after capture, and have not assessed the long-term impacts of capture or how its effects change with an increasing time in captivity or for individuals of different ages. This is important because it is currently unclear how long capture effects persist, and which age-groups are the most vulnerable. The long-term effects of capture can be explored by comparing wild-caught and captive-born individuals living in similar conditions, but such studies have produced mixed results. For example, a recent meta-analysis from 44 species reported that wild-caught animals have a 74% increased odds of reproductive success compared to their captive-born counterparts in captive environments (Farquharson et al. 2018). However, several studies present contradictory results, with lower reproductive success among wild-caught individuals in captivity. These studies are often from animals with slow life-histories and longer lifespans: gorillas (Ryan et al. 2002, Bolton et al. 2012), chimpanzees (Bolton et al. 2012), woolly monkeys (Mooney and Lee 1999), and polar bears (Curry et al. 2015). Some of the differences between wild-caught and captive-born animals can be attributed to the length of time wild-caught individuals have been in captivity (Kohler et al. 2006) (time since capture has generally been omitted but see Lahdenperä et al. 2018), selective survival (Lahdenperä et al. 2018), inbreeding depression and adaptation to captivity (Mason et al. 2013), early maternal effects (Mason et al. 2013), or differences between the captive and wild environments (Mason 2010).

Capture can influence an individual's life-history in the long-term through behavioral, physiological and immunological mechanisms (Lahdenperä et al. 2018). Reproduction may be affected by capture in several ways, both directly and indirectly. For example, drugs used in the capture process to sedate larger mammals can have potentially harmful effects on an animal's reproduction (Alibhai et al. 2001) if they are used at an incorrect dose. The capture of pregnant females can also lead to injuries and changes in foetal development or even abortion of the foetus (Adams et al. 2017). Stress can impair all aspects of fertility, from implantation of the ovum to permanent anoestrus (Alibhai et al. 2001). Furthermore, interactions with humans (handling/breaking/taming), changes in social system, unfamiliar living conditions, and intra- and interspecies competition can also exacerbate the adverse effects of capture on reproductive function (Morgan and Tromborg 2007).

Elephants have been a target of large-scale wild-capture for centuries (Lair 1997, Nijman 2014). Today, elephants are caught and held in zoos or other captive facilities under CITES, for working purposes (Lair 1997), or for illegal trade (mostly for tourism) in Asia (Nijman 2014). Elephants are slow reproducers, with long inter-birth intervals, gestation periods, and offspring dependency (Lahdenperä et al. 2016). Zoo elephants are also known to have several difficulties in breeding: many reproductive age females do not experience normal oestrus cycles and are infertile (Clubb and Mason 2002). In addition, abnormal deliveries and stillbirths are major issues in captive elephant populations (Hermes et al. 2008). However, these findings reflect the vast differences between zoos and wild environments (Clubb and Mason 2002), and it is largely unknown whether capture itself has an impact on reproductive success in elephants. Specifically, to determine capture effects we need long-term data and a detailed comparison of individuals of different birth-origins that live in a similar environment with shared food and disease sources, similar social interactions, and similar breeding opportunities.

Here we use an exceptionally detailed longitudinal, multi-generational dataset of timber elephants from Myanmar to study the effects of capture on lifetime reproductive success in Asian elephants. Myanmar has the largest captive population of Asian elephants in the world, with approximately 2700 government-owned individuals used in the timber logging industry. Historically, approximately half of the timber elephant population has been wild-caught. Wild-caught and captive-born elephants live, forage, and work side-by-side in the same environment and are governed by the same regulations and practices concerning data recording, workload, and rest periods. The dataset includes longitudinal information of reproductive events for 2,685 females over 64,823 elephant-year observations, with 1,362 wild-caught females (captured between 1951-2002) and 1,323 captive-born females (born between 1942-2011). Consequently, the dataset offers a unique opportunity to test the effects of capture on female lifetime reproductive success in a long-lived and slow reproducing mammal. Specifically, we compare lifetime reproduction probabilities, age-specific reproduction rates, age at first reproduction, and calf survival between wild-caught and captive-born individuals. Importantly, we investigate whether the effect of wild-capture on reproduction depends on an individual's age at capture and the time spent in captivity. Currently, there is a great need for animal welfare specialists, veterinarians, and ecologists to identify the potential effects of capture from the wild, especially in endangered species, for the success of the individuals and consequently populations.

2.3 Methods

Study population

The MTE (Myanma Timber Enterprise) elephants are used in the timber logging industry, and work in forest camps as riding, transport, and draft animals (Zaw 1997). At night and during rest periods, all elephants forage in the forest unsupervised. Breeding rates are natural, with many captive-born calves thought to be sired by wild bulls, and calves born in captivity are cared for by their biological and allo-mothers.

Our dataset has been collated from elephant log-books (monitoring life-history information for each individual, see e.g. Lahdenperä et al. 2018) and annual extraction reports archived and maintained by the MTE. Individual log-books are maintained by local veterinarians and regional extraction managers in order to check each elephant’s health condition and working ability each month. While the ages of captive-born elephants are known from precise dates of birth, wild-caught elephants are aged by comparing their height, body condition, and physical features with captive-born elephants of known age. The error in these estimates is unknown, but is likely to be within a couple of years for young animals that continue to grow (under 20), which form the majority of those captured (Lahdenperä et al. 2018).

The capture of elephants

The capture of wild elephants to supplement the timber elephant population has been controlled by the government. The estimates differ, and one stated that nearly 17,000 elephants were captured from 1911-1982 in Myanmar (Lair 1997). Capture was formally banned in Myanmar during the 1990s (Lair 1997), but smaller scale capture continues, primarily focusing on elephants involved in human-elephant conflict, yet also from illegal captures. Capture was usually practiced in the cool season by three alternative methods (Lair 1997): by stockades (“kheddah”) for whole groups, or immobilization by sedation, and lassoing (“milarshikar”) for specific individuals (for more detailed descriptions of the capture methods, see Lahdenperä et al. 2018). Government figures estimate that the mortality rates for all methods is between 5% and 30%, with most of these deaths happening during the months following capture (Lair 1997).

All captured elephants undergo an initial taming or “breaking” procedure immediately after capture that lasts 4-12 weeks, depending on the temperament of each elephant. Older elephants generally require a longer period of taming than animals caught from the wild at younger ages or captive-born individuals, which are tamed using similar methods (Min-Oo 2010). The taming undoubtedly incorporates stress and compromises welfare, especially during the first few days. Elephants commonly resist training and reject food/water for the first few days but are referred to as “broken” when they begin to accept food, water, and human contact later in taming. Captive-born elephants are also tamed around the age of 4-5 (Min-Oo 2010). Because captive-born elephants grow up in regular contact with both their maternal herd and mahouts (elephant handlers), and are rarely subjected to harsh taming, their training is thought to be considerably less stressful.

After taming, elephants are classified as trained elephants and assigned permanent individual registration numbers, mahouts, and logbooks to record biodata (sex, temperament, musth, mating, calving, veterinary intervention etc.). The government enforces strict workloads and rest periods for all individuals: all state-owned elephants are subject to the same regulations for hours of work per week, working days per year, and tonnage to extract per elephant according to their size and condition. Elephants 'retire' at 55, but their records are maintained until death. Working females are given rest from mid-pregnancy (11 months into gestation) until the calves reach their first birthday. Mothers are then used for light duties but are allowed to nurse the calves on demand.

Lifetime reproduction probability

We first investigated whether captive-born and wild-caught elephants differed in their lifetime reproduction probability using a linear mixed effects model. We only included females (both wild-caught and captive-born) that lived beyond the mean age at first reproduction (19.38 ± 5.59) and wild-caught females that were caught before this age, which resulted in 1,678 females (wild-caught = 766, captive-born = 912). Lifetime reproduction was scored as a time-invariant binomial trait (0 = did not produce any calves during lifetime; 1 = produced at least one calf during lifetime), and analysed using a generalized linear mixed-effects model (GLMM) with a binomial error structure and a logit link function in the R package lme4 (Bates et al. 2015, R Core Team 2017). The main effects of interest were the birth origin, included as a two-level factor (wild-caught vs. captive-born), and the age at capture (integer, range = 0-19 years for wild-caught females), which was included as an interaction term only with birth-origin. We set the age at capture as 0 for all captive-born elephants, ensuring that this effect did not exert any influence on the parameter estimation. We also controlled for other covariates as fixed effects, namely, whether the individual was censored (1 = died before the end of the study, 0 = was censored, e.g. Hayward et al. 2014), lifespan at death/censoring (mean 39.3 ± 11.8, range 19-76) and birth cohort (factor, each decade between 1930 and 1990), and we included an intercept-only random effect of regional division in Myanmar (see S1.1 for further details). Here, and in all subsequent reproduction models (excluding calf survival analysis), we assessed the significance of the terms using likelihood ratio tests (LRTs) with the Chi-squared ($\chi 2$) distribution.

Age-specific reproduction probability

Using the records of 2,685 females, we then examined whether captive-born and wild-caught females differed in their age-specific annual reproduction probability between ages 5-64 within a logistic regression model selection framework. The maximum age limit was selected because there were few births for females older than 64, and few ages of death or ages at censoring exceeding 64 years (max.

captive-born = 68, max. wild-caught = 76). To avoid the possibility of including birth events and pregnancies from wild-caught females before they entered the captive population (which would over-estimate their reproduction in captivity), we only included reproductive data from wild-caught elephants from two or more years after their year of capture (minimum time since capture = 2 years). Both captive-born and wild-caught individuals exited the analysis at their last known age alive, or at an age of censoring <= 64. We constructed a dataset where the annual reproduction of each female was scored as a binomial trait, where 0 = did not produce a calf in a given year of life and 1 = produced at least one offspring. We assessed age-specific reproduction probability using generalized linear mixed-effects models (GLMMs) with a binomial error structure and a logit link function in lme4. The data used in this analysis was comprised of 64,823 age-event datapoints from the 2,685 females (1,362 wild-caught females).

First, we built a 'base' model, in which the main effect of interest was birth origin to study the effect of capture on age-specific reproduction. We explicitly tested how the time since capture influenced reproduction probability using an interaction variable between birth origin and log-transformed years since capture (but no main effect, range = 2-54) following Lahdenperä et al. (2018). As with age at capture, time since capture was 0 for all captive-born elephants. We also controlled for other covariates, namely, whether or not an individual was censored, lifespan (mean 35.4 ± 16.5, range 5-76), birth cohort (each decade between 1920 and 2010) to control for temporal variation in keeping practices and vital rates (Jackson et al. 2019), and average-age (average of all ages the individual was included in the data) to control for selective (dis)appearance of individuals due to different entry and exit ages (Verhulst et al. 2014). Individual identification number and the regional division in Myanmar were included as intercept-only random effects terms in the final models to control for non-independent datapoints from the same individuals and spatial variation in vital rates (see S1 for further details).

We then explored the effect of age on reproductive success using a model selection framework, first including age as a linear term, a quadratic term, or as a factor, and then using threshold or piecewise regression (Toms and Lesperance 2003) models. Threshold models enabled us to capture complex non-linear relationships with age using the combination of more simple linear changes between threshold ages. We explored the fit of one-, two-, and three-threshold models, where annual breeding success changed as a linear function of age in two, three, or four age groups, respectively (following Hayward et al. 2014). We used all combinations of ages between 6 and 63 for the locations of the thresholds (21,089 combinations in total), which were selected at each one-year interval. The change in breeding success either side of (and between) threshold ages was captured in all models using an interaction between the linear age term and the age group. Interactions between the birth origin and age, birth origin and age-group were also included in all models to allow the effect of capture to change with age according to the thresholds. We then performed model selection (see S1.2 for further details) and compared the predictive performance of all models using the Akaike Information Criterion (AIC)(Burnham and Anderson 2003), where the best model had the lowest AIC value (see S1 for details). Finally, to test whether differences in lifetime reproduction probability influenced age-specific patterns, we repeated the age-specific reproduction model selection process, but only including females that reproduced at least once in their lifetime. This dataset included 38,492 time-event datapoints from 1175 reproducing females (wild-caught = 595, captive-born = 580).

Age at first reproduction

We assessed whether wild-caught females had a delayed onset of reproduction by investigating the age at first reproduction. To ensure that we captured the true age at first reproduction of wild-caught females, we only included wild-caught females caught before the age of 13 (onset of reproduction, mean reproduction probability = 0.002), and also only those captive-born females with an age at first reproduction after 13 (97% of all reproductive captive-born females). We tested the effect of capture on the log-transformed age at first reproduction for 843 females (wild-caught = 283, captive-born = 560), using a linear mixed effects model in lme4. The main fixed effect of interest was birth origin. We also included censoring, lifespan and birth cohort, and we included regional division as an intercept-only random effect.

Calf survival and mother's birth origin

To investigate the life-history implications of capture from the wild on subsequent generations, we investigated the survival of 2,423 calves (born between 1960-2016) to 5 years (calves from captive-born mothers = 1,290, calves from wild-caught mothers = 1,133; see S1.1 for more details). Survival to age 5 was selected because age-specific mortality is highest in the first 5 years of life and calves are separated from their mothers for training at this point (Mar et al. 2012). We constructed a time-event dataset, where the annual survival of each calf from birth to age 5 was scored as a binomial trait (0 = died during the focal year and 1 = survived the focal year), resulting in 10,192 datapoints (calves from captive-born mothers = 5,411, calves from wild-caught mothers = 4,781). We assessed age-specific mortality using GLMMs with binomial errors and a logit link function with a GLIMMIX procedure in SAS (SAS Institute Inc., release 9.4, 2014).

The main variables of interest were included similarly to previous analysis; the mother's birth origin (binary, captive-born vs. wild-caught) and the log-transformed time since the capture of the mother at each calf age (i.e. each focal year; interaction with mother's birth origin only). For calves born to wild-caught mothers, the time since mother's capture varied from 0 to 52 years at the time of the calf's birth. Several terms (e.g. calf age, maternal age and presence, calf sex and inter-birth interval) were controlled for in the analysis that are known to have an influence on calf survival probability in the population(Mar et al. 2012, Lahdenperä et al. 2016), for more details see S1.

2.4 Results

Differences in reproductive intensity and timing between captive-born and wild-caught females

First, we found that wild-caught females had a significant reduction in their lifetime reproduction probability, even when captured before the mean age of first reproduction (19 years) (figure 2.1; table S1.1a). Wild-caught females had a lifetime reproduction odds ratio of 0.72 relative to captive-born females, such that they were 28% less likely to ever reproduce, taking into account known differences in lifespan (Lahdenperä et al. 2018). Furthermore, females that were older at the time of capture were significantly less likely to reproduce during their lifetime (table S1.1a).

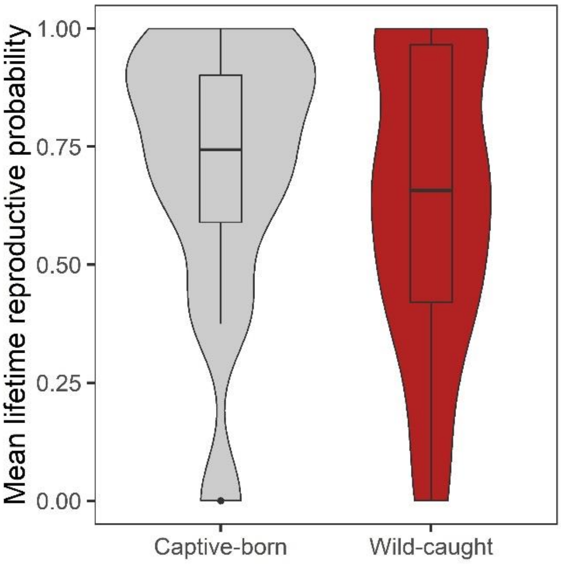

Figure 2.1 Wild-caught females had a lower probability to reproduce during their lifetime than captive-born females. Box plots indicate the median and interquartile range, violin plots indicate the density of raw (mean) data averaged for each birth cohort (decade), lifespan (grouped in to 20-year bins) and censoring group (dead or censored) between captive-born (n = 912) and wild-caught (n = 766) females.

Second, we found striking evidence of a reduction in the annual reproductive probability of wild-caught females at almost all ages, compared to females born in captivity that are not subjected to capture stress (table 2.1). The raw mean annual birth rate for all females across the study period was 0.043 ± 0.20 for all ages and birth origins, such that approximately 4% of females were breeding in a given year. We found that age-specific reproduction probability for all females was best described by a three-threshold model, such that breeding success changed as a linear function of age across four age groups (table S1.2; figure S1.1; figure 2.2). First there was an initial period of negligible reproductive success (mean = 0.002 ± 0.043) with a small increase between the ages of 5-12. Second, a rapid exponential increase in female reproductive success occurred from the age of 13 to the age of 19. The peak in reproduction occurred between the age of 19 and 20, at which the raw mean annual birth rate was 0.061 ± 0.24 for all females. Third, between the ages of 20-44, the age-specific reproductive success declined slowly, and finally, there was a rapid decline between ages 45-64.

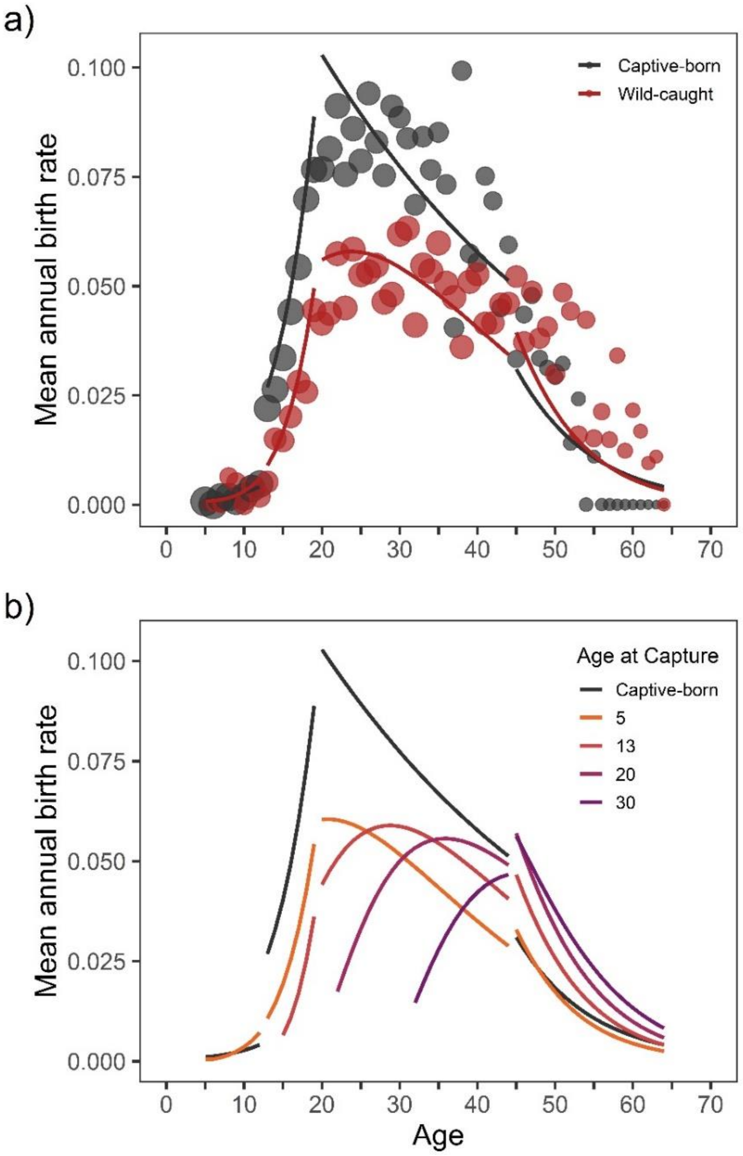

Figure 2.2 Wild-caught females had reduced age-specific reproduction probabilities compared to captive-born females (a) and the effect was more pronounced for females caught at older ages (b). The figures show age-specific patterns of reproduction from the best-fit threshold regression model (age groups: 5-12, 13-19, 20-44, 45-64) for all females (1,323 captive-born females and 1,362 wild-caught females). a) Points are the raw mean annual predicted birth rates at each age for all females, with the size of the points denoting the square root of the sample size at each age (range = 11-1,323 time-event data points). Lines are the mean predicted values for an extended dataset (observed females but extended to span all ages) of the observed females in the 1960 birth cohort, which were most similar to raw mean birth rates. b) Differences in mean predicted values from an extended dataset of observed females in the 1960 birth cohort between captive-born females (grey) and wild-caught females of different ages at capture (coloured lines).

However, the significant reduction in age-specific reproduction probability for wild-caught individuals depended on the age of the female (table 2.1, figure 2.2a). There was little discernable difference between captive-born and wild-caught females between the ages of 5-12 when fertility probability was low for all animals (raw mean annual birth rates of 0.002 ± 0.043 and 0.003 ± 0.053, respectively). At the onset of reproduction between 13 and 19, captive-born females had a significantly larger mean annual reproductive rate of 0.046 ± 0.21 relative to 0.022 ± 0.15 for wild-caught females. At the age of 13, a wild-caught female had an odds ratio of 0.36 with respect to a captive-born female, such that a wild-caught female was approximately 65% less likely to reproduce (figure S1.2). At peak reproductive age (19 years), captive-born females from the 1960 birth cohort (closest to mean age-specific birth rates, figure S1.3) had a mean predicted reproductive rate of 0.105 ± 0.042 relative to 0.057 ± 0.031 for wild-caught females, who were 42% less likely to reproduce (odds ratio = 0.58). Then, there were general declines in annual reproductive rates between the ages of 20 and 44. These were more pronounced in captive-born females (figure 2.2a), though their annual reproductive rate (raw mean annual birth rate of 0.078 ± 0.27) remained above that of wild-caught females (0.050 ± 0.22) (table 2.1). The mean annual reproductive rate in the oldest age-group (between ages 45 and 64) was 0.032 ± 0.18. Interestingly, wild-caught females had a higher annual reproductive probability with respect to captive-born females at these advanced ages (raw mean annual reproduction rates of 0.034 ± 0.18 and 0.027 ± 0.16, respectively; figure 2.2a). Given that wild-caught females have previously been found to have increased mortality (Lahdenperä et al. 2018), selective disappearance likely plays a role in this finding. The average odds ratio for wild-caught females aged 45-64 ranged between 1.63-1.95, meaning that, on average, wild-caught females were between 63%-95% more likely to reproduce than captive-born females between 45 and 64.

The effect of capture on age-specific reproduction also depended on the length of time spent in captivity, with a significant positive effect of the interaction between birth origin and log-transformed years since capture (table 2.1; figure 2.3). Specifically, there was a large reduction in annual reproductive rate compared to captive-born females immediately (2 years) after capture, which then increased slowly. It took approximately 12 years before wild-caught females reached the mean annual reproductive rate of captive-born females (figure 2.3). Furthermore, the decrease in reproductive rates immediately after capture was the most pronounced in wild-caught females that were captured at older ages (figure 2.2b; figure S1.2). Females caught at the ages of 13, 20, and 30 had reproductive odds ratios of 0.18, 0.07 and 0.08 two years after capture, relative to captive-born females (figure S1.2).

Table 2.1 Parameter estimates from the best-fit model of age-specific reproduction for all females (n = 2685; 64,823 elephant-year observations), fit using binomial generalised linear mixed effects models (GLMMs). Estimates and standard errors are present on the logit scale. The colon (:) depicts interaction terms. LRT denotes likelihood ratio test statistics.

Fixed effects	**Estimate**	**Standard error**	**LRT χ^2**	**p value**
Intercept	-7.20	1.00		
Age	0.20	0.10	273.3	<0.001
Age group			1061	<0.001
ages 13-19	1.53	1.03		
ages 20-44	6.37	0.94		
ages 45-64	9.32	1.22		
Birth origin			179.9	<0.001
wild-caught	-2.41	0.53		
Lifespan	-0.04	0.01	11.79	<0.001
Average age	0.10	0.02	17.59	<0.001
Birth cohort			74.27	<0.001
1930	-0.51	0.29		
1940	-0.55	0.29		
1950	-0.96	0.30		
1960	-1.24	0.31		
1970	-1.56	0.32		
1980	-1.85	0.34		
1990	-1.46	0.35		
2000	-2.21	1.00		
2010	-7.30	11.89		
Censored			1.50	0.221
dead (1)	0.08	0.07		
Age:Age group			143.1	<0.001
age:ages 13-19	0.01	0.10		
age:ages 20-44	-0.23	0.10		
age:ages 45-64	-0.31	0.10		
Age:Birth Origin			26.70	<0.001
age:wild-caught	-0.06	0.01		
Age group:Birth Origin			24.06	<0.001
ages 13-19:wild-caught	-1.61	0.47		
ages 20-44:wild-caught	-1.69	0.47		
ages 45-64:wild-caught	-1.01	0.54		
Birth Origin:ln Years since capture			95.35	<0.001
wild-caught:ln years since capture	1.66	0.18		

Random effects	**Variance**	**Standard deviation**
Individual ID	0.42	0.65
Regional division group	0.06	0.23

Third, the lower age-specific reproduction of wild-caught females was not only due to a lower lifetime reproduction probability, because wild-caught elephants that reproduced at least once also had lower age-specific reproduction rates. When restricting the dataset to include only reproductive females, wild-caught females had reduced age-specific reproduction rates, particularly at peak reproductive ages (figure S1.4; table S1.3), consistent with the previous analysis. There were slight differences in the thresholds for the best model for reproducers, which included four threshold age-groups at ages 5-12, 13-20, 21-51, and 52-64 (figure S1.4; table S1.3). Fourth, we found that wild-caught females started to reproduce later than captive-born females. The age at first reproduction for wild-caught females captured before the age of 13 was significantly later than for captive-born females (figure 2.4; table S1.1b): the mean age-at first reproduction for captive-born females was 2 years earlier (21.2 ± 6.1) than wild-caught females (23.3 ± 7.25 years).

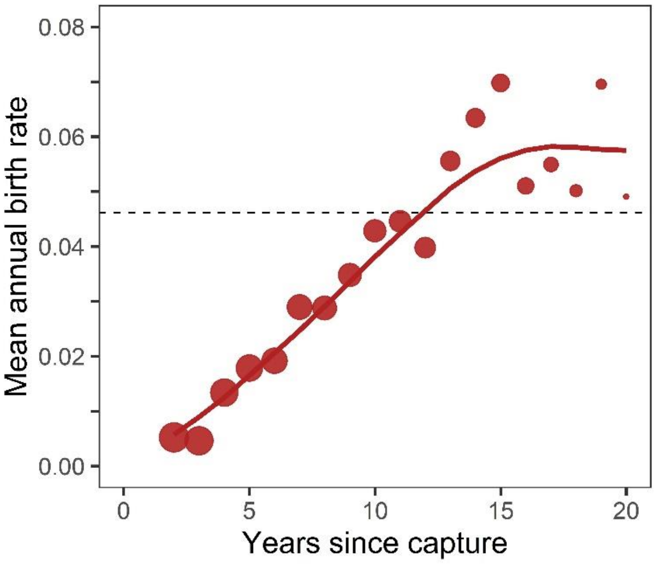

Figure 2.3 Age-specific reproduction for wild-caught females was lowest immediately after capture, and it took approximately 12 years before wild-caught females reached the mean annual reproductive rate of captive-born females (1,362 wild-caught females and 1,323 captive-born females- dashed line). figure shows mean annual birth rates for wild-caught females with the number of years since capture across all ages. Points are raw mean annual birth rates, with the size indicating the sample size (range = 856-1,338). Lines are the mean fitted values from the best-fit model including all females. Dashed line indicates the raw mean annual birth rate for captive-born females across all ages.

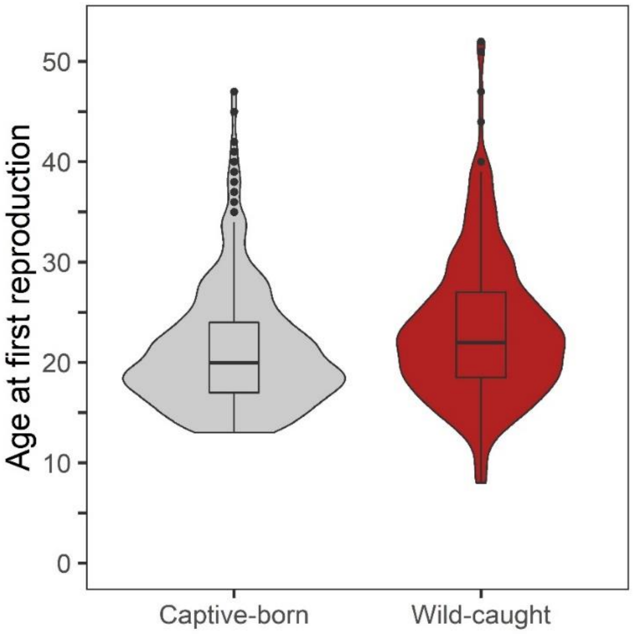

Figure 2.4 Wild-caught females had a later age at first reproduction than captive-born females. Box plots indicate the median and interquartile range, violin plots indicate the density of raw age at first reproduction data for captive-born (n = 560) and wild-caught females (n = 283).

Cross-generational effects of wild capture

Finally, we found evidence that wild-capture also affected the life-history of the following generations living in captivity. Elephants suffer from high infant mortality (Mar et al. 2012), with 23.5% of calves born in captivity in our sample dying before the age of 5. We found that the calves of wild-caught mothers had an increased mortality before the age 5 when compared to the calves of captive-born mothers. However, this effect depended on the number of years since the capture of the mother (table S1.4). Calf mortality was highest in the year immediately after their mother's capture, with an annual mortality rate of 0.134 ± 0.076 for the calves of wild-caught females compared to 0.058 ± 0.029 for the calves of captive-born mothers, decreasing thereafter (figure 2.5). The odds ratio of calf death in the first year was 2.50 compared to calves from captive-born mothers, declining exponentially with increased time since capture (figure S1.5). An equal odds ratio of calf mortality between wild-caught and captive-born females was only achieved 16 years after the mother's capture from wild.

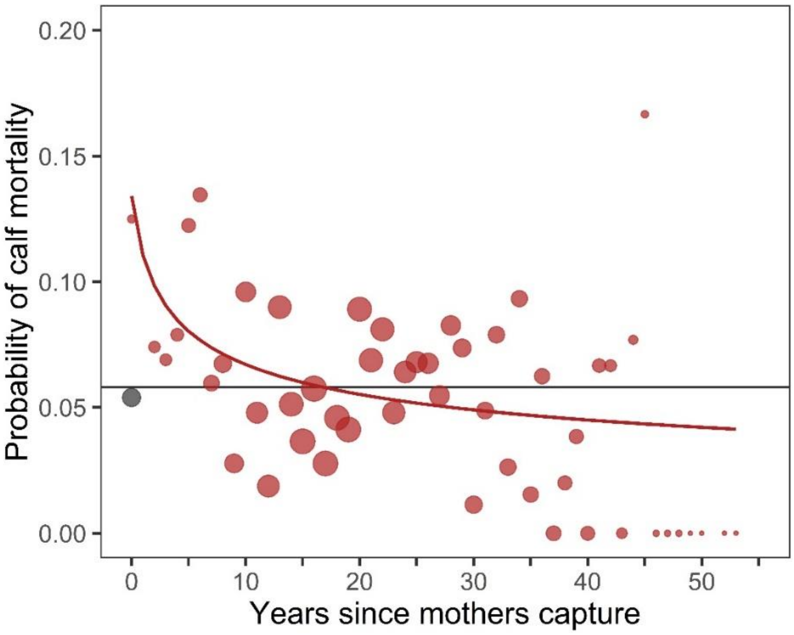

Figure 2.5 The wild-capture had effects on the next generation as calves of wild-caught mothers had an increased mortality to age 5 compared to the calves of captive-born mothers, the effect being strongest during the first years after mother's capture from the wild but lasting on average 16 years (n = 10,240 observations, 2,471 calves, 1,033 mothers). The red points are raw mean mortalities for calves from wild-caught mothers, with the size indicating the sample size (range = 1-226). The red line shows predicted values for calves born to wild-caught mothers as a function of the years since the mothers capture. The grey dot indicates the raw mean mortality of calves from captive-born mothers (n = 5,411). The black line shows the predicted value for calves born to captive-born mothers. Predicted values are mean values from birth to age 5 and calculated across other reference categories and mean values of terms in the model. One raw mortality value for calves of wild-caught mothers is not displayed (mortality of 0.28 1 year after capture).

2.5 Discussion

Large numbers of animals are routinely captured from the wild for many purposes including research and conservation, but surprisingly little is known about the consequences of capture for the subsequent long-term performance of those individuals. Using unique records of wild-caught and captive-born Asian elephants in Myanmar, we demonstrate for the first time that capture from the wild has lasting adverse effects on lifetime reproductive success in a long-lived mammal. Furthermore, these effects are most likely due to the capture process itself, as wild-caught and captive-born females experience the same conditions in captivity, and the effects wane with the number of years spent in captivity.

These results are timely given that 60-80% of the current captive elephants in zoos are wild-caught (Clubb and Mason 2002), and that the capture of wild elephants continues to supplement waning tourism and working populations worldwide (Clubb and Mason 2002, Nijman 2014). That wild-caught animals take more than 10 years to recover from their experiences, show higher lifetime infertility, and transfer the negative effect of capture on to the survival of the next generation in a long-lived social species such as the Asian elephant, has implications for captive animal welfare and research. Whilst some captive animals are healthier, live longer and have a higher reproductive success than their wild counterparts, other species perform less well in captivity (e.g. Mason 2010). Furthermore, depending on the species, wild-born animals constitute different proportions of the number of animals in captive populations (Kohler et al. 2006, Mason et al. 2013). This raises the questions of whether the observed negative effects of captivity are actually due to negative long-term capture effects, and whether captive populations can be used as reference groups for species-typical parameter values (Mason 2010). In addition to these long-term effects on captive populations, an increasing human population has seen more animals taken from the wild, imposing a strong negative impact on wild population growth rates (Leimgruber et al. 2008).

We found a consistent pattern of reduced reproductive success in wild-caught females compared to captive-born females. The adverse effects were stronger in elephants that were caught at older ages and immediately after capture from the wild and lasted for more than a decade. These findings are likely due to both the immediate and long-term effects of the capture process. First, captures during critical phases of gestation may lead to the abortion of fetuses, premature births, or reduced calf survival (Alibhai et al. 2001, Adams et al. 2017). Calf mortality was highest during the first year after capture, suggesting that mothers who were pregnant during capture may have suffered from physical trauma or complications risking the calf's subsequent survival. Second, reduced calf survival and impaired reproduction may be the result of high acute and chronic stress due to capture (Baker et al. 2013), also depending on an individual's age (Baker et al. 2013). For example, through the action of glucocorticoids, chronic psychological stress can impact reproductive hormone levels, function of the placenta, and fetus development (Joseph and Whirledge 2017). In support of this, we found that wild-caught females were less likely to reproduce during their lifetime, had an increased age at first reproduction, and a reduced age-specific fertility at peak ages. Other studies have found negative impacts of capture on reproduction, for example in chimpanzees (Bolton et al. 2012), gorillas (Ryan et al. 2002, Bolton et al. 2012), black rhinos (Alibhai et al. 2001), polar bears (Ramsay and Stirling 1986), pampas deer (Ungerfeld et al. 2008), and mountain goats (Côté et al. 1998), though many of these studies were carried out over short time scales or did not account for the length of time in captivity. Third, capture can lead to decreases in activity and feeding (Morellet et al. 2009), lower body condition (Cattet et al. 2008) and social disruption (Shannon et al. 2013), further reducing the long-term reproductive performance of wild-caught animals.

Interestingly we found that wild-caught females were more likely to reproduce at old ages than captive-born females. This finding can be explained partly by selective (dis)appearance (van de Pol and Verhulst 2006), which is known to bias fitness estimates in demographic studies. Previously, we have found that wild-caught Asian elephants had high mortality immediately after capture from the wild, which, similar to the results here, lasted for a decade after capture (Lahdenperä et al. 2018). Therefore, given the increased mortality rates following capture and an initial bias for capturing animals in good condition (Lahdenperä et al. 2018), it is feasible that only the most robust wild-caught animals or those more adapted to semi-captivity contribute to older age reproductive rates by being able to continue reproducing even at such advanced ages. Given that we controlled for individual variation, lifespan, censoring, and average age in age-specific analysis, our results present good evidence that there are strong selective disappearance effects. Furthermore, wild-caught females have a delayed first reproduction, lower reproductive output at peak reproductive ages and lower calf survival but continue to reproduce for longer, and thus exhibit a shift in reproductive strategy until older ages. Poor early life conditions have previously been associated with a delay in reproduction (Lindström 1999) and a change in life-history trajectories (e.g. Mumby et al. 2015) in a range of species, and our results suggest that similar cross-generational effects may arise from (presumably stressful) wild-capture. This highlights the importance of understanding the long-term evolutionary consequences of human disturbance and wild-capture for wildlife populations.

The long-term effects of capture are currently not considered in research and conservation programs, but our results suggest that the life-history of captured individuals may differ substantially compared to those born in captivity. Current evidence suggests that some species, often those with longer lifespan or slow life-history, may be more prone to the negative effects of capture (Mooney and Lee 1999, Ryan et al. 2002, Curry et al. 2015, Jett and Ventre 2015, Tidière et al. 2016). We therefore welcome more long-term studies in other animals to identify the species and individuals most at risk from capture. In elephants, although capture might be inevitable sometimes (e.g. for conservation, veterinary and anti-poaching purposes), consistent large-scale wild-capture should be avoided to supplement captive populations because it fails to provide a sustainable long-term strategy (Leimgruber et al. 2008, Jackson et al. 2019) and may have far reaching evolutionary consequences for captive populations.

2.6 Acknowledgements

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Chapter 3

Long-term trends in wild-capture and population dynamics point to an uncertain future for captive elephants.

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3.1 Abstract

Maintaining sustainable populations in captivity without supplementation through wild-capture is a major challenge in conservation that zoos and aquaria are working towards. However, the capture of wild animals continues for many purposes where conservation is not the primary focus. Wild-capture hinders long-term conservation goals by reducing remaining wild populations, but the direct and long-term indirect consequences of wild-capture for captive population viability are rarely addressed using longitudinal data. We explored the implications of changes in wild-capture on population dynamics in captivity over 54 years using a multigenerational studbook of working Asian elephants (*Elephas maximus*) from Myanmar, the largest remaining captive elephant population. Here we show that population growth and birth rates declined between 1960 and 2014 with declines in wild-capture. Importantly, wild-caught females had reduced birth rates and a higher mortality risk. However, despite the disadvantages of wild-capture, the population may not be sustainable without it, with immediate declines owing to an unstable age-structure that may last for 50 years. Our results highlight the need to assess the long-term demographic consequences of wild-capture to ensure the sustainability of captive and wild populations as species are increasingly managed and conserved in altered or novel environments.

3.2 Introduction

Captive management and conservation are considered to be important stop-gap measures in efforts to ensure that wild animal populations are sustainable (Redford et al. 2011, IUCN 2016). Although *ex situ* conservation strategies have been implemented successfully (e.g. Toone and Wallace 1994), captively managed populations are often small, and fail to be representative of the species as a whole, genetically robust or self-sustaining (Redford et al. 2011). Many studies have found that zoo populations are unsustainable (Lees and Wilcken 2009, Lacy 2013). An assessment of 87 mammalian zoo populations revealed that only half were breeding to replacement rate (Lees and Wilcken 2009). Although an increased effort is now being placed into maintaining sustainable captive populations through captive breeding and reproductive technology (Lacy 2013, Saragusty et al. 2016), captive populations in zoos and aquaria have long been supplemented through wild-capture (Faust et al. 2006). However, capture from the wild may impose long-term demographic consequences for captive populations (Lahdenperä et al. 2018), and therefore its implications for population viability must be explored.

Importantly but often overlooked, animals are also removed from the wild and kept in partially free-ranging or semi-captive conditions for many reasons other than conservation (Dierenfeld and McCann 1999, Golosova et al. 2017), most notably as research animals or for economic purposes as working animals (Mar 2007, Vors and Boyce 2009, Mason et al. 2013). Large numbers of individuals may be captured from the wild and conservation is not the primary goal of many semi-captive populations, but conservation management must still be considered, particularly where IUCN protection is in place (Win 2018). However, few systems enable the assessment of how variation in wild-capture rates influences demography and population viability in captivity. One such species is Asian elephants (*Elephas maximus*), which are endangered but have a captive population of over 16,000 individuals, up to a third of the total population, increasing the importance of captive management (Sukumar 2003). Asian elephants are slow reproducers, exceptionally long-lived (mean lifespan = 38.4 ± 11.6 years and age at first reproduction = 19.8 ± 5.7 years (Lahdenperä et al. 2014)) and have a matriarchal social structure that has a large impact on survival (Lahdenperä et al. 2016), making them sensitive to anthropogenic disturbance and slow to recover (Turkalo et al. 2016). In the wild, although there have been global population estimates and some assessments that indicate large population declines (Sukumar 2003, Leimgruber et al. 2008, De Silva et al. 2013), we have a poor understanding of population dynamics (Blake and Hedges 2004). In captivity, many studies have emphasized that elephant populations managed in zoos are not self-sustaining (Myroniuk 2004, Faust et al. 2006, Clubb et al. 2009), but this constitutes only a small number of individuals globally (~1000 individuals; (Sukumar 2006)). The vast majority of captive Asian elephants are partially free-ranging, semi-captive working animals in range countries, used primarily for timber logging, tourism and ceremonial purposes (Sukumar 2006, Mar 2007). Traditionally, wild elephants were captured to supplement the working population, which has been monitored in countries such as Myanmar for over a century (Toke Gale 1971, Mar 2007). Although the majority of captive elephants are primarily managed for economic purposes, conservation measures for the working population have also been incorporated in to local action plans e.g. in Myanmar (Win 2018). The case-study of working elephants therefore provides a unique opportunity to understand how wild-capture influences population-dynamics in captivity.

Here, we aim to assess how long-term variation in wild-capture has influenced population viability in the largest captive population of the long-lived Asian elephant. To address this issue, we use a detailed longitudinal studbook of government-owned female timber elephants (N = 3585) that were captive-born or wild-caught in Myanmar between 1960 and 2014. There has been substantial variation in wild-capture during this period; Aung (1997) estimated that at least 2000 individuals were caught from the wild between 1970 and 1993. Furthermore, systematic wild-capture was formally banned in 1994 (Uga 2000). Thus, this unique dataset enables us to capture detailed variation in wild-capture and vital rates across several decades, which provides rare insight into the demographic challenges faced by vulnerable species in captivity as a result of capture from the wild. From these extensive demographic records, we address two key questions: 1) Between 1960 and 2014, how much did wild-capture contribute to observed annual changes in the number of individuals in the population? and 2) Now that systematic wild-capture is no longer practised, and given observed variation in demographic rates, will the current population decline in the future? To address the first question, we captured historic trends in age-specific life-history traits in wild-caught and captive-born female elephants, and related observed changes in population size to wild-capture rates in each year from 1960-2014. For the second question, using age-specific demographic rates from years after capture was banned, we constructed individual-based, stochastic projection models to assess long-term population viability over 250 years. We explored population viability under model uncertainty of life-history rates, observed variation in the environment and demographic stochasticity. Finally, we performed sensitivity analyses of the projection models under different scenarios of changes to life-history rates, to provide targets for sustainable management in semi-captive elephants.

3.3 Methods

Study population

The Union of Myanmar has the largest working population of Asian elephants, with more than 5000 individuals, and approximately 2700 are state owned and used for timber extraction processes (Toke Gale 1971, Sukumar 2006). The timber elephant population is managed centrally by the state forestry commission, the Myanma Timber Enterprise (MTE), and keeping systems (including workload regulations) are consistent across Myanmar (Mar 2007). Although MTE elephants are held in captivity, we describe them as semi-captive: 1) they are free-roaming outside of working hours and in the 3-month annual rest period and forage naturally without supplementation, 2) there is no reproductive management of the population and individuals mate freely with captive or wild conspecifics, 3) there is no human intervention with the weaning of calves, which are cared for by the mother until training at the age of five (Mar 2007), and 4) culling is not practised and elephants only have access to basic veterinary care. Veterinarians diagnose disease and record deaths and their causes following broad post-mortem exams, increasing the reliability of mortality estimates (Lynsdale et al. 2017). Despite workload and work-related stress having the potential to influence life-history traits, population vital rates are more comparable to those of wild African elephants (Clubb et al. 2009) and Asian elephants (De Silva et al. 2013) than to those held in zoos (Clubb et al. 2008). Timber elephants have been monitored by the state for over a century, and the current studbook has been collated from individual elephant log-books and annual MTE reports. To our knowledge, the studbook covers most individuals in the working population between 1960 and 2000, but we had access to approximately 13% less demographic records between 2001 and 2014. The final studbook was a female-only dataset (N = 3585, wild-caught = 1215) with individuals from 11 out of the 14 regional divisions (or states) of Myanmar, including Ayeyarwady, Bago, Chin, Kachin, Magway, Mandalay, Rakhine, Sagaing, Shan, Tanintharyi, Yangon and Unknown regions (for data selection details, see S2.1, S2.2 and figure S2.1). This female-only dataset was used in all analyses of life-history traits and population projections.

Wild individuals were systematically captured in Myanmar until 1994 to supplement the working population, after which they were protected (Uga 2000, Mar 2007). However, individuals are still taken from the wild into captivity in instances of human-elephant conflict, but this occurs at much lower levels than historically (Mar 2007). For wild-caught individuals, specific birth date is unknown, and therefore age is estimated at the time of capture using shoulder height and a comparison of body condition with elephants of known age (Mar 2007). In addition, the extent of pigmentation on the face (including trunk and temporal areas), folding of the upper ear, tail hair, and wrinkliness of the skin are used to estimate age in wild-caught individuals (Lahdenperä et al. 2018). The exact error in age-estimation for wild-caught individuals is unknown, but thought to be within couple of years for individuals that continue to grow (up to approximately 25 years old; Mumby et al. 2015), which constitutes the majority (72%) of those captured (Lahdenperä et al. 2018). Using records of wild-caught females, we included a measure of wild-capture, which broadly assessed the number of individuals captured in each year. However, this does not necessarily include all individuals captured for two reasons. First, an estimated 5-30% of individuals die during capture (Lair 1997), and the studbook only includes individuals remaining in the working population (Lahdenperä et al. 2018). Second, we only included wild-caught females caught before an estimated age of 25, when their age-estimation is likely to be most accurate. We have no estimate on the level of poaching in the wild population, and to our knowledge, only very few individuals in the captive population are removed after they were born/captured. We restricted the studbook to a female-only dataset because we could not reliably estimate paternity and thus reproductive rates for male elephants from demographic records. There are differences in life-history traits between male and female elephants (Lahdenperä et al. 2018), and this is a limitation of the current studbook, but we could not include the dynamics of males in this study. However, A female-only design was appropriate for the current study because reproduction was not limited by the number/frequency of males, with a mean sex ratio of 1.34 across the study period (females:males, range = 1.23-1.45; figure S2.6) and 50.54% of births to male calves. Females also mate with both wild and captive bulls (Mar 2007). Thus, population growth and decline can be assessed reliably using the dynamics of females.

Long-term trends in the age-specific vital rates of wild-caught and captive-born females

Mortality and birth events within the studbook were used to quantify population vital rates through time for individuals of different birth origins, to parameterise population projection models. Age-specific rates of mortality and birth were estimated from the raw data using a generalised additive mixed modelling (GAMM) framework, run using the *gam* function in the R package *mgcv* (Wood 2011, R Core Team 2017). The raw data was smoothed using an additive modelling approach because there was a large variation in the density of life-history data spatio-temporally and across ages. Thus, raw age-specific data in a given year may not be representative of general population-level trends of life-history. An additive modelling approach also enables us to flexibly capture non-linear trends in vital rates across an individual's lifespan and through time. All analyses were carried out in R (R Core Team 2017).

For every year of a female's life from birth/capture (or any years of a female's life after 1960 if entering before 1960) to death/censoring, we coded the mortality and birth events of each individual as binary response variables (fitted with binomial error structures and a logit link function), where a 1 indicated an event (death or birth) in a given observation year. Individuals exited the analysis at death or at their last known age alive (censor date). The time series dataset contained 66,528 (wild-caught = 30,287) year-age observations from the 3585 females. We then modelled the probability of death and birth separately as functions of age (numeric integer), observation year (numeric integer, years from 1960 to 2014), and birth origin (binary factor, captive-born vs wild-caught). Using model selection, we explored the predictive performance of 18 models, which incorporated age as a linear predictor or smoothing term, and observation year as a linear term, factor (decade or half-decade), smoothing term and random effect smoothing term. We also explored interactions between age, observation year and birth origin, included as thin plate regression spline smoothers for each birth origin, or as tensor product interaction smoothing terms (Wood 2003, 2006). Models were selected based on the Akaike information criterion (AIC) (Akaike 1987, Burnham and Anderson 2004) (For full details of model selection see S2.2 and table S2.1).

We assessed the distributional assumptions of the best models by testing the under/overdispersion of scaled model residuals. Scaled model residuals were calculated from the *DHARMa* package of R, which uses a simulation-based approach to create readily interpretable scaled residuals for mixed effects models (Hartig 2018). We tested for under/overdispersion and uniformity in simulated residuals using 1000 simulations (figure S2.2). Then, we quantified the uncertainty in birth and mortality rate predictions from the best models. This enabled us to assess how much parameter uncertainty influenced variation in population size in future projections. Parameter uncertainty was quantified using posterior simulation of the best model, with 1000 replicates of model coefficients from the posterior mean and covariance matrix of the model. Posterior simulation was selected ahead of other bootstrapping techniques as it prevented the need to re-fit models, which would risk under-smoothing.

How was past population growth influenced by wild-capture?

To explore how past trends in population growth were influenced by wild-capture, we calculated realised changes in the number of females from demographic data. For each year between 1960 and 2014, we calculated the number of females alive and the realised annual growth rate was calculated as $\lambda_{t\ realised} = N_{t+1}/N_t$, where N is the number of individuals in year t. Population changes from 2000-2001 were ignored because there was a decrease in the number of demographic records available to us between 2000 and 2001. We partitioned out population change effects due to wild-capture and to annual vital rates alone by subtracting the observed annual wild-capture rate from the change in the number of individuals and re-calculating the realised annual population growth rate. We tested the difference in population growth rate with and without wild-capture when capture was still practised systematically (before 1995) using a linear model, with realised annual growth rate as the response variable and both year (numeric integer) and capture presence (binary factor) as predictor terms.

Population projection models for a future without wild-capture

To assess the future viability of the timber elephant population, we built female-only, stochastic individual-based projection models using predicted age-specific birth and mortality rates for years after systematic wild-capture was banned (1995-2014) (more details in S2.3, figure S2.9 and figure S2.10; Grimm et al. 2006). We opted to use an individual-based modelling framework to incorporate demographic stochasticity. All projection models were run on predicted values from the Kachin regional division; Kachin had a large number of life-history records, whilst having average predicted vital-rates most consistent with the overall mean vital rates across all divisions. We did not incorporate density dependence in projection models, as we found that population size did not improve model performance (table S2.1). Finally, we removed individuals over the age of 70 in each year of each simulation (i.e. mortality of 1 at age 70), as there was large variation in life-history parameters at these ages and very few individuals. For each year in all projections, birth and death events were randomly sampled from a Bernoulli distribution according to age-specific probabilities from the best models. For all projections, we assumed that all births were to females.

We first constructed a projection model for the average vital rates across observation years in this period (1995-2014), without incorporating parameter uncertainty or environmental stochasticity (S2.3). Thus, the first model was intended to explore the average long-term dynamics of the population with demographic stochasticity alone. The projection began with the age-structure present in 2014 (N = 1369; figure S2.10). Over 500 iterations, we projected 250 years into the future, which was selected to capture long-term trends over 10-12.5 generations in the future (generation time 20-25 years from Choudhury et al. 2008). This ensured that we captured stable long-term dynamics based on the average vital rates between 1995 and 2014.

We then performed a hierarchical population viability analysis under three levels of uncertainty; 1) parameter uncertainty from the best model, 2) environmental stochasticity (variation across years 1995-2014) and 3) demographic stochasticity (figure S2.11). 1) Parameter uncertainty was incorporated using posterior simulation of the best birth and mortality models, from which we calculated 200 sets of predicted values. Each set of predicted values included interannual (environmental) variation with observation year included as both a smoothing term and random effect (table S2.1). 2) Environmental stochasticity was incorporated by resampling both the random effect and smoothing term of observation year from the best models. We randomly sampled years for both the smoothing term and random effect term, and adjusted birth and mortality rates together according to the sampled years. We sampled 10 sets of years for each of the 200 sets of predicted values generated through posterior simulation. 3) Demographic stochasticity was incorporated by repeating each set of years 10 times. The total number of simulations when assessing population dynamics over a 50-year period with different levels of uncertainty was 20,000. We then projected 50 years into the future from the starting population size and age-structure in 2014 (N = 1369). Finally, we investigated the relative importance of the three different levels of uncertainty on population size in the population projection. We used nested hierarchical mixed effects models for each year in the projection, implemented in the *lme4* package (Bates et al. 2015), to partition the variance in $\ln population\ size$ attributable to demographic stochasticity within environmental stochasticity within parameter uncertainty (figure S2.11).

Identifying demographic targets for population management

To assess how age-specific rates influence population growth to identify demographic targets for population management, we performed numeric sensitivity analyses on the average long-term dynamics of the population excluding environmental stochasticity or parameter uncertainty. We first split age-specific demographic parameters of captive-born females into four main stages for life-history: juvenile (0-4 years of age before weaning), pre-reproductive (5-12 years old), adolescent (13-20 years old), reproductive adult (21-44 years old), senescent adult (45-70 years old). Life-history stages were selected based on previous findings of life-history patterns in timber elephants and raw age-specific data (Hayward et al. 2014, Crawley et al. 2017) (figure S2.7). Then, for each life-history stage, we increased birth rates by 10% or decreased mortality rates by 10%, perturbing birth and mortality separately. We selected 10% because it represented a realistic potential change in management for a given life-history stage, laying beneath the variation in life-history rates that was observed in the raw data between 1960 and 2014 (SD 19% and 14% for total birth and death rates, respectively). To assess population viability, we performed population projections for each scenario, performing 1000 simulations over 200 years, randomly assigning births and deaths to each individual in each year, with birth and death probabilities adjusted for each scenario. Finally, we compared population dynamics in each scenario to the baseline under current conditions, to identify targets for management.

3.4 Results

The average annual birth rate was 3.1% (range = 1.2-5.4%) and the average annual mortality rate was 2.1% (range = 0.3-4.2%) for female elephants (N = 3585) between 1960 and 2014 (figure S2.5a). Our measure of wild-capture for females entering the final studbook occurred at an average rate of 20.6 individuals per year, with the maximum number of individuals captured in a single year being 117 in

1972 (figure S2.5b). Capture rates between 1965 and 1975 were higher than other years within the study period, with 56% of all captures taking place within this 10-year period (figure S2.5b).

Birth rates varied across lifespan and years for both captive-born and wild-caught females (figure 3.1a). For captive-born females, birth rates increased at the age of 12 up to an average initial peak of approximately 10% between the ages of 20 and 22, after which generally there was a decline later in life (figure 3.1a; figure S2.7a). In earlier years before 1970, there were fewer old-aged individuals and the population was smaller, and so predicted birth rates increased later into life, but on average birth rates declined beyond the age of 44 (figure 3.1a; figure S2.7a). Birth rates were consistently lower on average in wild-caught females across ages, increasing more slowly from age 12 and reaching a maximum annual predicted birth rate of only 7%. However, at older ages wild-caught females exhibited higher birth rates, but also declined after the age of 50 (figure S2.7a). Overall, birth rates declined between 1960 and 2014, particularly for captive-born females (figure 3.1a; figure S2.8a). The best model for birth rates included a tensor product interaction smoothing term between age, year and birth origin, and an additional term for annual variation with year as a random factor (table S2.1). We did not find evidence for an effect of population size on birth rate as it did not improve predictive performance; the AIC difference between the best model and the model with population size was 0.42, but the more parsimonious model with fewer parameters was selected (table S2.1; figure S2.4a). The best model fit the data well because there was no evidence of overdispersion or non-uniformity in the simulated residuals (figure S2.2a). Furthermore, there was no observed covariance between simulated model residuals and explanatory variables (figure S2.3a; figure S2.3c).

Mortality rates were high in young individuals, declining until the age of 10 and remaining low until 45, after which mortality rates rapidly increased into old age (figure 3.1b). Mortality rates were also higher in wild-caught females than captive-born females, but at extreme ages (> 50 years of age), there was some evidence that wild-caught females had reduced mortality due to selective disappearance (figure 3.1b; figure S2.7b; Lahdenperä et al. 2018). Predicted mortality risk at all ages also fluctuated across the study period for both captive-born and wild-caught females (figure 3.1b; figure S2.8b). For mortality, the best model also included a tensor product interaction smoother between age, observation year and birth origin, with an additional random term of year. Again, we found no clear evidence of an effect of population size on mortality rate, with an AIC difference of 0.38 compared with the second-best explanatory model with more parameters (table S2.1; figure S2.4b). Furthermore, there was little evidence of non-uniformity, overdispersion, or covariance with explanatory variables in the simulated model residuals (figure S2.2b; figure S2.3b; figure S2.3d). For both birth and mortality models, the random effect of spatial division was accounted for in subsequent projections by using values from Kachin state, which was closest to the average birth and mortality values across divisions, with a large population size.

The number of individuals in the final female-only studbook dataset between 1960 and 2014 increased from 385 to 1369, with a maximum of 1677 individuals in 1992 (figure 3.2a). To investigate changes in population growth rate across the study period and to assess the implications of wild-capture for population growth, we calculated the observed annual population growth rate both with and without wild-capture from raw data. Realised annual growth rates were highly variable across observation years (figure 3.2b). Generally, growth rates declined between 1960 and 2014 (range = 0.93 – 1.14) (figure 3.2b) but remained above replacement rate (growth rate ≥ 1) before 1990 when capture was included. However, population growth rate was highly dependent on wild-capture, suggesting the population may not be sustainable, particularly as systematic wild-capture was banned in 1994. Growth rates excluding wild-capture before 1995 were 2.1% lower than those including wild-capture ($F_{2,67} = 22.1$, $p< 0.001$). Together, the historic changes in the female timber-elephant population suggest that large population increases were accompanied by intensive wild-capture rates, and population growth rate has fluctuated around 1 beyond 1995, making the population vulnerable to population decline in the future.

To assess the future outlook for timber elephants in a world excluding wild-capture, we performed individual-based, stochastic projection models of the population beginning with the starting age-structure in 2014. We first investigated long-term (250 years) dynamics over 500 simulations in a scenario excluding model parameter uncertainty or environmental stochasticity. Generally, as with historic population changes, the average change in the population was close to a population growth rate of 1, indicating little change over 250 years (figure 3.3a). However, the model projection had a long-lasting transient phase of fluctuation in the population of ~70 years, in which the population declined down to 1176 individuals in 2056. After this transient phase up to ~2080, the population reached a steady, but small stable annual growth rate of ~1.005 (figure 3.3a). Although population growth was predicted in the long-term, the proximity of the growth rate to 1 indicates that the population is susceptible to decline given changes in the environment. As expected, the variation in population viability was far greater when environmental stochasticity and parameter uncertainty were included (figure 3.3b). Including uncertainty in the environment and parameter uncertainty, we again found an average population decline of ~150 individuals over 50 years. However, decomposition of the different sources of uncertainty revealed that although demographic and environmental stochasity are drivers of variation in population viability, model parameter uncertainty was the most important driver of observed population changes (figure 3.3c). After 50 years, parameter uncertainty explained ~75% of the variance in population size (figure 3.3c). This suggests that understanding long-term variation in demographic rates is particularly crucial in this long-lived species.

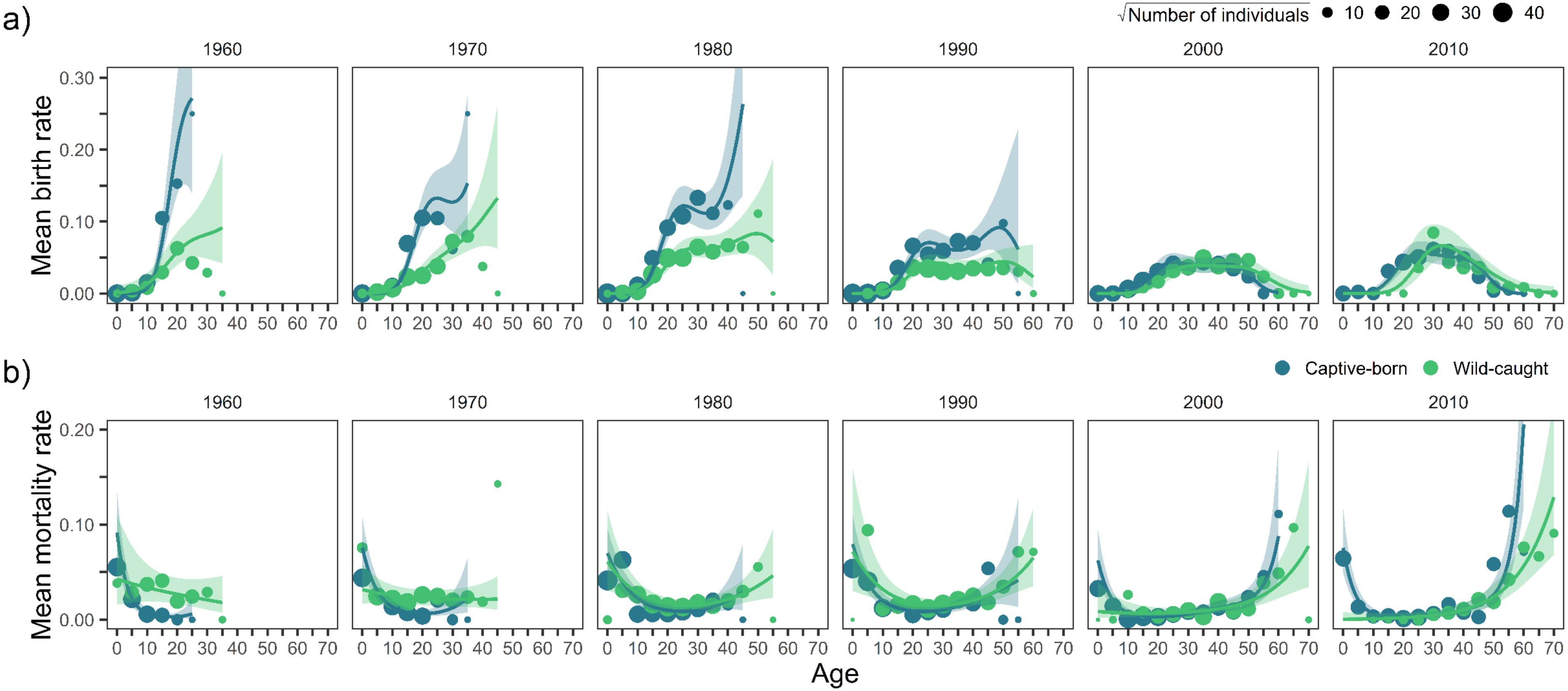

Figure 3.1 Mean age-specific birth (a) and mortality (b) rates in wild-caught (green) and captive-born (blue) female timber elephants for each decade between 1960 and 2010. Points are mean age-specific vital rates for each 5-year age-class across all regional divisions in Myanmar for each decade, with the size depicting the square root of the sample size (range = 1-1815 individuals). Lines are the mean model predicted values from the best birth (a) and mortality (b) models across regional divisions, with 95% confidence intervals from posterior simulations. Model predictions between 1995 and 2014 were used to parameterise individual-based projections.

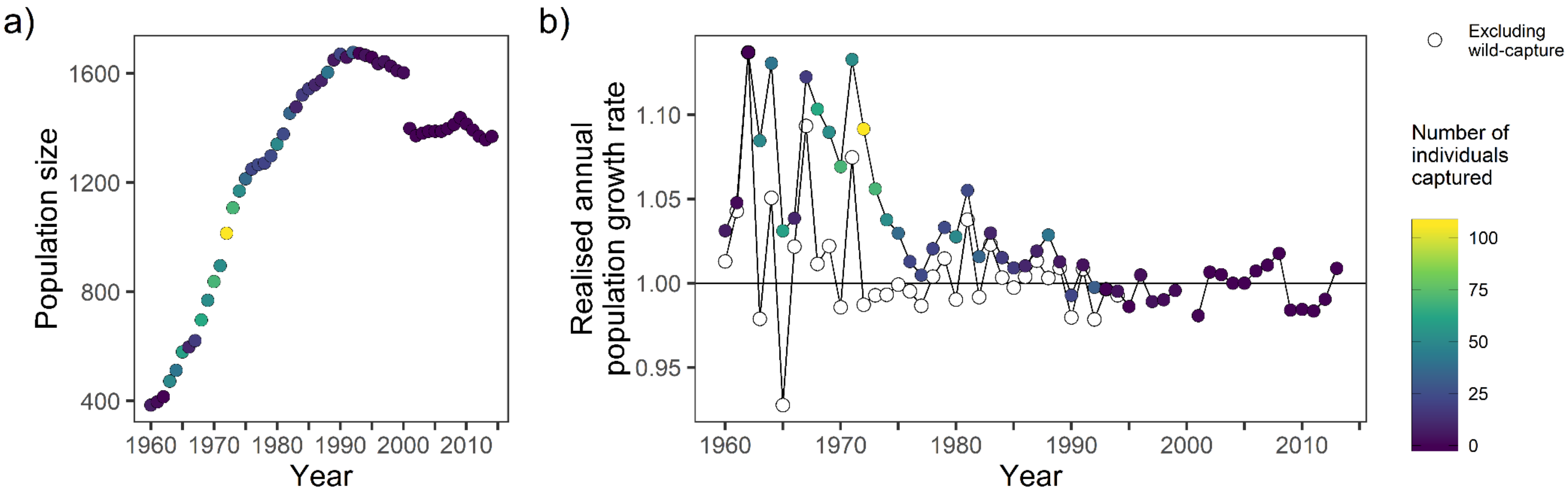

Figure 3.2 Historic trends in the female timber elephant population with wild-capture. a) The number of female timber elephants in each year between 1960 and 2014. The decrease in the year 2001 is due to a decrease in the number of demographic records. b) Changes in the realised annual population growth rate, both including (coloured points) and excluding (open points) capture from the wild. Solid line indicates annual growth rate of 1 i.e. replacement rate. For both (a) and (b), the colour indicates the annual capture rate in each year.

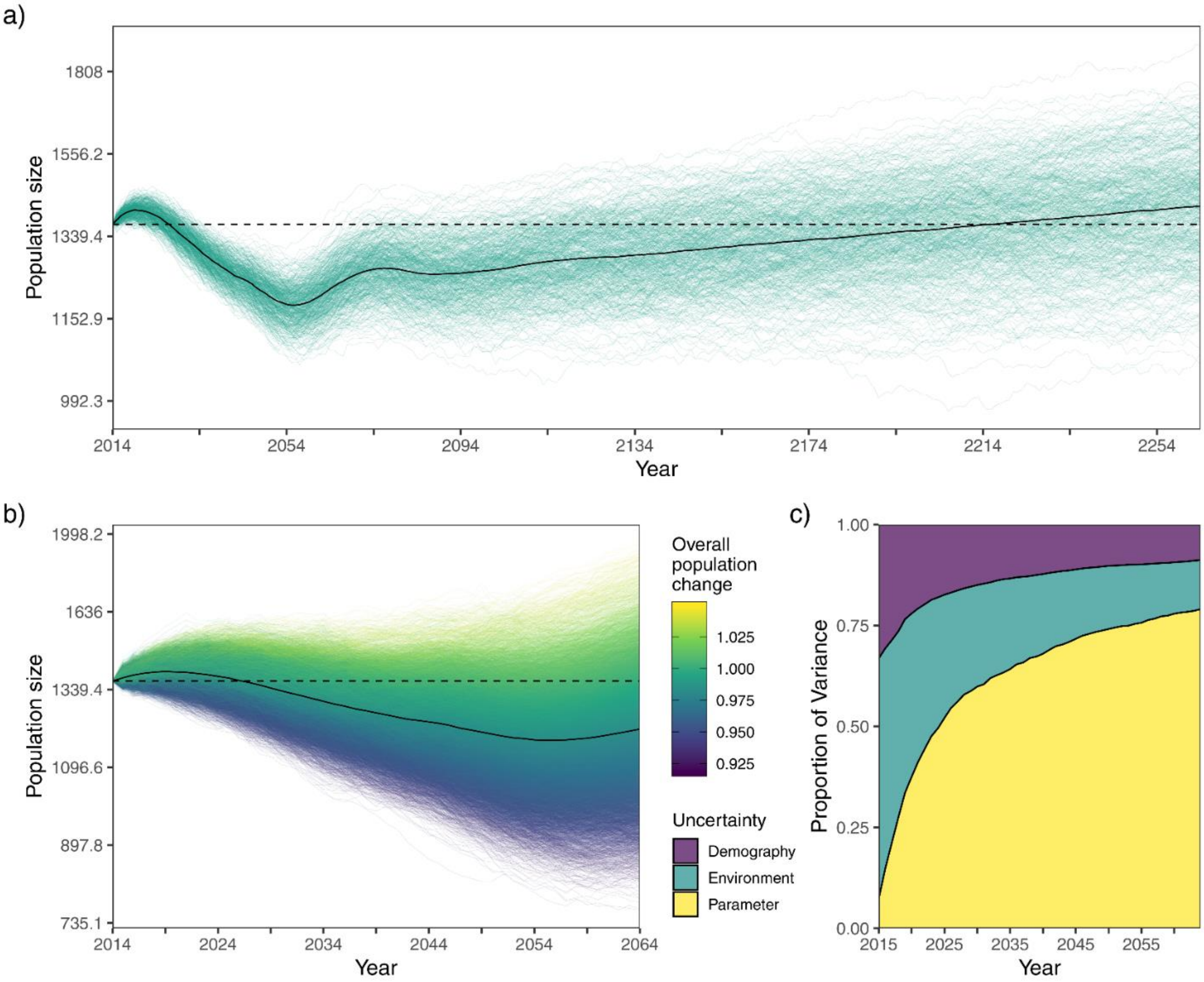

Figure 3.3 Population projections for female timber elephants in a world without wild-capture. a) Population projection over 250 years and 500 simulations representing the average dynamics of the population excluding model uncertainty in parameters and environmental stochasticity. Green lines represent the change in population size for each simulation, and the solid black line indicates the geometric mean. b) Short term changes (50 years) in the timber elephant population incorporating varying levels of uncertainty (parameter uncertainty and demographic/environmental stochasticity). Coloured lines indicate each simulation (20,000), and the colour denotes the overall population change in that simulation. Solid black line indicates the geometric mean of population size. For population projections, population size is on the natural log scale, and the dashed line indicates the starting population of 1369. c) The proportion of variance in ln(population size) explained by uncertainty in model parameters (yellow), and with both environmental (green) and demographic (purple) stochasticity over 50 years for 20,000 simulations.

We investigated which age-specific demographic rates had the largest impact on population growth by performing population projections under scenarios with changes to demographic rates at key life-history stages and comparing them to the baseline scenario. We investigated the sensitivity of population viability to 10% changes in each life-history stage (increase for birth rates, decrease for mortality). The majority of changes to age-specific rates had relatively little effect on population viability relative to the baseline scenario (figure S2.12). However, both a 10% increase to the birth rates of adult reproducers (21-44) and a 10% decrease in mortality of juveniles (0-4) had a substantial influence on population viability and resulted in a more rapid population increase (figure 3.4). Population increases of 5% and 2% were observed under adult birth rate and juvenile mortality rate scenarios, respectively, compared to a 0.01% increase under the baseline scenario over the 200-year period. Notably, increases in birth rates at older ages (45-70) and in early reproducers (13-20) also had an influence on population growth (figure S2.12).

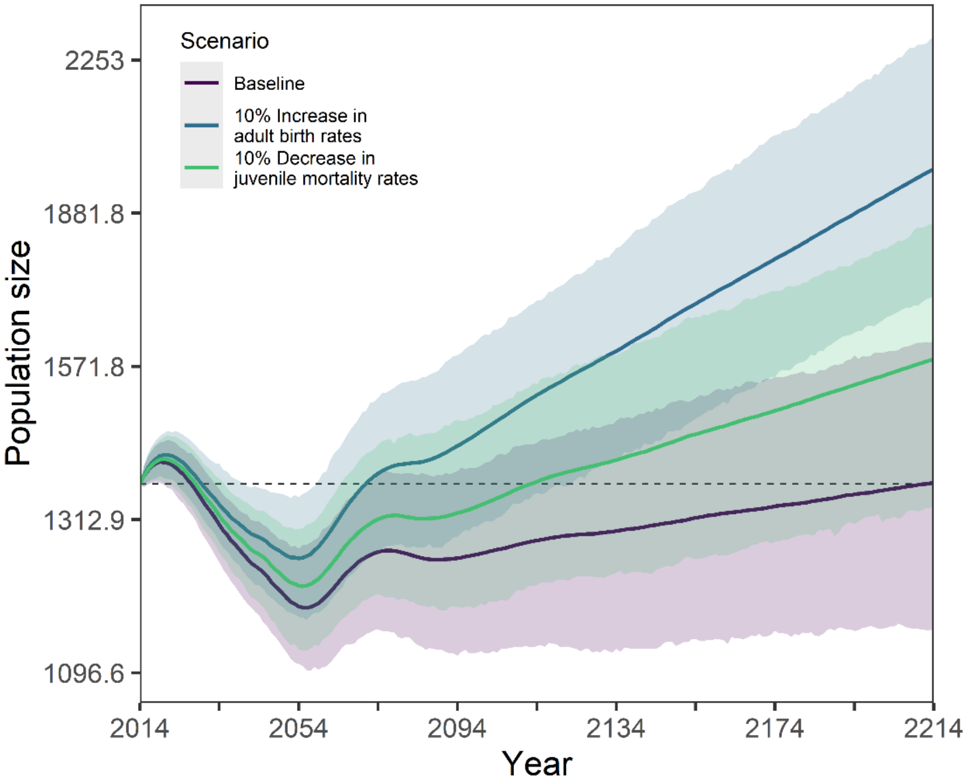

Figure 3.4 Increases to juvenile survival represent a realistic and meaningful target for conservation management. Individual-based, stochastic projections excluding parameter and environmental stochasticity over 200 years under three scenarios; baseline (average observed dynamics – purple), a 10% increase to adult birth rate (age 20-44 – blue), and a 10% decrease in juvenile mortality (age 0-4 – green). Solid lines are the population size on the natural log scale, with 95% CI across 1000 simulations, dashed line indicates the starting population size of 1369 females in 2014.

3.5 Discussion

Our results challenge the prospect of maintaining viable populations of captive elephants without the capture of individuals from the wild. Historic trends in population dynamics using demographic data spanning 54 years revealed that population growth rate was highly dependent on wild-capture. Given this dependence on wild-capture and an accompanied decline in birth rates between 1960 and 2014, the outlook for captive elephants excluding wild-capture is uncertain. Long-term population projections predict immediate population declines, but long-term stable population growths rates that are close to replacement rate, suggesting that the working population is vulnerable to environmental disturbance. However, due to an unstable age-structure, immediate transient population declines may last for approximately half a century, suggesting that management must be tailored to the slow life-history of Asian elephants. Although population viability excluding wild-capture is uncertain, our results also suggest that there are long-term demographic consequences for individuals that are caught from the wild; wild-caught females have lower life-time birth rates and higher death rates than captive-born females. Wild-capture reduces remnant wild populations, but also has a long-lasting demographic impact on the demography of the captive population, and we must focus on managing the demography of captive populations to prevent future declines.

Between 24% and 29% of the global Asian elephant population is held in captivity (Sukumar 2003, Choudhury et al. 2008), of which Myanmar's timber elephant population may constitute as much as a third. Thus, although this working population is often overlooked as a unit of conservation, sustainable management is crucial for the viability of this endangered species. However, our study shows that for decades, this has not been achievable without the capture of wild individuals. Wild-capture in Myanmar has been detrimental for the wild population, which is important for both Asian elephants and their surrounding ecosystem (Leimgruber et al. 2003). Leimgruber et al. (2008) postulated that capture rates of 100 individuals per year would result in the extinction of the wild population in under half a century. However, the exact dynamics of Myanmar's wild population in relation to changes in wild-capture rates is unknown. As well as decreasing the size of the wild population, we found evidence that wild-caught females have lower birth rates and survival, which is most likely a result of the stress of the capture process (Lahdenperä et al. 2018). However, despite the lower performance of wild-caught females in captivity, there were large declines in captive population birth rates with declines in wild-capture. In other words, the captive population depended on wild-capture. Furthermore, historic rates of wild-capture do not necessarily take into account capture-related mortality itself, and many more elephants may have actually been removed from the wild than are utilised in the timber industry (Lahdenperä et al. 2018). For example, the estimated instant mortality rate during the elephant capturing process in Myanmar is high, varying between 5% and 30% depending on the capture method (Lair 1997, Myint Aung 1997). The ongoing wild-capture of elephants is not limited to supporting Myanmar's timber elephants (which now continues in cases of human-elephant conflict, but not systematically): capture continues worldwide for both legal and illegal purposes (e.g. Fernando et al. 2012, Nijman 2014). Asian elephant populations currently held in Western zoos, safari parks, and circuses are not self-sustaining (Myroniuk 2004, Clubb et al. 2009), and 60% were wild-caught and imported from range countries (Clubb and Mason 2002). The reliance of captive Asian elephant populations on wild-capture is alarming, and management must be addressed to ensure the sustainability of this species without continued capture.

Although population viability in captivity is under threat, population extinction was not predicted in long-term population projections. A handful of studies have also aimed to assess the viability of semi-captive elephant populations (e.g. Leimgruber et al. 2008, Suter et al. 2014). Both studies forecasted that extinction was highly likely. Importantly however, both studies impose carrying capacities on working elephant populations, which limits population growth (Leimgruber et al. 2008, Suter et al. 2014). We did not find evidence for a correlation between realised population size and age-specific vital rates in this extensive demographic dataset spanning 54 years. Furthermore, the notion of density dependence in semi-captive populations is not trivial; individuals are not always subjected to habitat limitation or competition as with fully wild populations, because of human management. Another key difference in the current study was the incorporation of temporal variation in age-specific vital rates that were estimated directly from the demographic studbook, rather than static age-specific rates. Historic annual population growth rates displayed a large variation between 1960 and 2014. Understanding temporal differences in demography and life-history are therefore crucial for population dynamics. However, temporal differences in vital rates have been absent in previous projections in Asian elephants (Leimgruber et al. 2008, Clubb et al. 2009, Suter et al. 2014). Previous work has suggested that the quality of demographic and life-history data needs to be addressed in viability analyses (Coulson et al. 2001), but our results suggest that this may be accentuated in long-lived species, where many decades of data are needed to quantify vital rates. Slow intrinsic growth rates and life-history in species such as elephants may exacerbate external pressures, resulting in further population declines (Turkalo et al. 2016). Indeed, we observed transient population dynamics that last several decades in long-term projections, and previous work has found long-lasting mortality effects in working elephants (Lahdenperä et al. 2018). This result is important for the conservation of long-lived species; an unstable age-structure can lead to long-lasting transient dynamics with more rapid population declines. However, these changes may occur on significant timescales, increasing the importance of long-term monitoring and conservation strategies that reflect the life-history of target species.

Although our results suggest that captive elephants in Myanmar may not be sustainable without wild-capture, we are not suggesting that reinstating the capture of wild individuals is a potential solution, because it is clearly detrimental for the wild population (Leimgruber et al. 2008). Instead, we suggest that management should be focused on sustaining the current individuals in the captive population. Specifically, our results suggest that increased survival in juveniles may be an important driver of population growth in long-lived species, which are characterised by low annual reproductive rates. Although, as expected, birth rates in adult females had the biggest influence on population viability, increasing adult birth rates does not necessarily present a tractable target for population management, particularly as adult females are working animals. Targeting juvenile mortality however provides a clear and tractable target for population management in this captive population. Currently, juvenile elephants are tamed around the age of five in order to learn commands and begin light carrying work (Toke Gale 1971, Mar 2007, Crawley et al. 2019). Elephants are removed from the mother at this stage to undergo training, and this stress is may have a negative impact on survival (Mar 2007). Furthermore, mortality is highest in neonatal, pre-weaning elephants (Mar et al. 2012, Mumby et al. 2013). This phenomenon is common in other populations and in African elephants, particularly in captivity (Weise 2000, Clubb et al. 2008). Further to previous findings our results suggest that targeting the factors influencing juvenile mortality may have a disproportionately beneficial effect on population growth. This could be achieved by adjusting management to reduce stress during the taming process and for peak reproductive aged females, and to target neonatal mortality.

Ex situ conservation is now common to prevent extinction in wildlife populations, but removal of individuals from the wild may be detrimental to both populations *in situ*, and those in captivity. With human-managed populations becoming increasingly common, there is a need for an increased understanding of how human intervention influences demography and life-history.

3.6 Keywords

Individual-based model, population viability, demography, ex-situ conservation, life-history

3.7 Acknowledgements

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3.8 Conflicts of Interest

We have no conflicts of interest.

3.9 Data accessibility

The data and code supporting our results are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.rj237db

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Chapter 4

Long-term fluctuation in age-structure is a key determinant of population growth rate in a long-lived mammal

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4.1 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 variation in population growth rates has rarely been explored empirically in wildlife populations with long-term demographic data.

2. Here, we assessed how variation 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 variance decomposition to partition population growth rates into the independent contributions of age-structure and age-specific vital rates, relative to average conditions.

4. Age-structure was highly variable over the study period, with large proportions of juveniles in 1970 and 1985, and was responsible for a significant proportion of variation in population growth rates. High adult birth rates between 1970-1980 would have resulted in large positive population growth rates, but these were prevented by a low proportion of reproductive-aged females.

5. An understanding of both age-specific vital rates and age-structure is needed to assess short-term population dynamics. Furthermore, 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 undoubtedly drive population dynamics by influencing birth and mortality rates, but understanding demographic structure is crucial for assessing population growth.

4.2 Introduction

Population growth rates are valuable indicators of a population’s trajectory, informing us about how organisms 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 et al. 2005). As age-specific birth and mortality rates, or 'vital rates', are directly impacted by the environment (Stearns 1992, Pardo et al. 2013, 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. This concept has been formalised as population inertia, in which deviations away from a stable age-structure can lead to short term population growth or decline before stable dynamics are reached (Koons et al. 2007). Indeed, in a constantly changing environment we observe large fluctuations in the demographic structure of populations through time alongside changes in population size (Gaillard et al. 2000, Moss 2001, Trimble et al. 2009, Ezard et al. 2010). Thus, with variation in demographic structure we expect variation in population dynamics, even with identical environmental conditions (Coulson et al. 2001), and there is a need to explore how age-structure influences population growth independently of 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 significant driver of population dynamics in many populations (Ezard et al. 2010, Stott et al. 2011, Ellis and Crone 2013, Mcdonald et al. 2016). 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 (Stott et al. 2010, Gamelon et al. 2014). Furthermore, the role of age-structure in short-term population dynamics is likely to be inflated in populations that have been disturbed, where age-structure is expected to be unstable. 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 et al. 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 unpicking the independent drivers of population growth rates (Caswell 1989, Williams and Crone 2006, Kalisz et al. 2014, Maldonado-Chaparro et al. 2018). 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 et al. 2016). However, few studies have applied our understanding of transient dynamics empirically to test how variation in age-structure influences population growth independently of age-specific vital rates.

One key issue when assessing the impact of demographic fluctuations on population dynamics is that individuals may live for several years or even decades, making long-term studies crucial (Clutton-Brock and 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 et al. 2012). For example, life-history data in the wandering albatross gathered over 50 years revealed that demographic variation in foraging efficiency was a strong predictor of population decline (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 (Moss 2001, Kuussaari et al. 2009, Turkalo et al. 2016, Jackson et al. 2019, Lahdenperä et al. 2019). In elephants, elevated stress and investment to fecundity early in life can influence reproduction and survival several decades later (Lee et al. 2013, Hayward et al. 2014, Mumby et al. 2015). Age-structure may be particularly important for population growth rates in long-lived species, as delayed responses to the environment influence survival and reproduction and impact upon age-structure.

Here, we aim to assess how age-structure influences population dynamics in a long-lived mammal. Deviation away from a stable age-structure has been shown to drive short-term population dynamics (Ellis and 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= 2223) of female working 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 et al. 2019), with which we can estimate vital rates and population growth rates (Jackson et al. 2019). First, we explore fluctuations 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 variance decomposition to assess the independent contributions of starting age-structure and vital rates on population growth rate, relative to the average environment. We show that age-structure was highly variable across the study period and explained a significant proportion of variation in population growth rates over 45 years, highlighting the importance of demographic structure for population dynamics.

4.3 Materials and Methods

Study population

Asian elephants have a substantial ex situ population of approximately 16,000 individuals globally (Sukumar and Santiapillai 1996, Sukumar 2006). 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 5000 individuals (Toke Gale 1971, Sukumar 2006). Our study population is comprised of over 2700 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 of 19 (Hayward et al. 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 (Uga 2000, Jackson et al. 2019). 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 et al. 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 et al. 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 not limited by the number of males, and females also mated with wild individuals in rest periods. Second, we only used data from captive-born females, to reduce the potentially confounding effects of capture from the wild on age-structure and population growth (Lahdenperä et al. 2018, Jackson et al. 2019). 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 2568 captive-born females, ranging in birth year from 1941 to 2014, and this data was used in all subsequent analyses.

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 five-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 five-year age-classes to maintain a sufficient sample size for each age-class in each year to visualise 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 1970-2014, again to account for smaller sample sizes and a lack of old-aged individuals. All analyses were carried out using R version 3.4.2 (R Core Team 2017).

Parameterising an age-structured model

We parameterised 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 2568 females. We smoothed birth and mortality rates from raw demographic data using a generalised 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 tensor product interaction smoothing term (Wood 2006). Birth and mortality models also accounted for spatial variation in vital rates by incorporating a random effect smoothing term of regional division in Myanmar (grouped to make sample sizes more comparable, see S3.1), penalised 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 1000 simulations (Hartig 2018).

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 1970-2014, using 71 annual age-classes (0-70 years old):

$$\boldsymbol{n}_{t+1} = \boldsymbol{A}_t \boldsymbol{n}_t, \quad \text{eqn1}$$

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

$$\boldsymbol{A}_t = \boldsymbol{P}_t + \boldsymbol{F}_t, \quad \text{eqn 2}$$

where $\boldsymbol{P}_t$ is the matrix of survival and $\boldsymbol{F}_t$ is the matrix of fertility in year t. Here, we parameterised $\boldsymbol{P}_t$ 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 parameterised $\boldsymbol{F}_t$ 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. From annual population projection models, we calculated the short-term population growth rate, λ, in year t, given by

$$\lambda(\boldsymbol{A}_t, \boldsymbol{n}_t) = \frac{\|\boldsymbol{n}_{t+1}\|}{\|\boldsymbol{n}_t\|} = \frac{\|\boldsymbol{A}_t \boldsymbol{n}_t\|}{\|\boldsymbol{n}_t\|}, \quad \text{eqn 3}$$

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 realised 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.

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 decompose the variation in realised population growth rate $\lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$ into contributions arising independently from variation in the environmental component (projection matrix), $\boldsymbol{A}_t$, and the age-structure component, $\boldsymbol{n}_t$. The goal of this approach was to assess how the age-structure and environmental components in each year independently affected population growth rates relative to the average conditions across the study period. Thus, in addition to the realised population growth rate captured in equation 3, we also constructed population models to capture the average environment, and to incorporate the observed age-structure and environmental components independently.

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

$$\lambda(\bar{\boldsymbol{A}}, \bar{\boldsymbol{n}}) = \frac{\|\bar{\boldsymbol{A}}\bar{\boldsymbol{n}}\|}{\|\bar{\boldsymbol{n}}\|}, \quad \text{eqn 4}$$

where $\bar{\boldsymbol{A}}$ is the mean projection matrix across the study period, parameterised using mean age-specific predicted birth and survival rates between 1970-2014, 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. 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 10 years of demographic data before and after the observation year (maximum of 20 years/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, $\bar{\boldsymbol{A}}$, from the average environment. These projections capture the independent effect of annual variation in age-structure on population growth rates. The corresponding short-term population growth rate for these models, $\lambda(\bar{\boldsymbol{A}}, \boldsymbol{n}_t)$, in year t with the mean projection matrix $\bar{\boldsymbol{A}}$ is defined as

$$\lambda(\bar{\boldsymbol{A}}, \boldsymbol{n}_t) = \frac{\|\bar{\boldsymbol{A}}\boldsymbol{n}_t\|}{\|\boldsymbol{n}_t\|}. \quad \text{eqn 5}$$

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

$$\lambda(\boldsymbol{A}_t, \bar{\boldsymbol{n}}) = \frac{\|\boldsymbol{A}_t\bar{\boldsymbol{n}}\|}{\|\bar{\boldsymbol{n}}\|}. \quad \text{eqn 6}$$

With the average environment model terms as a reference ($\bar{\boldsymbol{A}}$ and $\bar{\boldsymbol{n}}$), in each year we partitioned the independent effects of age-structure and environment on observed population growth rates. To partition age-structure effects in each year we used an ANOVA decomposition. 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. 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 $\Delta\boldsymbol{A}_t x \Delta\boldsymbol{n}_t$, such that

$$\ln\lambda(\boldsymbol{A}_t, \boldsymbol{n}_t) = \ln\lambda(\overline{\boldsymbol{A}}, \overline{\boldsymbol{n}}) + \Delta\boldsymbol{A}_t + \Delta\boldsymbol{n}_t + \Delta\boldsymbol{A}_t x \Delta\boldsymbol{n}_t, \quad \text{eqn 7}$$

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. The resulting design of the simulation experiment was a fully factorial ANOVA without replication for each year (i.e. $\overline{\boldsymbol{A}}$ versus $\boldsymbol{A}_t$, and $\overline{\boldsymbol{n}}$ versus $\boldsymbol{n}_t$). 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 variation in population growth rates alongside the effect of age-structure, we further separated the effect of the environmental component ($\boldsymbol{A}_t$) into independent 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 decomposed variance in population growth rate following the same ANOVA framework but calculating average-environment terms for survival and birth separately ($\overline{\boldsymbol{p}}$ and $\overline{\boldsymbol{f}}$, respectively). Then, comparing the population growth rate when including the observed survival and birth probabilities ($\boldsymbol{p}_t$ and $\boldsymbol{f}_t$, respectively) independently to the average environment terms, we could estimate the contribution of survival and birth to 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, $\Delta\boldsymbol{p}_t x \Delta\boldsymbol{n}_t$ and $\Delta\boldsymbol{f}_t x \Delta\boldsymbol{n}_t$, such that

$$\ln\lambda(\boldsymbol{A}_t, \boldsymbol{n}_t) = \ln\lambda(\overline{\boldsymbol{A}}, \overline{\boldsymbol{n}}) + \Delta\boldsymbol{p}_t + \Delta\boldsymbol{f}_t + \Delta\boldsymbol{n}_t + \Delta\boldsymbol{p}_t x \Delta\boldsymbol{n}_t + \Delta\boldsymbol{f}_t x \Delta\boldsymbol{n}_t. \quad \text{eqn 8}$$

We estimated these effects using pairwise combinations of model terms, and the design of the simulation experiment was a factorial ANOVA. However, this design was not fully factorial because we excluded the 2-way interaction between $\Delta\boldsymbol{p}_t$ and $\Delta\boldsymbol{f}_t$ ($\Delta\boldsymbol{A}_t$ in equation 7) and the 3-way interaction between $\Delta\boldsymbol{p}_t$, $\Delta\boldsymbol{f}_t$ and $\Delta\boldsymbol{n}_t$ ($\Delta\boldsymbol{A}_t x \Delta\boldsymbol{n}_t$ in equation 7).

4.4 Results

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 4.1). 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 peak reproduction) increased across the study period (figure 4.1). 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 4.1). 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 4.1). 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 4.1). Together, these results suggest that there have been substantial fluctuations in the demographic structure of the captive-born population over 45 years, particularly in younger individuals.

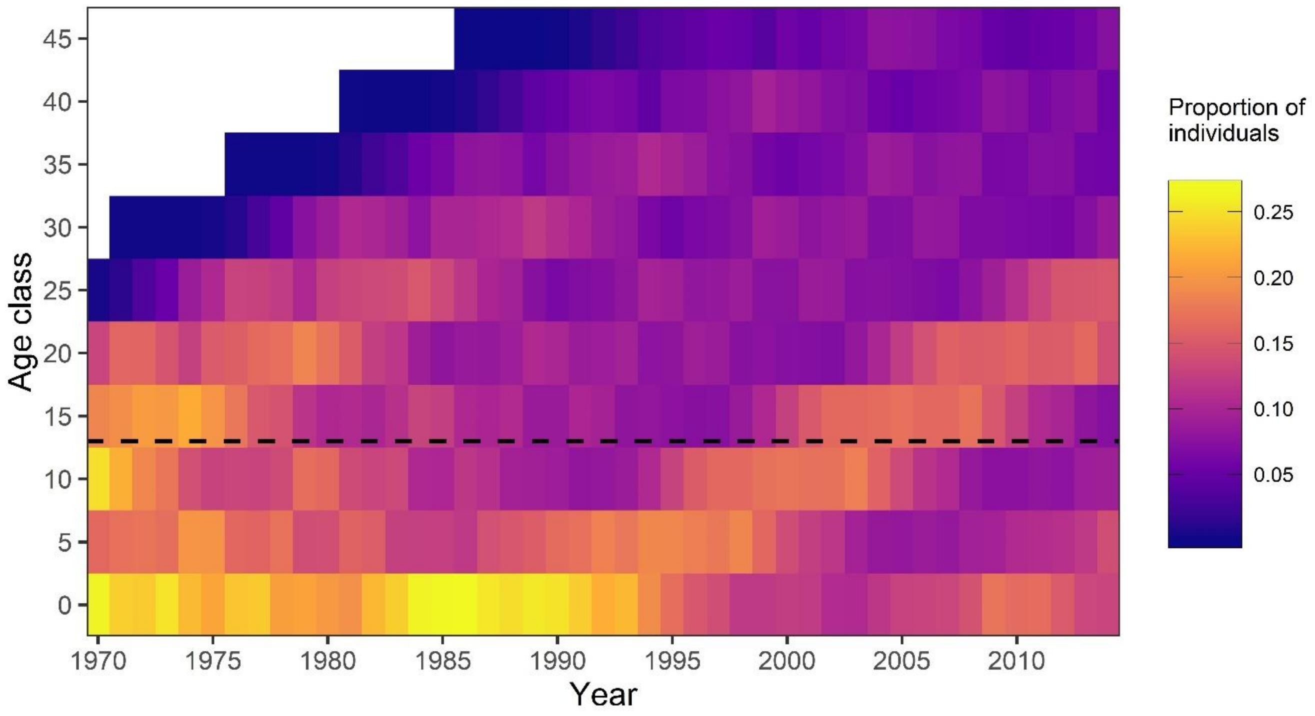

Figure 4.1 Fluctuations in the age-structure of captive-born female timber elephants between 1970 and 2014. A heatmap of the observed age-structure in each year for each five-year age-class, with the colour denoting the proportion of individuals. The dashed line indicates the age of the onset of reproduction i.e. age 13.

Age-structure is a significant driver of 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 S3.1). Mortality rates were higher in young and old individuals, particularly below 8 and above 45 years old, with lower mortality in adult individuals (figure S3.1). Mean birth rates declined across the study period, and this was particularly due to high adult birth rates in the 1970s and 1980s in comparison to later years (figure S3.1; figure S3.2). There was no evidence of non-uniformity or overdispersion in the simulated model residuals of the birth and mortality models (figure S3.3). 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 4.2a). Between 1985-2000, population growth rates were negative, but otherwise remained above replacement rate (>0) after 2002 (figure 4.2a).

The average-environment population growth rate was 0.015, equating to a 1.5% increase in the population in a single year, and was above the observed population growth rate (figure 4.2a). Importantly, the observed population age-structure explained a significant proportion of variation in population growth rate, in addition to effects from the environmental component (figure 4.2b). Between 1970 and 1985, population growth rates were markedly higher when including the environmental contribution (but holding the average-environment age-structure) relative to the average environment, ranging between 0.01 and 0.11, suggesting that age-specific vital rates were driving population growth (figure S3.4). However, the environmental contribution declined over the study period, becoming negative in 1985 and then stabilising after 2000 (figure 4.2b). Conversely, the contribution of age-structure to variation in population growth rates relative to the average environment increased across the study period (figure 4.2b). There were large negative contributions before 1978 when fewer old-aged individuals were present, with population growth rates including the observed age-structure substantially lower than the average environment population growth rate. Furthermore, there was a large negative interaction effect of age-structure and the environment early in the study before 1985, and negative interaction effects after 2000 (figure 4.2b). Importantly, the variance decomposition of observed population growth rates in each year highlighted both age-structure and the environmental component as crucial drivers. 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 ~0.04, lying above the average-environment popualtion growth rate. However, before 1993, the contribution of age-structure to population growth rates was negative, suggesting that the population age-structure was unstable for much of the study period (figure 4.2b). The importance of age-structure for population growth rates was also not dependent on the choice average-environment conditions, with similar patterns observed when including a time-varying average environment as a reference (figure S3.5).

Finally, we separated the influence of the environmental component (projection matrix) into its two contributing processes, age-specific birth and survival probabilities. The crucial environmental component governing population growth rates was age-specific birth probabilities, with large positive contributions between 1970 and 1985, and declining contributions that stabilised later in the study period (figure 4.3). Furthermore, 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 birth rates (figure 4.3; figure 4.2b; figure S3.2). 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 was a much weaker driver of population growth rates, with contributions close to 0 across the study period (figure 4.3). Combined with negative contributions of age-structure early in the study period and strong negative interaction effects, this result suggests that despite larger observed birth rates having the potential in increase population growth rates in the 1970s and 1980s, age-structure was unstable, and observed population growth rates were lower.

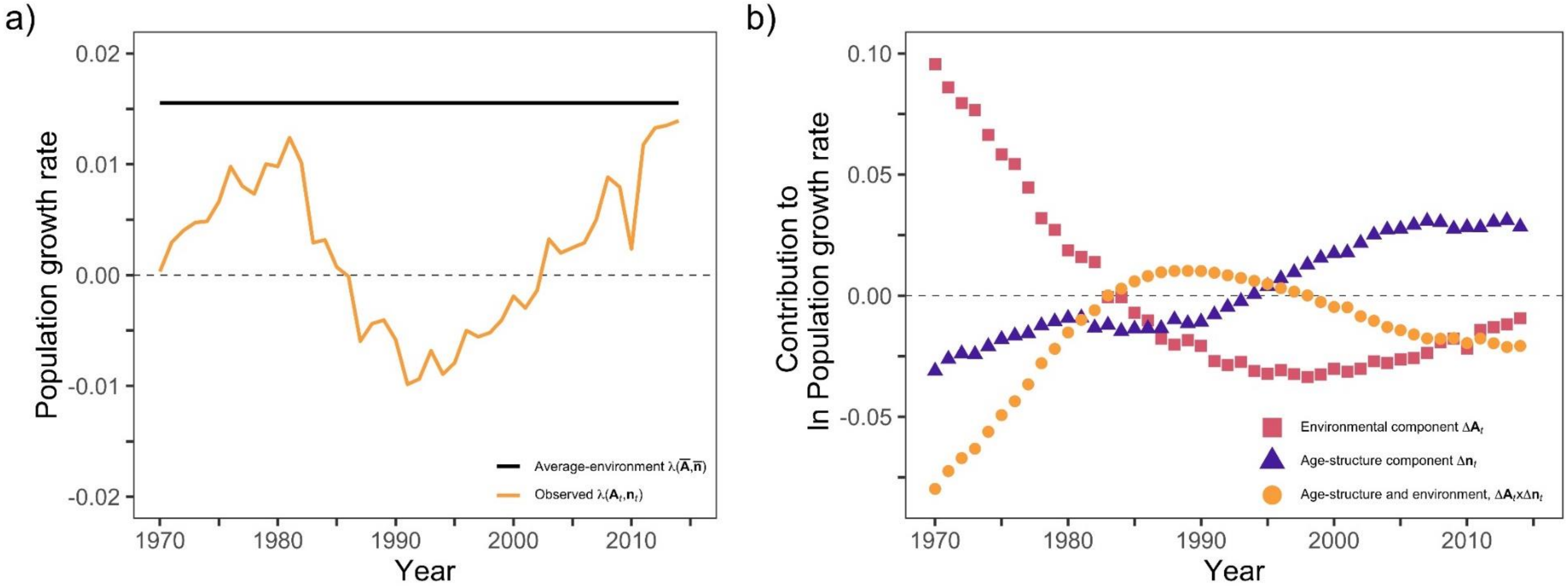

Figure 4.2 Age-structure is a key determinant of population growth rates. a) The observed log transformed short-term population growth rate (yellow line, ln $\lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$ from equation 3) between 1970 and 2014, relative to the average-environment short-term population growth rate (solid black line, ln $\lambda(\bar{\boldsymbol{A}}, \bar{\boldsymbol{n}})$ from equation 4). Dashed black line indicates a ln population growth rate of 0. b) The contribution of the age-structure component (purple triangles, $\Delta\boldsymbol{n}_t$) and environmental component (or age-specific vital rate component, pink squares, $\Delta\boldsymbol{A}_t$) to variation in annual log-transformed short-term population growth rates (ln $\lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$) between 1970 and 2014. Yellow circles indicate non-additive contributions from both the age-structure and environmental components in a given year ($\Delta\boldsymbol{A}_t x \Delta\boldsymbol{n}_t$). 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.

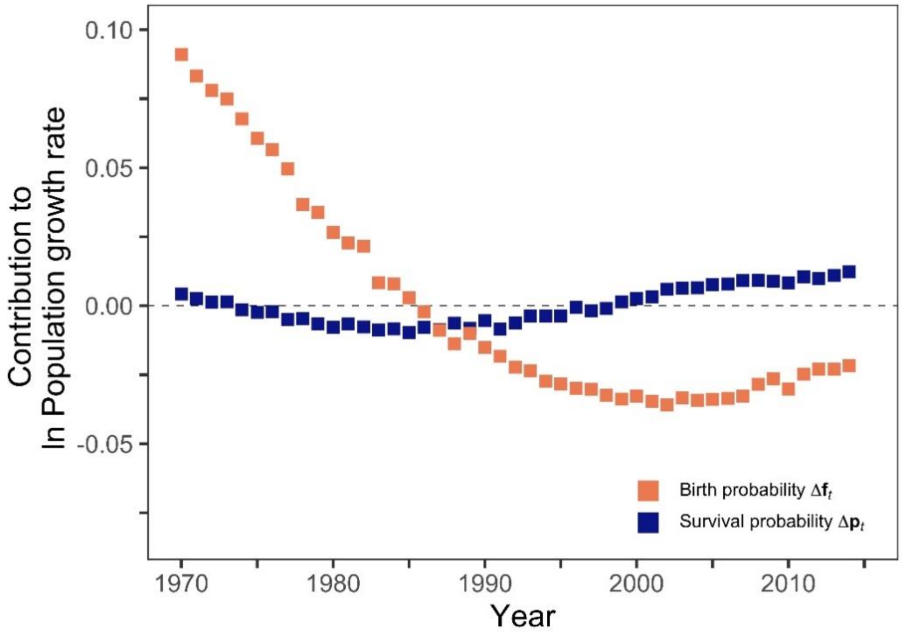

Figure 4.3 Age-specific birth probabilities are the key environmental component for population growth rates. The environmental component ($\Delta \boldsymbol{A}_t$) was partitioned in to its components of predicted age-specific birth (orange, $\Delta \boldsymbol{f}_t$), and survival (blue, $\Delta \boldsymbol{f}_t$) probabilities to assess their contribution to variation in log-transformed short-term population growth rates ($\ln \lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$) in captive-born females between 1970 and 2014. Dashed black line indicates a contribution of 0.

4.5 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 (Moss 2001, Boggs and Inouye 2012, Jenouvrier et al. 2014, Flockhart et al. 2015, Lusseau and Lee 2016). 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 population dynamics in long-lived species in addition to, and independently of, environmental contributions from vital rates. Using a retrospective variance decomposition, we found that a significant proportion of the variation in population growth rates was attributable to variation in age-structure, which exhibited large fluctuations over four and a half decades. The contribution of age-structure fluctuations to population growth rates was 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") still contributed significantly to variation in population growth rates between 1970-2014. Early in the study period (1970-1980), there was a substantial positive contribution of this component to variation in population growth rates relative to the average-environment, which was primarily driven by high birth rates. Furthermore, negative population growth rates between 1985-2000 were also associated with negative contributions from birth rates in the environmental component, and declines in the predicted birth rates across ages. These results support previous findings of a decline in adult birth rates in this population 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 (Coulson et al. 2000, Parker et al. 2009, Cook et al. 2013). For example, drought conditions in Kenya have been associated with lower birth rates in African elephants (Moss 2001). In the current population, monthly survival was highest at moderate temperatures and with increased rainfall (Mumby et al. 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). Interestingly, alongside a decline in habitat availability, declines in the wild elephant population over the last half-century may also have had an impact on fecundity in the captive population. Captive calves are often sired by wild bulls (Mar 2007), and so a larger wild elephant population in the past may have provided breeding opportunities to captive females, which would benefit birth rates in captivity. Despite uncertainty surrounding the mechanisms, our results clearly demonstrate significant contributions of this environmental component to variation in population growth rates.

Importantly, despite the significant positive contribution of birth rates to variation in population growth rates early in the study period, observed population growth rates were moderate due to an independent negative contribution from population age-structure, and large negative interaction effects between age-structure and the environment. 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. Furthermore, population growth rates were negative between 1985-2000 as birth rates declined and the contribution from age-structure remained negative, and after 2000 positive contributions from age-structure were dampened by negative environment effects. 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 1990-2014. We also observed short periods (around 1970, 1985 and 2009) with 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. The explanation for these trends is less clear, but changes in age-structure may be an indirect consequence of the capture of wild elephants in Myanmar. There was systematic capture from the wild in Myanmar until 1994, with approx. 3000 individuals wild-captured between the 1950s and 1994, but after this point wild-capture occurred at lower rates (Uga 2000, Mar 2007, Lahdenperä et al. 2018). Wild-capture may have been particularly influential on age-structure because it targeted younger individuals (Lahdenperä et al. 2018) who eventually gave birth to captive-born females, which were the focus of the current study. These initial imbalances in age-structure recovered over several decades as the population approached a more stable age-structure, resulting in positive contributions towards variation in 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 (Coltman et al. 2003, Bischof et al. 2018). Of course, poaching and hunting have immediate effects on age-specific vital rates, with implications for population viability and extinction risk (Lusseau and Lee 2016). However, they also have evolutionary implications by, for example, selecting for smaller bodied individuals with smaller auxiliary structures or disrupting social structure (Jachmann et al. 1995, Coltman et al. 2003, Gobush et al. 2008). 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 and 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 et al. 2018). Our results add to these studies across taxa, suggesting that the changes to population age-structure associated with human interference can have significant independent influence on short-term population dynamics.

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 (Stott et al. 2010, Gamelon et al. 2014, Mcdonald et al. 2016). Though a number of different methodological frameworks are available to assess such impacts (Ezard et al. 2010, Ellis and Crone 2013, Koons et al. 2016), these have not typically distinguished between contributions to population growth from vital rate variation and (st)age-structure fluctuations (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 sensitives, which can be cumbersome for complex models, and can be applied without modification to alternative frameworks such as Integral Projection Models (Ellner et al. 2016).

The long-term, multigenerational demographic studbook of timber elephants in Myanmar has provided novel empirical insights into the demographic drivers of population dynamics. However, the importance of demographic structure is not limited to age-structure. Sex ratios have also been linked with population dynamics and extinction risk (Coulson et al. 2001, Le Galliard et al. 2005), and have implications for human management (Clutton-Brock et al. 2002). An improved understanding of changes in demographic structure can provide novel insight into the mechanisms underpinning population dynamics. Therefore, long-term, individual-based monitoring of wildlife populations is crucial (Clutton-Brock and Sheldon 2010, Hughes et al. 2017). 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.

4.6 Acknowledgments

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Chapter 5

Identifying delayed climatic drivers of age-specific life-history in a long-lived mammal

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5.1 Abstract

Understanding how populations will respond to a changing climate is crucial to mitigate against widespread population declines. Life-history variation within populations may mean there are both immediate and delayed climate effects on vital rates such as mortality and reproduction. However, the mechanisms of how climate influences vital rates are poorly understood in long-lived species, for which decades of demographic/climate data is needed to unpick delayed effects. Here, we explored how the past climate influenced age-specific mortality and reproduction in the long-lived Asian elephant, using an extensive 45-year demographic dataset of semi-captive individuals from Myanmar, with detailed historic temperature/precipitation records and a broad climate index between 1962-2007. We tested delayed climatic drivers under two contrasting biological models; *continuous* effects, where mortality and reproduction are influenced by a cumulative effect of the past climate, and *risk window* effects, where climate variation in critical seasonal windows have a long-term influence on individual condition and thus vital rates. We find little support for the *continuous* and *risk window* hypotheses of delayed climatic effects in the past year on juvenile mortality, peak-age reproduction, or mortality and reproduction across lifespan. Our findings highlight the importance of exploring the long-term consequences of a changing climate on populations using a variety of mechanistic models.

5.2 Introduction

Climate change, alongside habitat loss, is one of the greatest threats to global biodiversity and predicted to cause widespread population declines and extinctions in the coming decades (Thomas et al. 2004, Brook et al. 2008, Butchart et al. 2010). Alarmingly, significant numbers of mammals and birds have already been negatively affected by climate change in at least part of their distribution (Pacifici et al. 2017). At the level of populations or individuals, climate change may result in range shifts or disruption to phenology and physiology, but responses are highly variable between species and often hard to detect (Both et al. 2006, Chen et al. 2011, Bellard et al. 2012). Pinning down the mechanisms that result in population decline under climate change is a challenge, but monitoring demographic rates provides a useful tool to investigate population-level responses to changes in the environment (Selwood et al. 2015). As such, profound effects on the demography and life history of populations have been documented in response to the climate, including biases to sex-ratio and impacts on survival and reproduction (e.g. Mumby et al. 2013, Herfindal et al. 2015, Campos et al. 2017, Peeters et al. 2017, Woodroffe et al. 2017, Paniw et al. 2019). However, not all species are equally prone to negative impacts from a changing climate, with key traits such as habitat specialisation and altitudinal range identified in vulnerable species (Pacifici et al. 2015, 2017). Life-history variation within and between taxa may also be a key predictor for how species or populations are influenced by environmental change (Fay et al. 2015, Herfindal et al. 2015, Cayuela et al. 2017). Ultimately, understanding demographic responses to a changing climate in animals presenting different life histories is crucial to prevent future population declines.

If a population is negatively affected by a changing in climate, questions arise regarding the mechanism of how climate variation, and which aspects of the climate, result in changes to vital rates such as survival or reproduction. Climate drivers may be more immediate, with physiological changes that influence body condition and metabolism, reducing individual performance and survival/reproduction (Johansen and Jones 2011, Cook et al. 2013, Walsh et al. 2018, Paniw et al. 2019). In contrast, the response may also be delayed and more complex, with multiple contributing factors that interact over longer timescales and more variation between individuals. For example, increased temperatures during the egg laying and incubation period were associated with reduced lifetime reproductive success in goshawks, but annual reproductive rates were higher when the egg laying period was hotter, and there was a large degree of individual variation in reproduction (Herfindal et al. 2015). Furthermore, populations may respond to different aspects of the climate, and both mean climate values or the variance in climate at a local scale, as well as broad-scale indices, may be important for vital rates (Stenseth et al. 2003, Jonzén et al. 2010, Campbell et al. 2012). The effect of climate on vital rates may also vary within populations, with age-classes or life-history stages (e.g. recruits) that are influenced more by climate (Gaillard et al. 2000, Coulson et al. 2001, Paniw et al. 2019), and so understanding climate responses across the lifecycle and at key life stages in long-lived species is crucial (Hindle et al. 2019). One key issue when assessing delayed responses to the climate is the necessity of long-term, individual-based demographic data in focal populations. Therefore, only few studies have investigated delayed climate effects, and further investigation into the long-term impacts of the climate on populations using long-term data is needed.

Several contrasting mechanisms may result in delayed responses to the climate. For example, where past climatic events result in defined and more predictable responses in vital rates, we may expect that continuous change in current vital rates is the result of a cumulative, weighted effect of the past climate (Roberts 2008). Continuous, cumulative responses to climate may be more prevalent where immediate physiological/phenological responses are present, and where vital rates are seasonal, with climatic conditions influencing traits such as growth or emergence (Parmesan 2006, Tenhumberg et al. 2018). African wild dogs present an example of a continuous response, in which high ambient temperatures were directly associated with reduced foraging times in females, and thus reduced recruitment at the end of the rearing season (Woodroffe et al. 2017). In contrast, past climatic events within a risk window (e.g. breeding season, critical development window) could result in changes to individual condition or frailty. Under this scenario, climate effects would not result in a predictable change in vital rates, but persistent average changes in vital rates in the future. A good example of risk window climate effects is the negative effect of temperature when a female was born on lifetime reproductive success in goshawks (Herfindal et al. 2015). Despite the potential differences in the mechanisms of delayed climate drivers, few studies have evaluated these contrasting mechanisms in the same species.

Long-lived species provide an interesting case study for understanding the impacts of climate change on demographic variation in wildlife populations. Theoretically, at the population level long-lived species are generally predicted to be buffered against climate variation. With increased longevity, which is associated with low annual mortality and reproduction, variance in vital rates (i.e. from annual variability in climate) has a smaller impact on population growth rates when compared to short-lived species (Morris et al. 2008). Furthermore, the demographic buffering hypothesis states that life histories should evolve to minimise the influence of environmental variation on fitness by buffering sensitive vital rates against environmental variation (Pfister 1998, Gaillard et al. 2000). Long-lived species may evolve to reduce the impact of climate effects on vital rates in sensitive age-classes (Rotella et al. 2012). However, several studies have found climate effects on vital rates in long-lived species. For example, drought years were associated with higher calf mortality in African elephants, and warm, wet and windy winter conditions were associated with reduced juvenile survival but increased adult fecundity and survival in Soay sheep (Forchhammer et al. 2001, Moss 2001, Foley et al. 2008). Thus, there is a need to investigate the pervasiveness of climate impacts on long-lived species, and for more studies assessing delayed climate impacts under contrasting mechanisms on vital rates.

In this study, we investigated delayed climate drivers of mortality and reproduction across lifespan in the Asian elephant (*Elephas maximus*) using a long-term multigenerational demographic dataset from Myanmar, alongside daily temperature and precipitation data and a broad-scale monsoon index between 1962-2007. Importantly, we explored two potential mechanisms of delayed climate effects; *continuous* effects where vital rates (over 5-day intervals) depend on a direct cumulative effect of the past climate, and *risk window* effects, where climate variation in a risk window (here seasons) influences subsequent annual vital rates. Among the world’s longest living terrestrial mammals, Asian elephants have a maximum lifespan of ~80 years and a mean age at first reproduction of 19.8, with inter-birth intervals of 5.99 years and reproduction to a maximum of 65 years old (Lahdenperä et al. 2014). Elephants are slow to recover from threats such as poaching (Turkalo et al. 2016), and current conditions have a long-lasting impact on fitness (Lee et al. 2013, Mumby et al. 2015). There are direct climate effects on vital rates in African elephants, for which extreme drought conditions decrease calf survival (Moss 2001, Foley et al. 2008). Asian elephants have seasonal patterns of survival in relation to the climate, and survival is higher in months with intermediate temperatures and more rainfall (Mumby et al. 2013). Across much of the range of Asian elephants, the climate follows monsoon patterns, with distinct hot, cold and wet seasons, which has the potential to influence factors such as the availability of food, disease transmission and thermoregulation (Sukumar 2003, Weissenböck et al. 2012, Mumby et al. 2013). However, despite seasonal variation, birth and mortality still occur throughout the year for Asian elephants, without a clear breeding season (Sukumar 2003).

We tested the effects of climate on vital rates in semi-captive Asian elephants used in the timber industry; although these elephants are managed in captivity, survival/breeding rates are largely natural, comparable to wild populations, and higher than those in zoos (Clubb et al. 2008, 2009, De Silva et al. 2013). Climate effects were explored on vital rates at two sensitive life-stages; juvenile mortality (0-4 years old) and peak-age reproduction (19-25 years old). In analyses, we tested the effect of climate on vital rates using both the mean and variance of climate anomalies (deviation from average climate conditions), and delayed climate effects of up to one year in the past under these contrasting hypotheses. To explore the different mechanisms of delayed climate drivers, flexible methods that capture past climatic variation in relation to demographic data are also important. Functional linear models (FLMs) are one emerging set of tools that have recently been applied to the investigation of past climate effects, and allow the effect of climate to be a smooth function through time based on the assumption that climatic conditions are correlated (Roberts 2008, Teller et al. 2016, Tenhumberg et al. 2018, Hindle et al. 2019). We used FLMs to capture i) *continuous* effects of past temperature and precipitation on juvenile mortality and peak-age reproduction at 5-day intervals, and ii) *risk window* effects, where the weighted effect of climate in each season (Cold: Nov-Feb, Hot: Mar-May, Monsoon: Jun-Oct) was tested against subsequent annual vital rates, for juveniles, peak-aged reproducers and for age-specific mortality/reproduction across ages. Finally, in addition to local climate effects, we tested the *risk window* effects of three broad-scale monsoon indices (Tsai et al. 2015) on subsequent annual vital rates.

5.3 Methods

Demographic data

Asian elephants are listed as endangered on the IUCN red list, with a declining and fragmented wild population of 40,000-50,000 individuals, which is mainly threatened by habitat loss and poaching (Choudhury et al. 2008). Alongside the wild population, there is a substantial captive population of approximately 16,000 individuals globally, which are mainly used for logging, tourism and ceremonial purposes in range countries (Sukumar 2003, 2006, Choudhury et al. 2008). Myanmar has the largest population of Asian elephants in captivity (>5000), and currently around 2700 elephants are state-owned and managed centrally by the Myanma Timber enterprise (MTE) for logging. Importantly, we define this population as semi-captive: elephants forage naturally without human supplementation outside of working hours, breeding and mortality rates are largely natural and elephants are not managed reproductively or culled, and elephants only have access to basic veterinary care. Individual-based records are kept for all elephants in the population in the form of logbooks, which are regularly updated and maintained by local veterinarians and mahouts (elephant riders). Records have been maintained by the MTE for over a century, and keeping systems are consistent across the country. The current study population is comprised of >9000 MTE elephants that were born in captivity or caught from the wild and demographic data has been compiled from individual logbooks and annual extraction reports.

Individual-based life-history data is available for all MTE elephants, and includes birth origin (captive-born or wild-caught), birth date (estimated if wild-caught), calves, and death date or last known date alive (for further information on life-history data see Lahdenperä et al. 2018). To assess the climatic drivers of vital rates, we restricted the initial demographic dataset to data from the Sagaing and Kachin regional divisions in the north of Myanmar. Sagaing and Kachin contain the largest area of unfragmented natural habitat remaining for Asian elephants (Leimgruber et al. 2003) and the majority of semi-captive Asian elephants are managed within deciduous forests in these regions and experience similar climatic conditions. Sagaing and Kachin also have a large number of elephants, which enabled us to maintain a sufficient sample size to investigate age-specific life-history variation. We only used reproduction events from females elephants because we could not reliably quantify reproductive rates in males. We further restricted the demographic data to include only individuals that were born in captivity after 1940, or caught from the wild after 1951, before which record keeping systems were not consistent, and we discarded approximately 5% of individuals due to contradictory death/departure/birth information.

We only considered demographic records and climate data between 1962-2007 for analyses, which enabled us to compare the predictive performance of models across climate variables. First, we assessed age-specific mortality and reproduction across ages for 1371 females between 0-65 years old. However, these analyses assumed that climate effects were consistent across ages. Although there may be covariance in the environmental drivers of vital rates for different life history stages (Rotella et al. 2012, Hindle et al. 2018), the impact of environmental variation often depends on an individual's age and sex (Gaillard et al. 2000). Thus, in subsequent analyses we mainly focussed on two vital rates at key life history stages: juvenile mortality (ages 0-4) and peak-age reproduction in females (ages 19-25; Hayward et al. 2014). These age-classes exhibit high rates of age-specific mortality/reproduction (Mar et al. 2012, Hayward et al. 2014), and population growth rates are most sensitive to changes in vital rates at these ages (Jackson et al. 2019).

Juvenile mortality data was available for 1705 calves (850 = females, 855 = males), and peak-age reproduction for 694 adult females between 1962-2007. For reproduction analyses, we assessed conception, which was the occurrence of a birth event from a given female 670 days (~22 months, the gestation period in Asian elephants; Sukumar 2003) in the future. The choice of conception probability allowed us to distinguish between climate drivers of mating decisions and conception, as opposed to potential climate drivers in utero. For all analyses, we scored time-dependent mortality and conception events as binomial response variables. All analyses were carried out in the R statistical package, version 3.5.3 (R Core Team 2019).

Climate data

Temperature (1961-2007) and precipitation (1951-2007) data were obtained from the APHRODITE daily gridded dataset for monsoon Asia (60°E-150°E, 15°S-55°N) at a spatial resolution of 0.25°, versions AphroTemp V1204R1 and V1003R1, respectively (available at http://www.chikyu.ac.jp/precip/; Yatagai et al. 2012). To assess climate variation at a scale consistent with demographic data, we restricted the full dataset to include only deciduous forest regions in the Sagaing and Kachin regional divisions of Myanmar. The climate data mask was obtained from the state and region boundaries and land use geospatial maps from the Myanmar Information Management Unit (MIMU, available at http://themimu.info/). We calculated the intersection between the 'deciduous forest' land use category and the Sagaing/Kachin regional divisions, and smoothed the final climate mask using qGIS version 3.5 (QGIS development team. 2018). We calculated mean daily temperature and precipitation values across the climate mask using the Climate Data Operators package, version 1.9.3 (Schulzweida 2018). We considered three seasonal periods in Myanmar, which were the Cold (November-February), Hot (March-May), and Monsoon (June-October) seasons (figure S4.1).

In addition to daily temperature and precipitation values, we also investigated vital rates with respect to a broad-scale climate indicator to test how annual climate variability influenced demography. Broad climate indices such as the North Atlantic Oscillation, which describe general climate patterns across large regions of the globe, are often better predictors of ecological processes than local weather patterns, and so it is important to compare local patterns to broad scale indices (Stenseth et al. 2003). We included the three annual scaled monsoon indices developed by Tsai et al. (2015), which are constructed from monsoon wind data for three monsoon season periods: March-May (early monsoon), June-August (mid monsoon) and September-November (late monsoon). The monsoon indices correlate to broad monsoon precipitation patterns in Southern Myanmar, and thus are a proxy for the strength of the monsoon in a given period in each year.

We aimed to explore how deviation away from average climate conditions influenced vital rates, rather than describe seasonal patterns, and so we decomposed raw daily temperature and precipitation data to extract climate anomalies (figure S4.2 & S4.3). First, we reduced the large variation in daily climate data by square root transforming mean data over 5-day increments. Then, we performed a Seasonal and Trend decomposition using Loess (STL) additive decomposition for each 5-day timeseries, using 1000 5-day increments for the trend-cycle window and 15 years for the seasonal window, and extracting the remainder (anomaly) components (figure S4.2 & S4.3; Cleveland et al. 1990). The 5-day temperature and precipitation anomalies and monsoon indices were used in all subsequent analyses on vital rates. In addition to mean temperature and precipitation values, the absolute magnitude, or variance, of climate anomalies may be just as critical for survival and reproduction (Campbell et al. 2012). Therefore, we also explored models using the absolute, squared values (variance) of climate anomalies.

Two contrasting models of delayed climate effects

Delayed climate effects in Asian elephants may occur through differing mechanisms; direct drivers such as capture from the wild have a direct and long-term effect on reproductive success and survival (Lahdenperä et al. 2018, 2019), and there are seasonal patterns in survival in relation to climatic variation (Mumby et al. 2013). The availability of detailed demographic data and accurate dates of birth/death enabled us to investigate delayed climatic drivers of vital rates under two contrasting biological models, which we define here as the *continuous* model and the *risk window* model (summarised in figure 5.1). In the *continuous* model (figure 5.1a), we assumed that the instantaneous, ~continuously varying probability of mortality/reproduction depended on a predictable, weighted, and summed effect of climate in the past over a discrete, pre-defined climate window. Here, we considered the continuous variation in mortality/reproduction rates over 5-day increments between 1962-12-31 and 2007-12-30. We explored the following set of discrete past climate windows: 60, 180, and 365 days. Within each of these climate windows, we tested varying climate increments, and the full set of past climate window/increment combinations in *continuous* analyses were 60 by 5 days, 180 by 10 days, 365 by 5 days, and 365 by 20 days.

In the *risk window* model (figure 5.1b), we assumed that climate variation in a discrete, pre-defined climate window influenced an individual's condition, which increased/decreased their subsequent probability of mortality/reproduction over a discrete, pre-defined demographic window. We considered the three climate seasons in Myanmar (Cold: Nov-Feb, Hot: Mar-May, Monsoon: Jun-Oct) and the three monsoon season periods (Mar-May, Jun-Aug and Sep-Nov; Tsai et al. 2015) as the focal climate windows. Seasonal models included climate increments of 10 days, and monsoon periods included a single index for each period. The demographic window was the subsequent year, such that climate variation within each season or monsoon season influenced subsequent annual mortality and reproduction e.g. if the focal season was the hot season (Mar-May), then the demographic window was Jun-Feb. The maximum past climate window was one year for each of the two mechanisms, and although this does not present a fully comprehensive test of delayed climate effects across lifespan in Asian elephants, the current framework enabled us to directly compare *continuous* and *risk window* effects.

Past climate effects on continuously varying vital rates

For *continuous* model analyses, we tested the cumulative, weighted effect of the past climate anomalies on juvenile mortality and peak-age conception probability. We constructed discrete-time datasets at 5-day intervals between 1962-12-31 and 2007-12-30 (total = 3288 increments), where each row represented an individual in a given 5-day interval. Individuals entered the dataset at the 5-day window of their birth

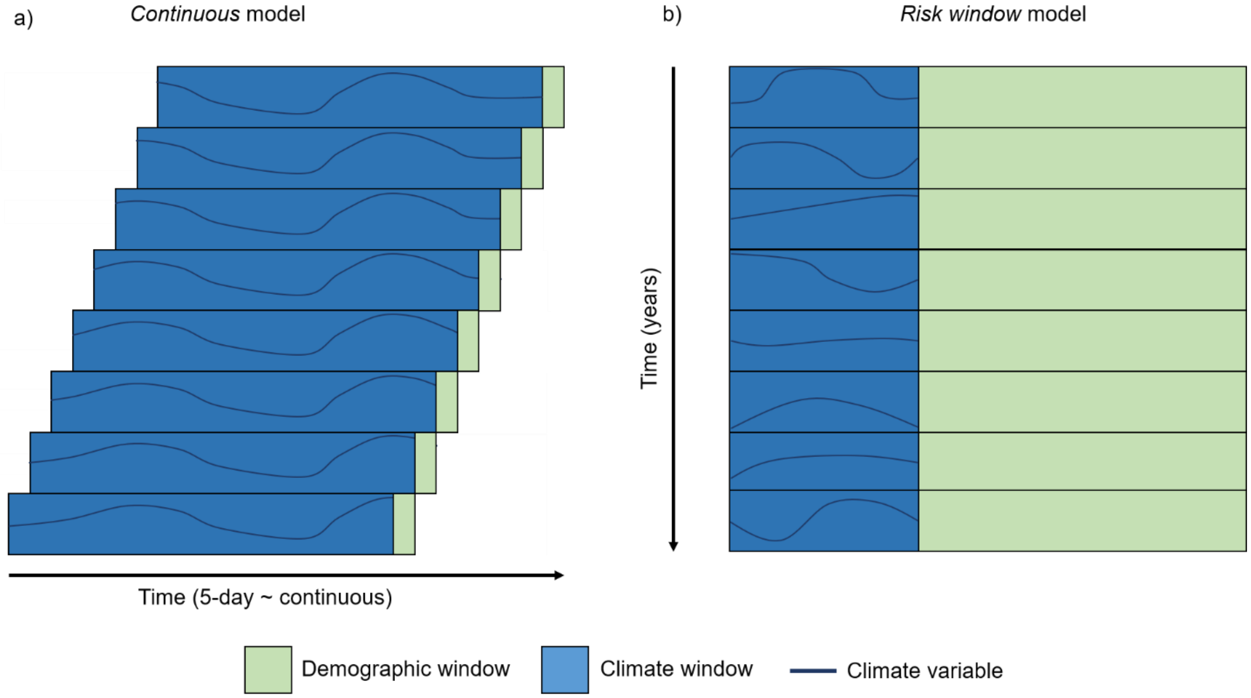

Figure 5.1 Two models of delayed climatic drivers of life history in long-lived species. a) In the *continuous* model, we assumed that the ~continuous probability of mortality/reproduction in 5-day demographic windows (green boxes) depended on the weighted effect of a past climate variable (blue lines) in a pre-defined climate window (blue boxes). b) In the *risk window* model, we assumed that the weighted climate effect acted in a pre-defined climate window (seasons or monsoon seasons) and influenced subsequent mortality/reproduction over an extended, pre-defined demographic window (years).

(mortality) or 19 years old (conception), and exited the analysis at their age of death or age at censoring (4 and 25 years old for mortality and conception, respectively). The demographic datasets used in *continuous* analyses consisted of 387793 and 258378 time-event observations for mortality and conception, respectively. We tested *continuous* past climate effects using functional linear models (FLMs) with binomial error structures and logit link functions. FLMs use the temporal relationship between climate covariates and assume that the effect of climate is a smooth function over time (Teller et al. 2016). All FLMs were fit using the *gam* function in the package *mgcv* (Wood 2017).

We explored FLMs in *continuous* analyses under three scenarios, i) using mean 5-day climate anomalies for all climate windows, ii) using the variance (square) of climate anomalies for a 365 by 5 day climate window, and iii) partitioning analyses by season and exploring 180 by 10 day climate windows. We partitioned the effects by season in scenario iii because the impact of climate anomalies may not be consistent throughout the year, with for example, positive temperature anomalies being beneficial in the cold season and detrimental in the hot/dry season.

Thus, for individual i in 5-day interval t, the probability of mortality μ is given by

$$logit(\mu_{it}) = \beta^0 + \beta^a a_{it} + \beta^s s_i + \beta^\tau \tau_t + f_v(v_t) + \sum_{l=1}^{L} f_C(l)\, C_{lt}, \text{ (eqn 1)}$$

where β^0 is the intercept, $\beta^a a_{it}$ is a continuous linear term with coefficient β^a for the age a (in days) of individual i at time t, $\beta^s s_i$ is a categorical linear term with coefficient β^s for the sex s (Male vs. Female) of individual i, $\beta^\tau \tau_t$ is a continuous linear term with coefficient β^τ for the scaled time point of the study at time t to account for temporal trends in vital rates, and $f_v(v_t)$ is a term to account for seasonal vital rate variation, where f_v is a cyclical smoothing function and v_t is the day of the year at interval t. f_C is a smoothing function of past climate over time, where l is the climate increment over the full climate window L, and C_{lt} is the climate C at climate increment l from time point t. The smoothing function f_v is a cyclic cubic regression spline with 12 knots, parameterised by spline basis expansion (Wood 2017). The climate smoothing function f_C is a cubic regression spline with 8 knots parameterised by spline basis expansion. Both smoothing functions were penalized with quadratic smoothing penalties, up to the second derivative (Wood 2017), with smoothing parameters that were estimated using restricted maximum likelihood (REML; Wood 2011).

For reproduction models, the probability of conception φ for individual i at 5-day increment time t is given by

$$logit(\varphi_{it}) = \beta^0 + \beta^a a_{it} + \beta^O O_i + \beta^\tau \tau_t + f_v(v_t) + \sum_{l=1}^{L} f_C(l)\, C_{lt}, \text{ (eqn 2)}$$

Where $\beta^O O_i$ is a categorical linear term with coefficient β^O for the birth origin O (captive-born vs. wild-caught) of individual i.

Seasonal risk window climate effects

For *risk window* models, we tested the effect of climate anomalies in focal seasons on subsequent annual vital rates, first across lifespan and second for key life-history stages (juvenile mortality and peak-age conception). We constructed discrete-time datasets on annual timesteps for each of the focal seasons in Myanmar: cold, hot, and monsoon. For each focal season in each year, we included subsequent annual demographic data for all individuals who entered (born/captured) the population before the end of the focal season. We assessed subsequent annual vital rates using FLMs under two scenarios, i) using mean climate anomalies, and ii) using the variance (square) of climate anomalies.

Thus, for analyses of age-specific mortality across lifespan (between 0-65 years of age), the subsequent annual mortality μ for individual i in focal year y is given by

$$logit(\mu_{iy}) = \beta^0 + f_a(a_{iy}) + \beta^O O_i + \beta^\tau \tau_y + \sum_{q=1}^{Q} f_C(q)\, C_{qy}, \text{ (eqn 3)}$$

where f_a is a smoothing function of a_{iy}, the age a (in days) of individual i during focal year y, $\beta^\tau \tau_y$ is a continuous linear term with coefficient β^τ for the scaled time point τ of the study in focal year y, and f_C is a smoothing function of climate over the focal season, where q is the climate increment over focal season climate window Q, and C_{qy} is the climate C at climate increment q in in focal year y. The smoothing functions were cubic regression splines parameterised by spline basis expansion. The number of knots in the climate smoothing function f_C depended on the focal season (Cold = 4, Hot = 3, Monsoon = 6). The subsequent annual conception φ for individual i in focal year y is given by

$$logit(\varphi_{iy}) = \beta^0 + f_a(a_{iy}) + \beta^O O_i + \beta^\tau \tau_y + \sum_{q=1}^{Q} f_C(q)\, C_{qy}. \text{ (eqn 4)}$$

For *risk window* models of subsequent juvenile mortality and subsequent peak-age conception, the FLMs were similar to equations 1 and 2, respectively, but the time increment was year y, and they excluded the cyclical smoothing term $f_v(v_t)$.

Broad-scale monsoon season effects

The impact of the monsoon index in the focal monsoon period on subsequent annual juvenile mortality and peak-age conception was estimated using generalised linear models (GLMs), and the age-specific mortality and conception at all ages using generalised additive models (GAMs), with binomial error structures and logit link functions. The form of the monsoon period models was identical to the other *risk window* models, but included a single continuous linear covariate for monsoon index in the focal period.

Model predictive performance

For all models in both *continuous* and *risk window* analyses, to assess whether there was support for the addition of a delayed climate effect, we tested the predictive performance of each model using cluster cross validation. Then, we compared the predictive performance of the model with the climate covariate or smoothing term to a base model excluding the climate effect. The *continuous* FLMs and base models were refit on a test dataset excluding data at the level of each climate window e.g. if the climate window was 365 days, 1 year of data was excluded in each step. *Risk window* models and base models were refit excluding each year of data, and consecutive blocks of 5 years for the age-specific models at all ages. The test models were used to predict the vital rate in the out-of-sample dataset. We calculated the predictive performance using the log loss function for each set of out-of-sample predictions, as follows:

$$Log\ loss = \sum_{p=1}^{P} \sum_{i=1}^{I} -o_{ip}\ \log(e_{ip}) - (1 - o_{ip}) \log(1 - e_{ip}), \text{ (eqn 5)}$$

where for individual i in out-of-sample cross validation step p, o_{ip} is the observed binomial response, and e_{ip} is the model predicted out-of-sample probabilities. Lower $Log\ loss$ scores indicate higher predictive performance. In addition to cross validation, we also compared the Schwarz's Bayesian information criterion (BIC) between the base model and climate models, which was selected due to its higher penalty for the addition of model parameters, which was greater in FLMs (Burnham and Anderson 2004).

5.4 Results

Between 1962-2007, the mean annual juvenile mortality was 0.065 ± 0.005 (Standard error; range = 0-0.16), and 30.5% of calves died before the weaning age of 5 (range = 26.9-34.1%). The mean annual peak-age conception rate was 0.084 ± 0.007 (range = 0-0.221), such that 50.2% of females between 19-25 conceived offspring. The median number of juvenile mortality events in each year was 7 juvenile mortality, with a total of 337 across the study period, but the number of juvenile mortality events was variable between years, with range of 0-16. The median number of peak-age conception events was 5, with a total of 296, but these were also variable, with between 0-17 in each year (figure 5.2a & figure 5.2b). Juvenile males had an annual mortality rate of 0.071 ± 0.005 relative to 0.056 ± 0.004 for females (figure 5.2a), and at peak reproductive ages the average conception rate for wild-caught females was 0.07 ± 0.006, compared to 0.10 ± 0.008 in captive-born females.

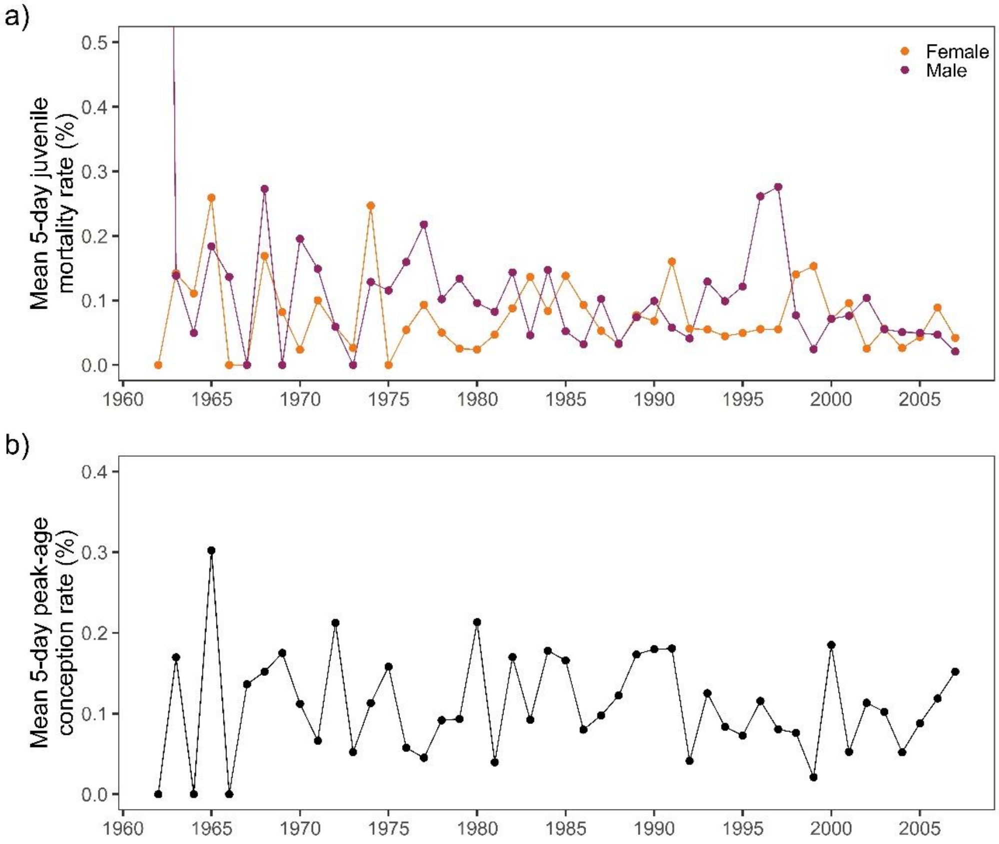

Figure 5.2 Average annual trends in juvenile mortality (a) and peak-age reproduction (b) in the Sagaing and Kachin regional divisions of Myanmar at 5-day increments. a) The mean annual 5-day mortality rate for juveniles (0-4 years old) between 1962-12-31 and 2007-12-30, for females (orange) and males (purple). b) The mean annual 5-day conception rate for peak reproductive-aged females (19-25 years old) between 1962-12-31 and 2007-12-30.

There was a large variation in temperature (1961-2007) and precipitation (1962-2007) within years across the study period. The cold season between November-February was dry and cold, with a mean temperature of 18.7°C ± 2.26 (standard deviation [SD]) and a mean precipitation of 0.60 mm ± 2.07 (figure S4.1). The hot season between March-May was hot and dry, the mean temperature was 25.4°C ± 2.49 (SD), with a mean daily rainfall of 2.51 mm ± 4.35 (figure S4.1). The monsoon season, between June-October, was most hot and wet, with a mean temperature of 26.5°C ± 1.35 and an average precipitation of 8.86 mm

± 7.84 (SD), (figure S4.1). Between years, average seasonal temperatures ranged between 17.2-20.0°C, 23.9-26.6°C, 25.8-27.6°C, for the cold, hot and monsoon seasons, respectively. Precipitation was also variable between years, with season averages of 17.2-20.0 mm, 17.2-20.0 mm, 17.2-20.0 mm, for the hot, cold and monsoon seasons, respectively. Generally, there was an even distribution in both precipitation and temperature anomalies (deviations from the average climate values) across the study period (figure S4.2 & figure S4.3). Precipitation decreased slightly after the year 2000, and temperature increased over the study period (figure S4.2c & figure S4.3c).

Buffering against past climate

For *continuous* models, we aimed to assess the past climate effect on juvenile mortality and peak-age conception at 5-day intervals. We found little evidence of delayed climate effects of juvenile mortality or peak-age reproduction for different climate windows, different seasons, or for the variance in climate anomalies (figure 5.3; table 5.1; table S4.1). Juvenile mortality models suggested that higher temperatures in the past 6 months improved survival (figure 5.3a & figure S4.4). This result was supported by cross validation results; for the models of 365 by 5 and 365 by 20 day climate windows, the difference in log $loss$ between the test model and base model was -2 (table 5.1; table S4.1). However, a comparison of BIC between the test model and base model indicated little support for past temperature effects on juvenile mortality, and the increase of BIC in the test model suggests that the differences observed from cross validation may be due to overfitting (table 5.1; table S4.1). Therefore, we conclude that we do not have support for a temperature effect on juvenile mortality. Similarly, when exploring the variance of climate anomalies on juvenile mortality, initial models suggested that there was a negative effect of variance in temperature and precipitation anomalies on juvenile mortality, i.e. larger variance in climate anomalies improved survival, but BIC results indicated improved predictive performance in the base model without climate (table 5.1; table S4.1; figure S4.7). We also found no evidence of past climate effects on juvenile mortality for different seasons (figure S4.6; table S4.1). For peak-age conception models, we found no support for past climate effects under any scenario for both cross validation and BIC (figure 5.3c & figure 5.3d; figure S4.5-7; table 5.1; table S4.1). The results from *continuous* models suggest that for key vital rates, there was no evidence for past climate effects on ~continuous patterns of mortality or reproduction.

For *risk window* models, we aimed to assess how climate in seasonal windows influenced subsequent annual mortality and reproduction. Similarly, found little evidence for delayed climate effects in focal seasons/monsoon seasons on subsequent annual vital rates. When using focal seasons as the climate windows, for juvenile mortality there was little support for delayed *risk window* effects (figure 5.4a & figure 5.4b; table 5.1; figure S4.8; table S4.2). There was support from cross validation for an effect of the precipitation anomaly in the cold season on subsequent annual juvenile mortality ($\Delta \log loss = -2.5$), with larger precipitation anomalies associated with lower mortality, but no support from BIC (table S4.2). In addition, when exploring subsequent mortality at all ages with respect to seasonal climate, there was no support for *risk window* effects across lifespan (table S4.1). Similarly, for peak-age conception and conception probability across lifespan, we found no support for delayed climate effects for focal seasons (figure 5.4c & figure 5.4d; table 5.1; figure S4.8; table S4.2). There was a suggestion that larger cold season precipitation anomalies were associated with a higher conception probability across lifespan, but again no support from BIC (table S4.2).

When investigating the monsoon index in focal monsoon season periods and its effect on subsequent annual vital rates, again we found little support for delayed climate drivers under any scenario (figure 5.4c & figure 5.4d; table 5.1; figure S4.9; table S4.2). There was an indication that stronger monsoon periods

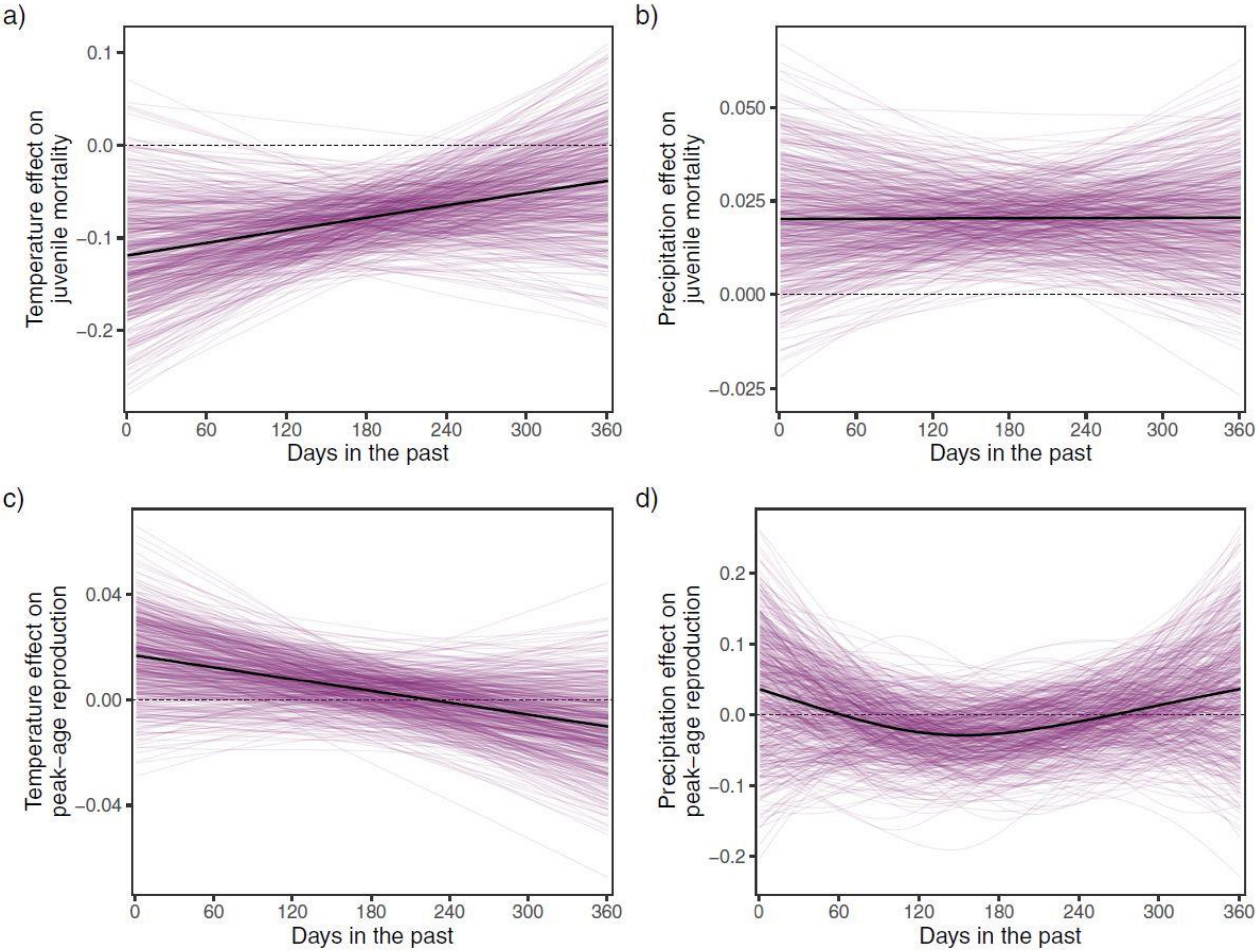

Figure 5.3 Past climate effects on juvenile mortality (a & b) and peak-age reproduction (c & d) from *continuous* models of delayed climatic drivers. The effect of anomalies in temperature (a & c) and precipitation (b & d) in the previous year (by 5-day increments) on 5-day juvenile mortality (a & b) and peak-age conception (c & d) rates. Coloured lines are simulated past climate coefficients from 500 posterior simulation iterations of each test model, solid black lines are mean past climate coefficients from the model, and dashed lines are a coefficient of 0 i.e. no effect of past climate.

between March-May decreased the conception probability across lifespan, but similarly we found no support in BIC (table S4.2). Overall, we find little evidence for either *continuous* or *risk window* models of delayed climate drivers in the past year for juvenile mortality, peak-age conception, or mortality and reproduction across lifespan.

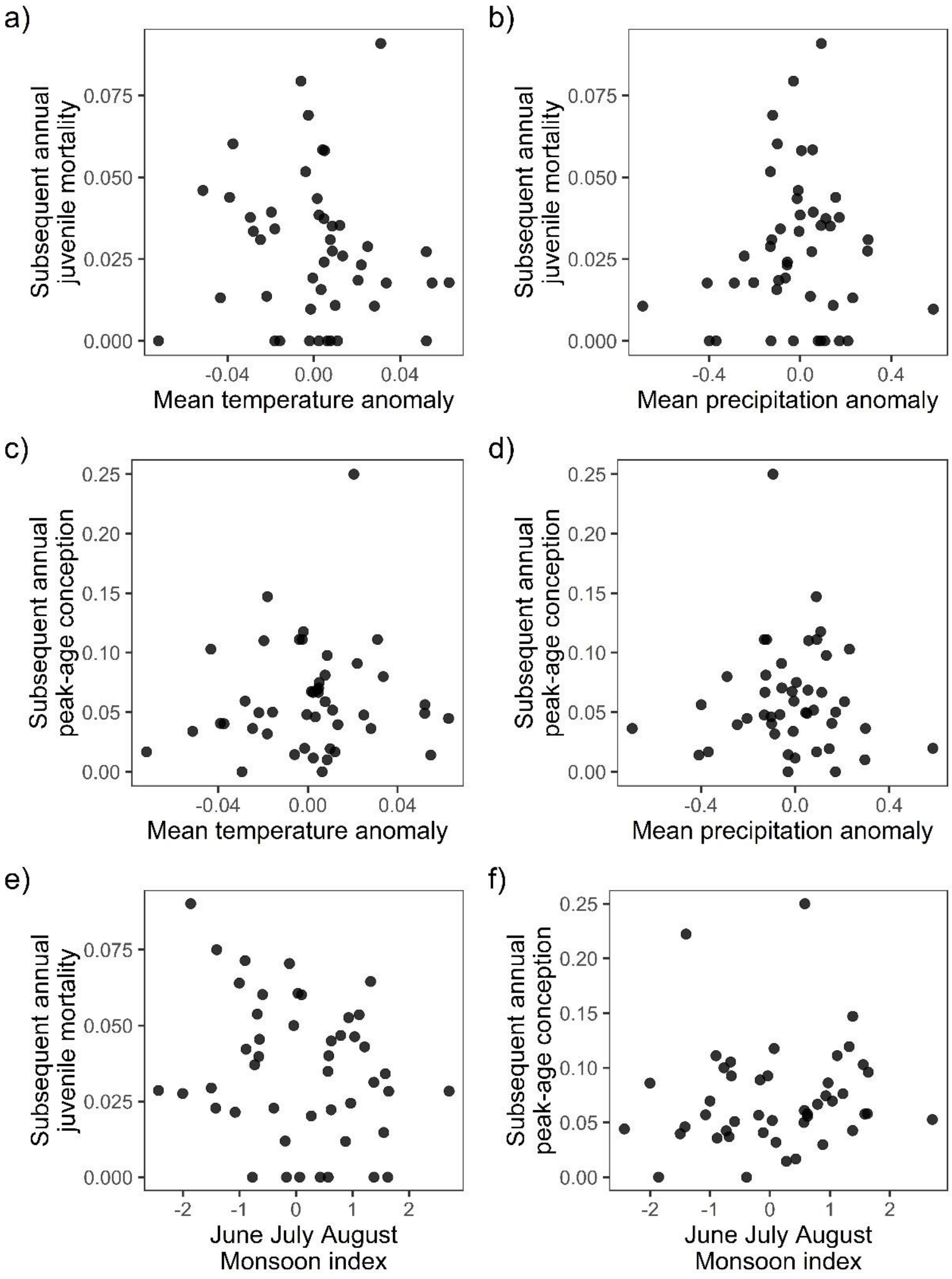

Figure 5.4 Past climate effects on juvenile mortality (a, b & e) and peak-age reproduction (c, d & f) from *risk window* models of delayed climatic drivers. Panels a-d display the mean temperature and precipitation anomaly in the monsoon season between 1961-2007 (a proxy for the weighted climate effect in the focal season) and its effect on subsequent annual vital rates. Panels e and f display the June July August Monsoon index from Tsai et al. (2015) and subsequent annual vital rates.

Table 5.1 Key cross validation results for *continuous* and *risk window* models of delayed climate drivers of life history in Asian elephants. $\Delta\, log\, loss$ and ΔBIC indicate the difference between the test model (with the climate variable) and the base model (without the climate variable) in $log\, loss$, the cross-validation metric, and Schwarz's Bayesian information criterion (BIC), respectively. $\Delta\, log\, loss$ values <= -2 are highlighted in bold, indicating cross validation support for the model.

Delayed climate model	Climate window	Response variable	Climate variable	$\Delta\log loss$	ΔBIC
Continuous	365 by 5 day past climate window	Juvenile mortality	Precipitation	-0.6	18.6
			Temperature	**-2.0**	**15.6**
		Peak-age conception	Precipitation	1.5	21.2
			Temperature	4.8	35.0
		Juvenile mortality	**Temperature variance**	**-5.4**	**28.0**
			Precipitation variance	**-3.1**	**19.2**
		Peak-age conception	Temperature variance	2.8	34.3
			Precipitation variance	1.5	23.5
Risk window	Focal season by 10 days	Subsequent juvenile mortality	Monsoon season temperature	7.2	20.7
			Monsoon season precipitation	11.9	22.8
		Subsequent peak-age conception	Monsoon season temperature	3.0	16.9
			Monsoon season precipitation	1.5	21.7
		Subsequent mortality all ages	Monsoon season temperature	7.1	21.8
			Monsoon season precipitation	13.2	18.8
		Subsequent conception all ages	Monsoon season temperature	11.5	20.4
			Monsoon season precipitation	5.0	27.1
	Single monsoon index value	Subsequent juvenile mortality	June July August Monsoon index	0.3	6.3
		Subsequent peak-age conception		0.9	7.0
		Subsequent mortality all ages		2.0	10.0
		Subsequent conception all ages		8.6	10.1

5.5 Discussion

A changing climate can have both immediate and long-term consequences for life history in populations of long-lived species (Foley et al. 2008, Herfindal et al. 2015). However, we found little evidence of delayed climate effects in the previous year on mortality and reproduction for key life history stages and across lifespan for Asian elephants. Importantly, in the current study we present two contrasting models of delayed climate drivers on vital rates for long-lived species: *continuous* effects and *risk window* effects, which can provide insights into the mechanisms of how a changing climate influences population dynamics. Studies have investigated *continuous* (Campos et al. 2017) and *risk window* (Herfindal et al. 2015) effects independently, but to our knowledge no study has explored contrasting potential mechanisms in the same population. We welcome more studies assessing different mechanisms for climate drivers in other taxa, particularly where direct climate effects are unknown, to disentangle how climate change results in population decline.

One potential explanation for a lack of delayed climate effects is that Asian elephants are buffered against climate variation, but the current study does not present a comprehensive assessment of buffering. This explanation would be in support of comparative evidence, which suggests that long-lived species will be buffered against environmental variation; annual variability in vital rates imposed by a change in climate have less impact on population growth rates in long-lived species (Morris et al. 2008). However, we cannot rule out demographic responses to the climate for several reasons. First, we tested delayed climate effects only in the previous year on demography under two contrasting hypotheses. In long-lived species climate effects may actually occur over much greater timescales or act on critical windows of development that were not captured in the current study. For example, with capture from the wild, which is another crucial driver of population dynamics in this system, reductions in reproduction and survival last for over a decade following capture (Lahdenperä et al. 2018, 2019). Therefore, any cumulative effects of changes in climate may act over several decades, impacting lifetime measures of fitness. Environmental effects occurring at critical development windows may also play a crucial role in Asian elephants; birth in the high-stress working season or in drought conditions can have a lasting impact on fitness across lifespan in elephants (Lee et al. 2013, Mumby et al. 2015). Ultimately, exploring delayed climate effects under a broad range of potential mechanisms is crucial where direct climate effects are unknown.

Second, in the current study we addressed demographic responses to deviations away from average climate conditions (anomalies) rather than direct responses to temperature and precipitation values. However, there is evidence for seasonal patterns of survival in the current population with respect to the climate; monthly survival was highest at intermediate monthly temperatures and with higher monthly rainfall (Mumby et al. 2013). Although Mumby et al. (2013) suggest seasonal patterns in vital rates, they do not separate seasonal variation from climate effects. Furthermore, human management is also seasonal, with rest periods in the Hot season and higher workloads in the Monsoon season, that have implications for long-term fitness in the current population (Mumby et al. 2015). Therefore, seasonal patterns alone may not capture true direct climate effects on elephant life history, and further investigation of these effects is needed. Third, extreme climatic events, which were not captured in this study, may be more important for population dynamics in elephants. In African elephants, drought years are associated with higher juvenile mortality rates, which suggest a direct climate influence on vital rates (Moss 2001, Foley et al. 2008). Although Asian elephants occur in different habitats, and their response to extremes in climate remains unclear (Sukumar 2003), relating extreme climate events such as drought or monsoon conditions to population dynamics in Asian elephants may be crucial in future studies.

The role of a changing climate on population dynamics can be complex and indirect, and factors such as density dependence have the potential to mediate or exacerbate environmental effects (Kausrud et al. 2008). Under this scenario, changes in the environment caused by the climate influence the availability of resources needed for growth and reproduction, which influences intraspecific competition and other density dependent processes (Coulson et al. 2000, Sæther et al. 2000). Climate change and density dependent effects have been demonstrated to have immediate impacts on vital rates and population dynamics (Kausrud et al. 2008), and to have delayed impacts where early-life conditions influence survival and recruitment later in life (Forchhammer et al. 2001, Payo-Payo et al. 2016). Furthermore, Albon et al. (2017) revealed that changes in the climate directly influences density-dependent body mass changes in Svalbard reindeer, which in turn influences population vital rates. Density dependence was excluded from the current study because a relationships between annual population size and vital rates were not found in this semi-captive population, for which the notion of density dependence is not trivial (Jackson et al. 2019). However, density dependence may mediate delayed climate effects in long-lived species such as Asian elephants. Future studies investigating how delayed climate effects under a variety of different mechanisms influence density dependence and population dynamics will be crucial in understanding how populations respond to climate change.

Two additional hypotheses that may explain the observation of a lack of delayed climate effects on vital rates in this study are the management strategies employed in this population and the availability of demographic data. Although the current study population has natural breeding/mortality rates and is able to forage naturally outside of working hours, individuals are still managed directly by veterinarians and mahouts for use in the timber industry (e.g. Robinson et al. 2012, Lahdenperä et al. 2018). As a result, it is plausible that instead of a form of demographic buffering, timber elephants are buffered by the adaptive management of humans. Under this scenario, when climate conditions are extreme, veterinarians and mahouts take steps to reduce workload, thus reducing the risk of mortality and increasing reproduction probability. Indeed, workload restrictions depend on the weather conditions, and elephants are given rest at the hottest time of the year (Robinson et al. 2012). Nevertheless, mortality and reproduction rates in this population are largely natural and comparable to wild populations (De Silva et al. 2013). Furthermore, the exact influence of human management is unknown; it is equally plausible that work-related stress would exacerbate any effect of climate on elephants.

The availability of data for the current study, particularly for *continuous* models of delayed climate drivers, may also mean that we were unable to detect past climate effects on vital rates. By selecting demographic windows of 5 days, while useful to assess ~continuous vital rate patterns, we reduced the number of mortality and conception data points in each window. Although our ability to detect climate effects at this increased resolution may have been reduced, generally our results were supported in *risk window* models, which were at annual timesteps. Therefore, human management and data availability have the potential to influence our observations.

Ultimately, human-induced climate change remains one of the greatest threats to global biodiversity (Butchart et al. 2010). Despite differences across taxa, rapid and extreme climate change will undoubtedly decrease wildlife populations in the coming decades (Pacifici et al. 2017). Even if populations of long-lived species such as Asian elephants are buffered, extreme changes in climate associated with future runaway climate change, which tip demographic rates beyond sustainable levels, are still likely to have a large impact on populations (Steffen et al. 2015, de Silva and Leimgruber 2019). However, diversity in life-history rates across taxa influences species' responses to climate change (Morris et al. 2008). We add to a small group of studies investigating delayed climate impacts on vital rates using long-term data, which are vital to understand how climate change will influence populations. Furthermore, the assessment of different mechanisms for delayed climate effects is crucial where more direct mechanisms are unknown.

5.6 Acknowledgements

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Chapter 6

Management Recommendations

I intend to submit this chapter to the Myanma Timber Enterprise.

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To whom it may concern,

The Myanmar timber elephant project has the privilege of studying the unique population of working elephants owned and managed by the Myanma timber enterprise. One of the key aims of our scientific research is to provide evidence that is useful for management practitioners in Myanmar, and we hope that our work can contribute towards the sustainable management of timber elephants in the future.

I have recently completed the PhD thesis entitled *Using semi-captive Asian elephants to examine population dynamics in long-lived mammals* at the University of Sheffield. The results of this thesis have direct implications for the management of timber elephants in Myanmar, which are as follows:

1. Females caught from the wild produce half the number of calves as captive-born females, and this effect lasts for over a decade. Adult females are also important for the growth of the population. We recommend improving the working conditions, nutrition and conditions for reproductive wild-caught females (391 wild-caught females in 2014) to benefit for the population.
2. Around 25% of young elephants die before taming ages, and this is important for population growth. We recommend improving care for mothers early in their calf's life, and introducing soft taming techniques to improve the growth of the population.
3. There may be fluctuations in the number of young elephants born in the population in future, changing the need for training and workload.

We welcome the addition of maintaining a sustainable captive population to the 2018 Myanmar Elephant Conservation Action Plan (MECAP). Fortunately, population extinction was not predicted in this thesis, and this suggests that sustainably managing the MTE population can be positive for the conservation of Asian elephants. Improving the survival of young calves the reproduction in adult females by just 10% would be beneficial for the population in future, The Myanma timber enterprise population of ~2800 individuals may be up to 7% of the remaining Asian elephant population, and so I argue that these elephants are a significant unit of conservation.

Queries arising from these recommendations are welcomed, and we are happy to give more detailed information on any of the topics discussed. Please find enclosed a copy of the PhD thesis. We endeavor to work closely with the Myanma timber enterprise to improve the sustainability of management in timber elephants, and once again take this opportunity to thank the Union of Myanmar for the opportunity to work with this population.

Yours sincerely,

John Jackson

PhD candidate, University of Sheffield

Chapter 7

General discussion

7.1 Wild-capture and population dynamics in Asian elephants

Few wildlife populations have been unaffected by the exponential increase of the human population. Three quarters of the terrestrial environment and two thirds of the marine environment have been significantly altered by human actions, and up to 1 million species are threatened with extinction in the coming decades (Díaz et al. 2019). Therefore, understanding the processes underpinning population decline is crucial to develop effective conservation strategies (Caughley 1994). The anthropogenic drivers of population decline, namely, land-use (or sea-use) change, direct exploitation, climate change, pollution, and invasive species, have immediate negative impacts on wildlife populations. However, populations may also exhibit indirect, long-lasting responses to changes in their environment, and we need more studies investigating population dynamics using long-term demographic data. In the current thesis, I have explored the drivers of population dynamics in a semi-captive population of Asian elephants, using a long-term, individual-based demographic dataset from timber camps in Myanmar.

The key driver of population dynamics in semi-captive Asian elephants that I identified in the current body of work was the capture of individuals from the wild, which has had both immediate and long-lasting demographic impacts on this population. First, in chapter 2 I demonstrated that females captured from the wild had a consistent reduction in breeding success relative to those born in captivity, with a reduced reproduction probability over their lifetime and at peak ages, and an increased age at first reproduction. The effects of capture from the wild on reproductive success lasted for over a decade, and calves from wild-caught mothers had reduced survival until the age of 5. These results highlight that human disturbance can have lasting demographic consequences on wildlife populations. From a demographic perspective, wild-capture bears comparison to other human disturbances such as poaching, hunting and translocations, in which individuals are artificially removed from/added to populations. Poaching and hunting have recently been shown to have a lasting impact on wildlife populations. Low population growth rates and reproductive potential in African forest elephants (*Loxodonta cyclotis*) indicate that recovery from poaching may take several decades (Turkalo et al. 2016), and increased hunting pressure in brown bears

(*Ursus arctos*) has altered reproductive value and life expectancy (Bischof et al. 2018). The lasting negative effects of human disturbance on wildlife populations may mean that the potential of population recovery is overestimated, and this must be incorporated into conservation management strategies.

Human disturbance and its long-lasting impacts on demography have important implications for population dynamics. Sex-biased selective harvest from hunting and selective poaching influence extinction risk in wildlife populations, and so it is important to incorporate human disturbance in to population projections (Saether et al. 2004, Milner et al. 2007, Lusseau and Lee 2016). For wild-capture, in addition to our findings in chapter 2 there are lasting negative impacts on mortality in this population (Lahdenperä et al. 2018), and severe negative consequences for the wild elephant population (Leimgruber et al. 2008). Therefore, it was also important to explore the implications of changes in the number of individuals captured on population viability. In chapter 3, I found that observed historic population growth rates were highly dependent on wild-capture, and 2.1% lower on average when wild-capture was excluded. In the future, without wild-capture there may be transient population declines that last for half a century, before population growth rates stabilise near replacement rate. This result highlights critical features of population dynamics in long-lived species that has implications for conservation management, namely, the importance of short-term, transient dynamics and the length of time that is required for the population to recover from disturbance. Long-lived species are expected to have transient dynamics with a higher amplitude (Stott et al. 2010, Gamelon et al. 2014), and here I demonstrate strong immediate transient dynamics in this human-dominated system. Furthermore, low annual reproductive and mortality rates in long-lived species mean that transient effects last for several decades, which has also been found in other species (Gerber and Kendall 2016, Turkalo et al. 2016). Transient dynamics are likely to be of particular importance in populations dominated by human activity, such as those that are in captivity, subjected to hunting or poaching, or experiencing rapid environmental change, in which there are changes to demographic structure (Ezard et al. 2010).

To further explore the role of transient population dynamics in semi-captive Asian elephants, in chapter 4 I investigated the importance of age-structure on short-term population growth rates. Age-structure was highly variable between 1970-2014 and was responsible for a significant proportion of variation in annual population growth rates. In particular, high adult birth rates would have resulted in high population growth rates in the 1970s, but this was prevented by a low proportion of reproductive-aged females. Changes to age-structure have long been predicted to impact upon population dynamics in wildlife populations (e.g. Coulson et al. 2001, Koons et al. 2007), and transient dynamics are receiving greater attention in population ecology research (e.g. Gerber and Kendall 2016, Koons et al. 2016, Mcdonald et al. 2016). The current study highlights the importance of changes in age-structure on short-term population dynamics and has implications for the conservation management of populations in human-dominated systems. The number of wildlife populations with disruptions to age-structure and thus exhibiting strong transient dynamics is unknown, most likely because of the necessity of long-term demographic data to assess both demographic structure and population dynamics. Nonetheless, the addition/removal of individuals in a population associated with poaching, hunting, capture and translocations, perturbs the age-structure of populations, which, in addition to direct impacts on vital rates, can have a significant independent effect on short-term population dynamics.

In addition to the influence of direct human disturbance (wild-capture) in the current study, other drivers may also be important for population dynamics, and further exacerbate population declines. Previous studies on African (*Loxodonta africana*; Moss 2001, Foley et al. 2008) and Asian elephants (Mumby et al. 2013) have found that climate influences survival, particularly in juveniles. In chapter 5, I extended previous work and investigated the delayed climate drivers of mortality and reproduction in semi-captive Asian elephants. Importantly, I explored two contrasting biological mechanisms of delayed climate effects; *continuous* effects where ~continuous (5-day windows) vital rate patterns were dependent on a cumulative effect of the past climate, and *risk window* effects where climate variation across a risk window, hear seasons, influenced subsequent annual vital rates. I found little support for either *continuous* or *risk window* models of climate effects on juvenile mortality and peak-age reproduction.

I argue that the principal driver of population dynamics in Myanmar's timber elephants was wild-capture. From the start of the study period in the 1950s, large numbers of wild individuals were targeted by systematic capture, with particularly high numbers captured during the 1970s (chapter 3; Lahdenperä et al. 2018). Furthermore, capture from the wild was focussed predominantly on younger individuals that posed less of a risk to mahouts and were easier to train (Lahdenperä et al. 2018). Capture first had both immediate and long-lasting negative consequences for survival (Lahdenperä et al. 2018) and reproduction (chapter 2). However, in addition to these negative impacts on vital rates, capture from the wild altered the age-structure of the timber elephant population. Generally, the population is buffered against environmental variation (chapter 5), but changes to age-structure were the key factor driving short-term population dynamics. The perturbation of demographic structure, which is still present today in this population, will result in long-lasting transient dynamics in future. However, population growth rates were highly dependent on the addition of new individuals through capture, and the population may not be sustainable in future without it.

7.2 Conservation implications

The findings of this thesis have implications for the conservation of Asian elephants. First, there are around 5000 working elephants in Myanmar, which may be up to 10% of the remaining global Asian elephant population (Sukumar 2006), and so I argue that this population is a significant unit of conservation. Indeed, the captive elephant population in Myanmar has now been incorporated in to the local action plan for Asian elephants (Win 2018). In chapter 6, I summarise the key management recommendations from the current body of work to aid in the conservation of semi-captive elephants in Myanmar. First, the capture of wild elephants is detrimental to the wild elephant population and has long-lasting negative consequences for survival and reproduction that influences subsequent generations, and so management should be directed to maintain a sustainable semi-captive population. Sensitivity analyses carried out in chapter 3 indicated that population growth may be more sustainable with increases to juvenile survival and reproduction rates in adults. Adult females are used more in the working population, and therefore improving juvenile survival is the most suitable course of management. Furthermore, the perturbation of age-structure has resulted in a population that will undergo long-lasting transient dynamics in the future, and the introduction of young individuals through wild-capture may mean that there are birth-pulses in the population, which may impact training and the availability of working animals. Fortunately, extinction was not predicted under long-term projection models in this population, which suggests that sustainable management in this population may be beneficial for the conservation of Asian elephants.

7.3 Limitations

There are several limitations that have arisen from the current work, which are predominantly the reliability and utility of the current demographic dataset and the applicability of this semi-captive system to other wildlife populations.

The dataset used in all chapters of this thesis is a longitudinal demographic dataset of registered Myanmar Timber Enterprise (MTE) elephants used in the timber industry between the 1950s and 2014 (e.g. Hayward et al. 2014, Mumby et al. 2015, Lynsdale et al. 2017). Limitations of this dataset that must be acknowledged are the availability of data early in the study and the reliability of life-history data. In analyses of temporal variation in vital rates and population dynamics, I used data from 1951 onwards, because before this time record keeping systems in the MTE were incomplete. Demographic data was compiled from individual logbooks and MTE reports, and was verified from different sources where possible, however historically the availability of data was reduced. In particular, the number of individuals, especially at older ages, was reduced until the 1970s. However, the number of individuals that are not in the current dataset, but that were present in the population during this time is unclear. Importantly, I accounted for temporal variation in vital rates, and only constructed population projection models using data after this period, but it is important to acknowledge this limitation.

The reliability of the data recorded is also a potential limitation of the current study, although the timing of key life-history events is largely accurate (to the day) and verified for each individual by government staff and veterinarians. One limitation however is the age estimation in wild-caught individuals. Age is estimated in wild-caught individuals at the time of capture using shoulder height and comparison of body condition and physical attributes such as pigmentation with elephants of known age. The exact error in age-estimation for wild-caught individuals is unknown but thought to be within a couple of years for individuals that continue to grow (up to 25 years old), which constitutes the majority (72%) of those captured. Overall, the reliability of life-history data in the current dataset is high, because elephants are individually monitored, and records are maintained centrally by the MTE. In analysis, we discarded approximately 5% of the original data due to discontinuous birth/capture/death/censoring data, but the exact degree of error in the whole dataset is unknown. Therefore, while the reliability of demographic data is potential limitation that must be acknowledged, generally the quality of data in the current study is high.

The second key limitation of the current thesis is the utility of the current system of semi-captive elephants as a model for other wildlife populations. The management system in this population is relatively unique, and timber elephants do not fit the binary definitions of *in situ* or *ex situ* populations (Redford et al. 2011). Only few species have populations with comparable semi-captive management systems, including reindeer (*Rangifer tarandus*) (Suominen and Olofsson 2000) and some other mammals (e.g. Dierenfeld and McCann 1999, Golosova et al. 2017). Whether temporal trends in vital rates and population dynamics reflect environmental conditions or simply changes in management is unknown. However, importantly, only few wildlife populations are undisturbed by human activity (Redford et al. 2011), and therefore understanding population dynamics in semi-captive systems such as timber elephants is still relevant to other systems. Therefore, while the application of this system to other wild populations should be approached with caution, it still provides insights into human disturbance and population dynamics in long-lived mammals.

7.4 Future work

There are a number of potential avenues of research to explore in extension to the work carried out in the current thesis, namely, the investigation of spatial trends in vital rates and population dynamics, other drivers of population dynamics including human management and habitat availability, and the interplay between the captive and wild elephant populations. Demographic data used in the current thesis covered the whole of Myanmar, and elephants are held in different states and regions of the country, with differences in habitat availability and climate. I accounted for this in demographic models by incorporating regional division as a random effect. However, explicitly investigating differences in vital rates population dynamics between regions may offer an opportunity to highlight spatial priorities for conservation in Myanmar and may also elucidate how habitat availability influences demography in Asian elephants.

Understanding other drivers of population dynamics, especially anthropogenic factors such as logging and workload would be useful for the management of this population. There are individual differences in the number of logs extracted and the amount of work carried out, and therefore relating this workload to vital rates may inform population managers about optimal workload strategies to maximise the sustainability of the population and the export of timber. Furthermore, despite the region containing the largest remaining unfragmented habitat for wild Asian elephants, a significant proportion of the forest cover (and thus natural habitat for elephants) has been lost in recent decades (Leimgruber et al. 2003, 2005). Understanding how habitat loss influences population dynamics in both wild and semi-captive populations would provide invaluable insight for conservation strategies in Asian elephants. Finally, a crucial feature of the current population is the role of the wild elephant population at sustaining the captive population; it has been documented that wild males breed with captive females, and also that captive males mate with wild females (Shell 2019). The precise contribution of the wild population to the captive population is currently unknown, but genetic analysis could shed light on the contribution of captive males to captive offspring. Furthermore, with widespread declines in the wild population, not least due to wild-capture, the future contribution of wild males to captive population dynamics is unknown but is likely to be reduced.

Understanding the interplay between the wild and captive populations is therefore crucial for the conservation of Asian elephants in the region.

More generally, the pervasiveness of short-term transient dynamics and the role of human disturbance in population dynamics is an interesting area of future research. Many populations, particularly in vulnerable species, are small in number, under threat of poaching and hunting, or subjected to translocations. Therefore, exploring the long-lasting demographic consequences of human disturbance in vulnerable populations, and the role of transient dynamics and age-structure is potentially crucial for understanding population declines. Furthermore, how long negative impacts from drivers of population dynamics such as poaching or climate change last is an important question in other populations.

7.5 Conclusions

In this thesis, I have provided novel insights into the impacts of human disturbance on demography and population dynamics in a long-lived species. For semi-captive Asian elephants, capture from the wild to supplement the working population has had long-lasting impacts on vital rates, demographic structure and population dynamics. With an increasing human population, the number of wildlife populations that are influenced by human activity will only increase. However, the number of long-term studies investigating patterns in demography is still relatively small. Here, I add to this small number of studies with the case study of timber elephants. Ultimately, understanding how human disturbance influences population dynamics is crucial to prevent future population declines in vulnerable species.

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Supplementary information

S1. Supplementary information for chapter 2

Capture from the wild has long-term costs on reproductive success in Asian elephants

References included in chapter 2

S1.1 Data selection

Age-specific reproduction

The demographic dataset of Myanmar timber elephants for age-specific analyses includes 2,685 females with known birth origin (captive-born vs. wild-caught) and survival information, which lived beyond the earliest age of reproduction, 5 years. Of these females, 1,323 were captive-born between 1942-2011 and 1,362 were wild-caught, captured between 1951-2002 at estimated ages of 0-55 years (mean capture age 16.13 ± 10.91). Exact lifespan was known for 1,079 females. Elephants were born (or estimated to be born) between 1921-2011 and come from 11 out of 14 regional divisions in Myanmar: Ayeyarwaddy (N = 39), Bago (N = 314), Chin (N = 31), Kachin (N = 266), Magway (N = 104), Mandalay (N = 401), Rakhine (N = 91), Sagaing (N = 928), Shan (N = 242), Tanintharyi (N = 6), Yangon (N = 8) and unknown (N = 255). In these analyses, we grouped regions together based on proximity, elevation and sample size: Ayeyarwaddy, Tanintharyi, Bago, Rakhine and Yangon were grouped together, Chin and Shan were grouped together, and Magway and Mandalay were grouped together. This made sample sizes in each region group more comparable for analyses. Approximately 95% of the original demographic data was retained with reliable birth, capture, departure and death information.

Calf survival and mother's birth origin

To investigate whether captive-born and wild-caught females show differences in calf survival before age 5, we analyzed 2423 calves (F = 1,235, M = 1,188; 1,290 born to captive-born females and 1,133 born to wild-caught females) born between 1960 and 2016 to 1030 mothers (500 captive-born and 530 wild-caught mothers). Generally, age-specific mortality in this population is greatest within the first 5 years (Mar et al. 2012), and therefore we concentrated on this age range in the analysis. We excluded stillborn calves, calves born to mothers captured before 1952, twins, and calves with mistakes or missing information (on sex, calf or mother's exact or censored lifespan after calf's birth). These calves come from 11 regions in Myanmar: Ayeyarwaddy (N = 59), Bago (N = 282), Chin (N = 4) Kachin (N = 130), Magway (N = 344), Mandalay (N = 255), Rakhine (N = 29), Sagaing (N = 956), Shan (N = 196), Taninthary (N = 7), Yangon (N = 9) and unknown (N = 152). In the analyses, regions were grouped in the same way as in age-specific reproduction analyses above resulting in 6 grouped regions.

Calf age was included as a linear and quadratic term to control for the quadratic age effect on calf mortality before age 5 (Mar et al. 2012). Birth cohorts and regions were also controlled for in the model (the same way as in age-specific reproduction analyses). Maternal death is known to increase calf mortality (Lahdenperä et al. 2016), and maternal presence was therefore coded as a time-dependent variable in every year from birth to calf age 5 (0 = mother died during the focal year/had died during previous years; 1 = mother was alive during the focal year). We also included an interaction term between calf age and maternal presence to control for the changing effect of maternal death on calf mortality at different calf ages (Lahdenperä et al. 2016). Maternal age at the birth of the calf was included in the model, which ranged from 7-63 years old in the current sample. Maternal ages above 60 were grouped together because of small sample size (N = 6 calves). Short previous birth intervals are known to increase calf mortality (Mar et al. 2012), and we categorized birth intervals as short, medium, long, and firstborn categories based on the 25% and 75% quartiles of birth-interval length (3.84 and 7.44 years, respectively; average = 6.28 ± 3.75 years). Birth order was not included because of its collinearity with maternal age and birth interval. We also controlled for the differences in survival between male and female calves (Mar et al. 2012), and an increased effect of maternal death on male calves by including calf sex and an interaction between maternal presence and calf sex in the model (Lahdenperä et al. 2016). Finally, the mother's individual identification number was included as an intercept-only random effect to account for repeated births by the same female (ranges of 1-8 calves for wild-caught mothers and 1-10 calves for captive-born mothers; average = 2.35 calves).

S1.2 Age-specific reproduction model selection – additional details

The model selection was carried out in two phases. First, we explored the full set (21,089 models) of age term models with generalized linear models (GLMs) with binomial error structures, incorporating all fixed effects, but excluding the random effects terms. Then, we re-ran the best 100 models using GLMMs, to incorporate the random effects terms of individual ID number and regional division group. We used this approach to reduce the computational power needed to assess all models, while maintaining a large enough subset of models incorporating the random effects. We compared the predictive performance of each model using the Akaike Information Criterion (AIC) (Burnham and Anderson 2003). The use of AIC was appropriate for the current study because each of the model parameters and interactions were considered *a priori* in the base model, and so all models contained the same number of parameters and interactions. The best 'final' model was the model with the lowest AIC value (Table S1). We assessed the significance of the terms in the best-fit model using likelihood ratio tests (LRTs) with the Chi-squared ($\chi 2$) distribution. Where a model term was included as both a fixed effect and an interaction, all terms with that effect were removed in the LRT calculation.

The AIC value of the best model was 0.04 lower than the second explanatory model with three thresholds (different thresholds at 20 and 44, as opposed to 19 and 44 years of age; Table S2; Figure S1). This small difference is therefore consistent with a peak of reproduction of between 19 and 20. The difference between the best and twentieth explanatory models was 2.74, indicating clear support for the best model relative to other competitive models (Figure S1). The best-fit 20 three-threshold models are shown in Table S2. Of the best 100 models, all were three-threshold models, and we found little support for linear, quadratic or cubic age terms relative to threshold models.

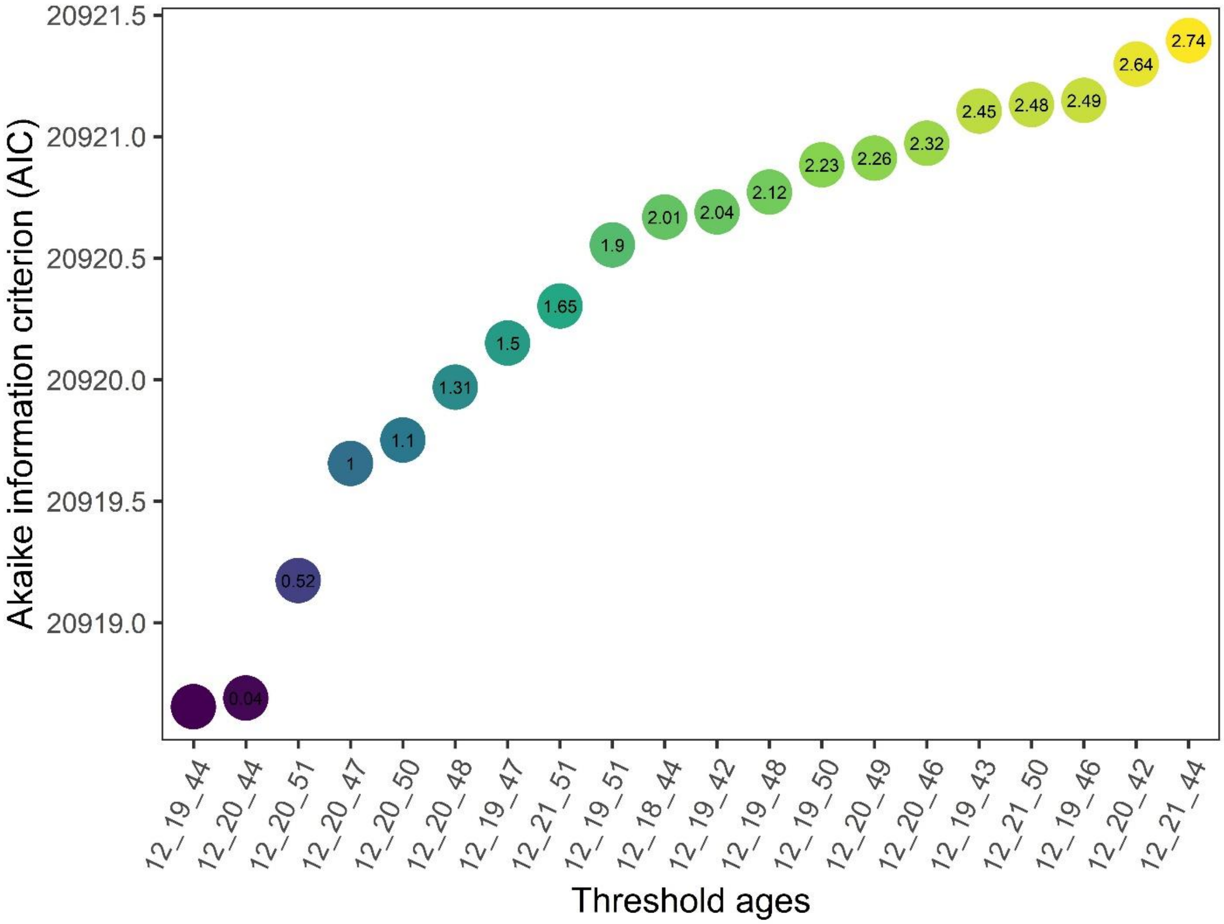

Figure S1.1 The best age-specific model was a three-threshold model with a peak reproductive age of 19. Figure shows AIC scores and threshold ages for the best-fit 20 models incorporating age terms. Colour denotes the AIC value, and the numbers within the points are the differences with respect to the best-fit model. The AIC differences indicate small differences between the first- and second-best models, but clear support for peak age of reproduction between 19 and 20.

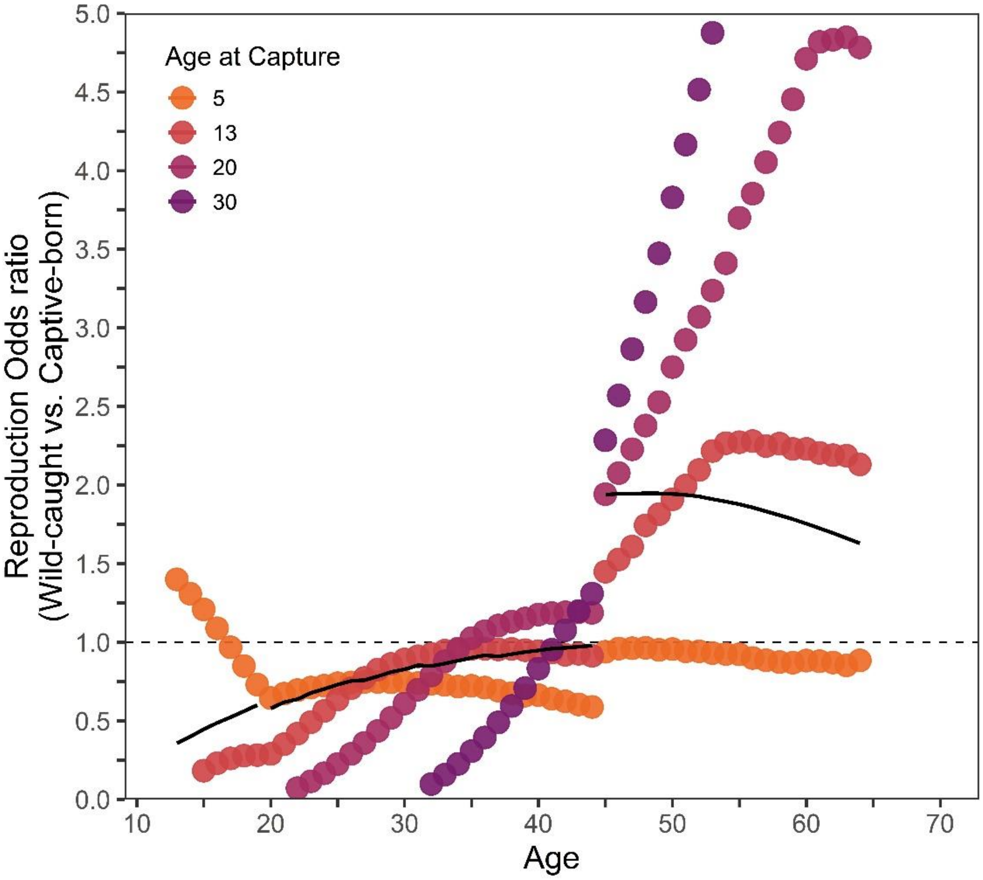

Figure S1.2 Wild-caught females had a greatly reduced odds of reproduction at peak reproductive ages (20-44) and at the onset of reproduction (13-19). Age-specific reproduction odds ratios comparing wild-caught to captive-born, for all individuals (1323 captive-born females and 1362 wild-caught females). Points are age-specific odds ratios for wild-caught females relative to captive-born females, colours are specific capture ages. Solid black line is the average age-specific odds ratio of reproduction irrespective of capture age. Dashed black line at odds 1 indicates an equal odds for wild-caught and captive-born females.

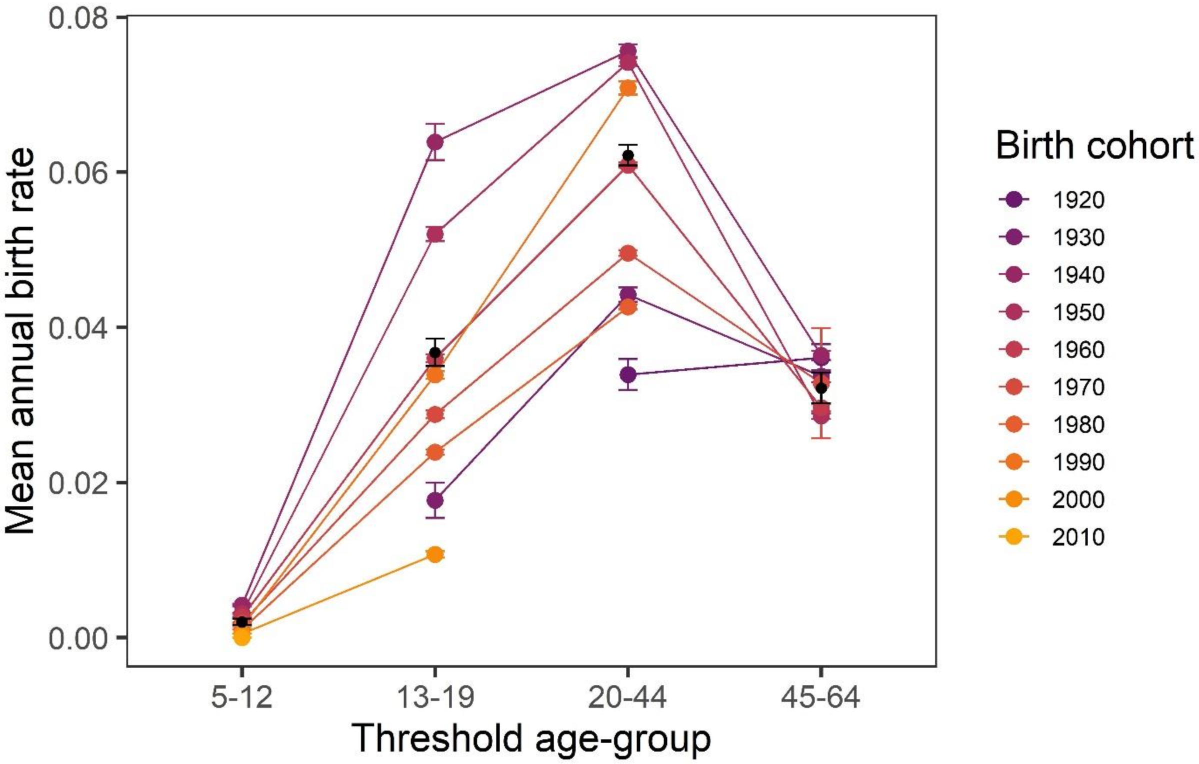

Figure S1.3 The age-specific birth rates from the 1960 birth cohort most adequately describe the mean reproductive rates in the raw demographic data. Mean annual birth rate in each of the threshold age-groups selected in the best-fit model for all females depending on the birth cohort (decade of birth). Coloured points lines represent mean±SEM model predicted annual birth rate in each age-group. Black points denote the raw mean±SEM annual birth rate in each age-group from demographic data. There was significant variation in age-specific reproduction depending on birth cohort.

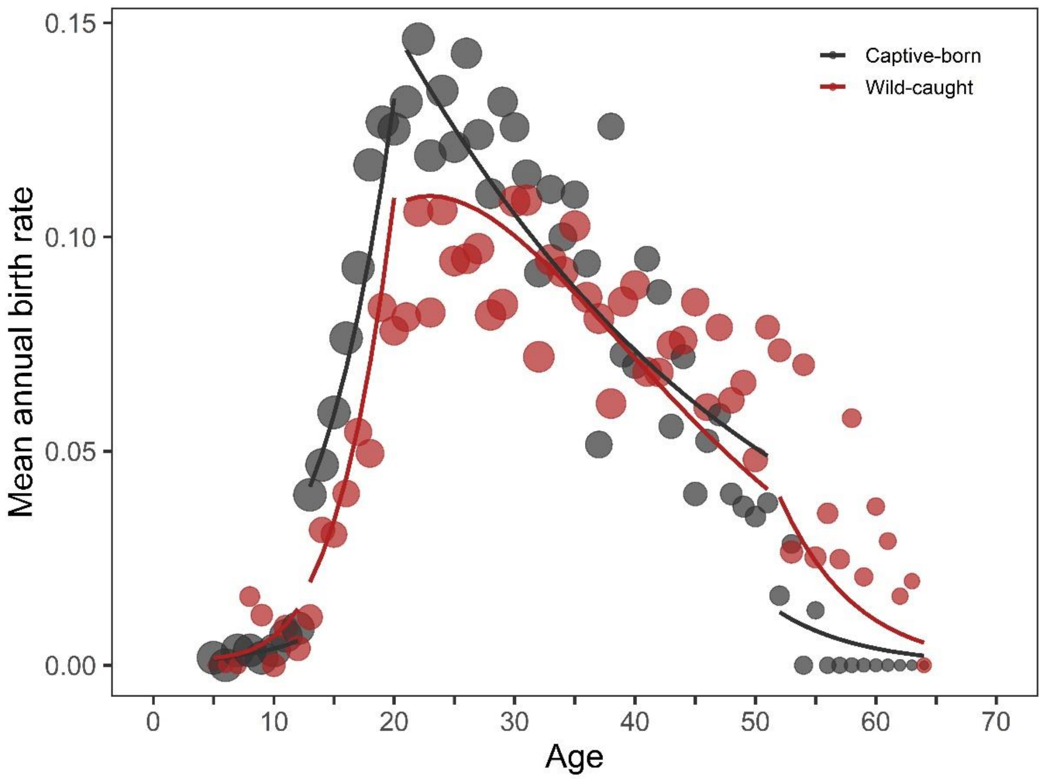

Figure S1.4 Wild-caught females that reproduced at least once had a reduced age-specific reproductive probability compared to captive-born females. The figure shows age-specific patterns of reproduction for captive-born and wild-caught females that reproduced at least once in their lifetime from the best-fit threshold regression model (age groups: 5-12, 13-20, 21-51, 52-64). Points are the raw mean annual predicted birth rates at each age for reproductive females only, with the size of the points denoting the square root of the sample size at each age (range = 8-580 time-event data points). Lines are the mean predicted values for an extended dataset of the observed females in the 1960 birth cohort, which were most similar to raw mean birth rates.

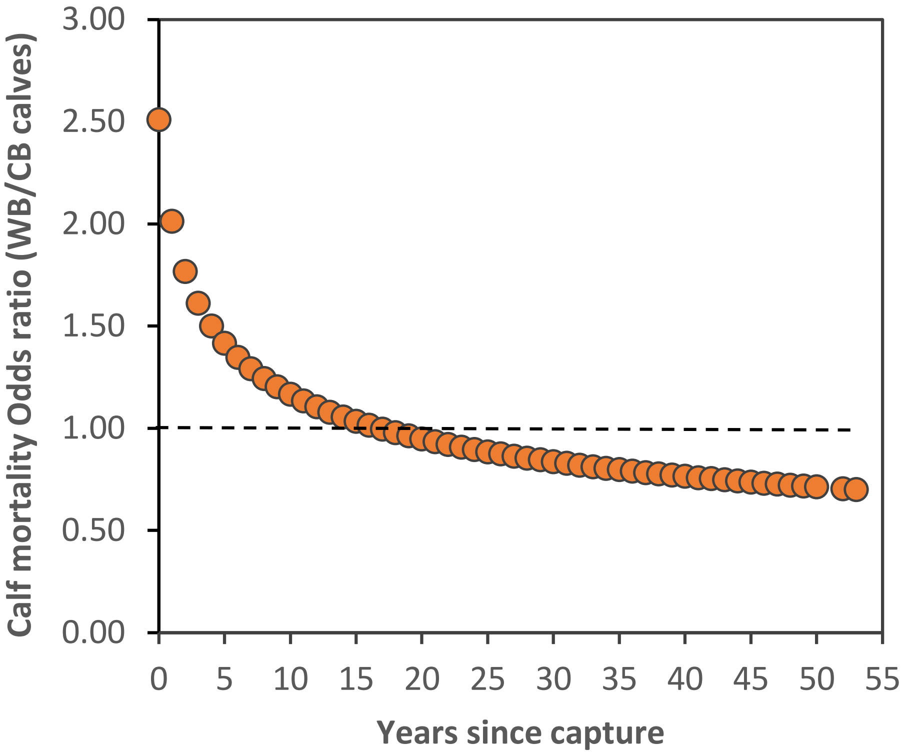

Figure S1.5 Calves of wild-caught (WB) mothers had increased mortality odds ratios (at each age from birth to age 5) compared to calves of captive-born (CB) mothers, the effect decreasing slowly and lasting ~16 years after mother's capture from wild (n=10,240 observations, 2471 calves, 1033 mothers). Points are yearly odds ratios after the mother's capture for calves born to wild-caught females relative to calves born to captive-born females. Dashed black line at odds 1 indicates an equal odds for calves of wild-caught mothers and calves of captive-born mothers.

Table S1.1 Parameter estimates and likelihood ratio tests (LRTs) for the effect of birth origin on lifetime reproduction (a- binomial mixed effects model, n = 1678) and log-transformed age at first reproduction (b- linear mixed effects model, n = 843) for female timber elephants. Estimates and standard errors presented on the logit scale for table a). Colon (:) denotes an interaction terms.

a)

Fixed effect	Estimate	Standard Error	LRT χ^2	p value
Intercept	0.02	1.19		
Birth origin			40.1	<0.001
wild-caught	-0.37	0.22		
Censored			15.1	<0.001
dead (1)	0.54	0.17		
Lifespan	0.07	0.01	93.1	<0.001
Birth cohort			17.1	0.02
1940	-1.93	1.11		
1950	-1.99	1.11		
1960	-2.34	1.12		
1970	-2.56	1.12		
1980	-2.53	1.13		
1990	-2.17	1.15		
Birth origin:Age at capture			4.9	0.03
wild-caught:age at capture	-0.04	0.02		

b)

Fixed effect	Estimate	Standard Error	LRT χ^2	p value
Intercept	2.67	0.08		
Birth origin			15.3	<0.001
wild-caught	0.08	0.02		
Censored			0	0.90
dead (1)	0.00	0.03		
Lifespan	0.01	0.00	17.3	<0.001
Birth cohort			37.6	<0.001
1950	0.09	0.05		
1960	0.12	0.05		
1970	0.16	0.05		
1980	0.30	0.06		
1990	0.14	0.07		

Table S1.2 Model selection results for the incorporation of age terms via threshold regression. The best 20 models are shown based on the Akaike information criterion (AIC). All of the best models had three thresholds, and thus four threshold age groups. The best model is highlighted in bold, and was selected in both stages of model selection (GLM and GLMM models).

Threshold age groups	Threshold ages	AIC	ΔAIC	GLM rank
four	**12, 19, 44**	**20918.65**		**1**
four	12, 20, 44	20918.69	0.04	2
four	12, 20, 51	20919.17	0.52	3
four	12, 20, 47	20919.66	1	4
four	12, 20, 50	20919.75	1.1	10
four	12, 20, 48	20919.97	1.31	7
four	12, 19, 47	20920.15	1.5	5
four	12, 21, 51	20920.3	1.65	14
four	12, 19, 51	20920.55	1.9	19
four	12, 18, 44	20920.67	2.01	8
four	12, 19, 42	20920.69	2.04	6
four	12, 19, 48	20920.77	2.12	17
four	12, 19, 50	20920.88	2.23	25
four	12, 20, 49	20920.91	2.26	18
four	12, 20, 46	20920.97	2.32	9
four	12, 19, 43	20921.11	2.45	13
four	12, 21, 50	20921.13	2.48	21
four	12, 19, 46	20921.15	2.49	16
four	12, 20, 42	20921.3	2.64	12
four	12, 21, 44	20921.4	2.74	11

Table S1.3 Parameter estimates from the best model of age-specific reproduction for only reproductive females (n = 1175; 38,492 elephant-year observations), fit using binomial generalised linear mixed effects models (GLMMs). Estimates and standard errors are present on the logit scale. The colon (:) depicts interaction terms. LRT denotes likelihood ratio test statistics.

Fixed effects	Estimate	Standard Error	LRT χ^2	p value
Intercept	-5.28	1.05		
Age	0.19	0.10	309.0	<0.001
Age group			973.2	<0.001
ages 13-20	1.99	1.06		
ages 21-51	6.51	1.01		
ages 52-64	10.63	2.58		
Birth origin			167.3	<0.001
wild-caught	-2.24	0.55		
Lifespan	-0.09	0.01	59.5	<0.001
Average age	0.15	0.02	48.0	<0.001
Birth cohort			88.7	<0.001
1930	-0.96	0.26		
1940	-1.06	0.25		
1950	-1.42	0.26		
1960	-1.61	0.27		
1970	-1.76	0.28		
1980	-1.97	0.29		
1990	-1.61	0.30		
2000	1.67	1.16		
Censored			9.53	<0.01
dead (1)	-0.14	0.05		
Age:Age group			142.1	<0.001
age:ages 13-20	-0.01	0.11		
age:ages 21-51	-0.23	0.10		
age:ages 52-64	-0.34	0.11		
Age:Birth origin			30.5	<0.001
age:wild-caught	-0.06	0.01		
Age group:Birth Origin			28.5	<0.001
ages 13-20:wild-caught	-1.76	0.49		
ages 21-51:wild-caught	-1.92	0.50		
ages 52-64:wild-caught	-0.53	0.69		
Birth origin:ln time since capture			96.4	<0.001
wild-caught:ln time since capture	1.67	0.18		

Random effects	Variance	Standard deviation
Individual ID	0.00	0.00
Regional division group	0.004	0.06

Table S1.4 Discrete-time survival model of the effects mother's birth origin on offspring risk of death during 0-4 (4.99) years in semi-captive timber elephants in Myanmar (Total n = 10,192 observations (2,423 calves and 1030 mothers). Positive estimates reflect increasing mortality risk. Reference categories are given in brackets. Mother's identity was fitted as a random term. The colon (:) depicts interaction terms. CB= captive-born, time= years since mother's capture, prev. =previous, M=male, F=female.

Fixed effects		Estimate	Std. Error	F value	Numdf, Dendf	P value
Intercept		-3.4812	0.2627			
Calf age		-0.5587	0.1214	51.96	1,9183	<0.0001
Calf age:calf age		0.1549	0.02785	30.92	1,9183	<0.0001
Mother's Origin (CB)		0.9266	0.4079	5.16	1,9183	0.0231
Mother's Origin:time (CB)		-0.3221	0.1355	5.65	1,9183	0.0175
Prev. birth-interval (medium)				3.54	3,9183	0.0141
	first-born	0.4380	0.1754			
	short	0.5981	0.1996			
	long	0.3532	0.2097			
Calf age:prev. birth-interval (medium)				5.61	3,9183	0.0008
	first-born	-0.2062	0.07229			
	short	-0.3786	0.1013			
	long	-0.2054	0.09526			
Birth cohort (1980)				2.86	5,9183	0.0138
	1960	0.07900	0.2241			
	1970	0.003297	0.1480			
	1990	0.1421	0.1260			
	2000	-0.3903	0.1627			
	2010	-0.4369	0.2270			
Mother's death (alive)		2.0369	0.4230	23.19	1,9183	<0.0001
Calf age:Mother's death (alive)		-0.4704	0.1668	7.95	1,9183	0.0048
Calf sex (F)		0.4366	0.2470	3.12	1,9183	0.0771
Calf sex (F):Mother's death (alive)				2.92	1,9183	0.0876
	M, mother dead	2.4734	0.5337			
	M, mother alive	0.01554	0.09558			
	F, Mother dead	1.6158	0.4415			
Calf division (Sagaing)				40.51	5,9183	<0.0001
	Ayeyarwaddy group (see S1)	-0.4616	0.1781			
	Chin and Shan	0.8292	0.1807			
	Kachin	1.6393	0.1828			
	Magway and Mandalay	0.2806	0.1304			
	Unknown	2.1089	0.1882			
Mother's age		0.01108	0.006420	2.98	1,9183	0.0844

Random effects		Variance	Std. dev.
Maternal ID		0.33	0.13

S2. Supplementary information for chapter 3

Long-term trends in wild-capture and population dynamics point to an uncertain future for captive elephants.

References included in chapter 3

S2.1 Data selection

The data recorded for all registered elephants includes: identification number and name, birth origin (captive-born or wild-caught), date and place of birth, mother's identification number and name, year and place of capture (if wild-captured), year or age of taming, identities of all calves born, date of death or last known date alive, and cause of death. The initial studbook contained data from 1876 to 2014. Further restrictions to the studbook were made because only sparse records were available until the 1950s. Therefore, only females born after 1920 if captive-born were included, and both mortality and birth records for females present in the population before 1960 were discarded. Records for wild-caught individuals were incomplete before 1951 and age estimates for wild-caught elephants may have lower accuracy after the individuals have achieved full body height (at the age of 25 years in this working population) (Mumby et al. 2015). Therefore, only wild-caught females entering the population after 1951 and caught before the age of 25 (~70% of those captured), were included here to increase the reliability of our age-specific mortality and fertility estimates. Thus, our measure of annual wild-capture rate does not reflect the total number of individuals caught from the wild each year, but instead general trends of wild-capture through time in Myanmar. Nevertheless, the majority of wild-caught elephants were below an estimated age of 25 at capture: during 1951-1999 the median age at capture varied between 8 and 13 years, depending on the method of capture (Lahdenperä et al. 2018), and capturers generally targeted young, healthy-looking individuals which were easier to train than older ones. There was also a female bias in wild-capture, who comprised 60% of wild-caught individuals in the initial studbook. Finally, individuals with erroneous or discontinuous death/departure/birth information were removed (5% of elephants). The final studbook was a female-only dataset (N = 3585, wild-caught = 1215) with individuals from 11 out of the 14 regional divisions of Myanmar, of which 2117 were censored. This female-only dataset was used in all subsequent analyses.

S2.2 Model selection

We used model selection in order to explore the fit of linear and non-linear explanatory variables on female birth and mortality rates, as well as on the interaction between age, year and birth origin (table S1). We assessed the fit of models incorporating the age and year parameters as 1) linear parametric terms, 2) smoothing terms fitted using thin plate regressions splines (Wood 2003), 3) separate smoothing terms for wild-caught and captive-born females, to capture the interaction between age/year and birth origin, and 4) a tensor product interaction smoothing term, with separate terms for wild-caught and captive-born females, to capture the interaction between all explanatory variables (Wood 2006). Finally, we also explored the fit of models incorporating a linear term for population size in each year, to assess density dependence in life-history traits and whether there was a need to incorporate density dependence in future projections. All models also had a linear parametric term for birth origin, to assess the differences in mean vital rates between wild-caught and captive-born females. Although a previous study found an effect of the time in captivity on survival in this population (Lahdenperä et al. 2018), because we aimed to assess population viability without continued wild capture (after 1995) this was not included in our model selection. All models also had a random effect smoothing term of spatial division group in Myanmar, penalized with a ridge penalty. We had life history records from 11 out of 14 spatial divisions (Ayeyarwady = 878, Bago = 7167, Chin = 1066, Kachin = 7252, Magway = 3322, Mandalay = 11650, Rakhine = 2004, Sagaing = 25713, Shan = 5749, Tanintharyi = 142, Yangon = 356, Unknown= 4984; figure S1). In the analyses, to make sample sizes more comparable we grouped divisions by proximity and elevation: Ayeyarwady, Yangon, Bago, Rakhine, and Tanintharyi regions were all grouped together because of low sample size and their coastal locations. Chin and Shan regions were grouped together because of their similar elevation and low sample sizes. Finally, Magway and Mandalay regions were grouped together because of similar altitude, proximity and low sample size. The best-fit models were selected using the Akaike information criterion (AIC), and where the difference in AIC between the two best models was less than 2, the simpler model with fewer interactions was selected (Akaike 1987, Burnham and Anderson 2004).

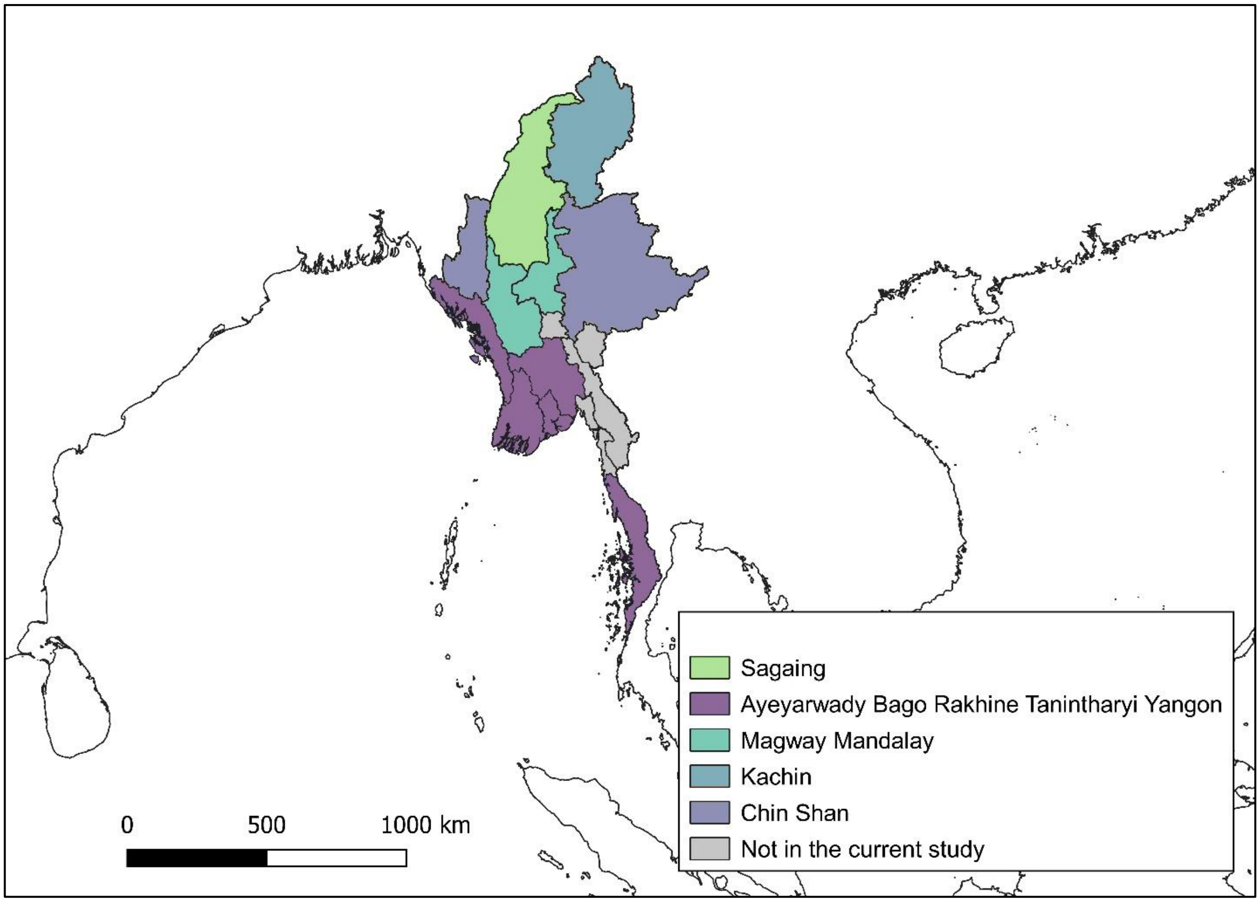

Figure S2.1 Regional divisions of Myanmar used in the current study. Colour denotes the regional division groups used in analysis.

Table S2.1 (overleaf) Model selection results for age-specific life-history traits through time in female timber elephants. Best model highlighted in bold. All models also included a binary response variable of birth or mortality, a parametric term for birth origin, and an additional random effect smoothing term predictor for regional division. The function $f(x)$ describes a thin plate regression spline smoother, the function $g(x)$ describes a tensor product interaction smoothing term fit with a thin plate regression spline, and the function $re(x)$ described a random effect smoothing term penalised with a ridge penalty. Terms without functions delineate parametric, linear predictors.

Birth model predictors	**AIC**	**ΔAIC**
g(age, year, birth origin = captive-born) + g(age, year, birth origin = wild-caught) + re(year factor)	**12712.61**	
g(age, year, birth origin = captive-born) + g(age, year, birth origin = wild-caught) + population size + re(year factor)	12713.03	0.42
f(year, birth origin = captive-born) + f(year, birth origin = wild-caught) + f(age, birth origin = captive-born) + f(year, birth origin = wild-caught) + re(year factor)	12732.73	20.12
g(age, year, birth origin = captive-born) + g(age, year, birth origin = wild-caught)	12758.12	45.51
f(year, birth origin = captive-born) + f(year, birth origin = wild-caught) + f(age) + re(year factor)	12759.73	47.12
f(year) + f(age, birth origin = captive-born) + f(year, birth origin = wild-caught) + re(year factor)	12764.91	52.31
f(year, birth origin = captive-born) + f(year, birth origin = wild-caught) + f(age, birth origin = captive-born) + f(year, birth origin = wild-caught)	12768.62	56.01
f(year, birth origin = captive-born) + f(year, birth origin = wild-caught) + f(age)	12795.52	82.92
f(year) + f(age, birth origin = captive-born) + f(year, birth origin = wild-caught)	12800.55	87.94
f(year) + f(age)	12863.94	151.34
Half-decade + f(age)	12872.52	159.91
Decade + f(age)	12952.38	239.77
year + f(age)	12987.26	274.65
year + age + year: age	13958.57	1245.96
f(year) + age	14204.45	1491.84
year + age + age: birth origin	14375.57	1662.96
year + age + year: birth origin	14414.02	1701.41
year + age	14415.25	1702.64

Mortality model predictors		
g(age, year, birth origin = captive-born) + g(age, year, birth origin = wild-caught) + re(year factor)	**8807.11**	
g(age, year, birth origin = captive-born) + g(age, year, birth origin = wild-caught) + population size + re(year factor)	8807.49	0.38
f(year, birth origin = captive-born) + f(year, birth origin = wild-caught) + f(age, birth origin = captive-born) + f(year, birth origin = wild-caught) + re(year factor)	8839.35	32.24
f(year) + f(age, birth origin = captive-born) + f(year, birth origin = wild-caught) + re(year factor)	8844.44	37.33
g(age, year, birth origin = captive-born) + g(age, year, birth origin = wild-caught)	8862.64	55.53
f(year, birth origin = captive-born) + f(year, birth origin = wild-caught) + f(age) + re(year factor)	8873.19	66.07
f(year, birth origin = captive-born) + f(year, birth origin = wild-caught) + f(age, birth origin = captive-born) + f(year, birth origin = wild-caught)	8883.63	76.52
f(year) + f(age, birth origin = captive-born) + f(year, birth origin = wild-caught)	8886.88	79.77
f(year, birth origin = captive-born) + f(year, birth origin = wild-caught) + f(age)	8916.00	108.89
Hal-decade + f(age)	8930.60	123.49
f(year) + f(age)	8936.67	129.56
Decade + f(age)	8947.66	140.55
year + f(age)	9004.32	197.21
year + age + year: age	9480.85	673.74
year + age + age: birth origin	9515.23	708.12
f(year) + age	9526.44	719.33
year + age + year: birth origin	9581.47	774.36
year + age	9583.10	775.99

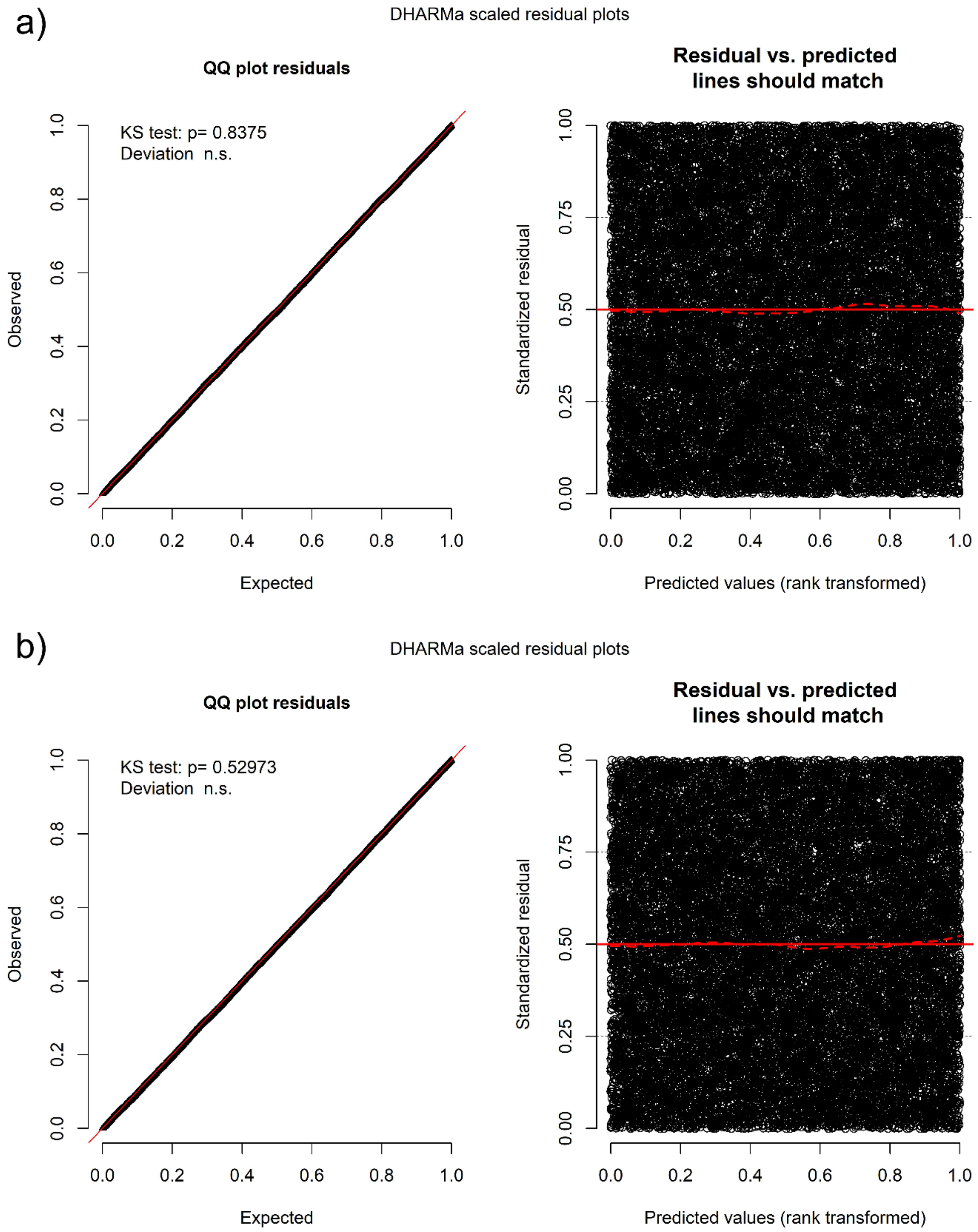

Figure S2.2 Scaled model residual diagnostics for the best-fit birth (a) and mortality (b) models over 1000 simulations. In neither birth nor mortality models was their evidence for deviation from uniformity in the residuals (left), or a relationship between predicted values and residuals (right).

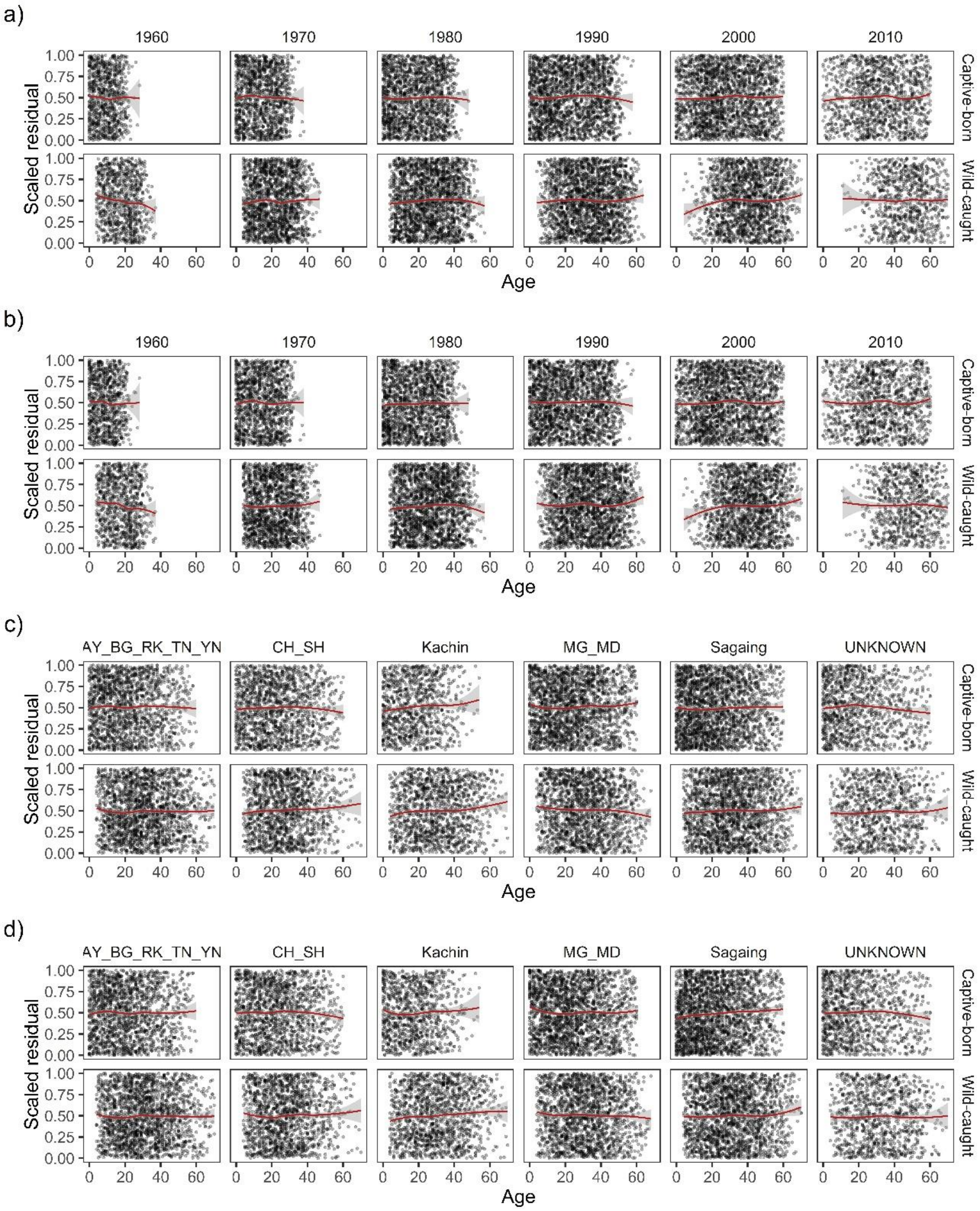

Figure S2.3 Scaled model residual covariance plots for the best-fit birth (a and c) and mortality (b and d) models. Scaled, simulated residuals were assessed against age, birth origin, decade (a and b) and regional division (c and d). Grouped regional division abbreviations: AY - Ayeyarwady, YN- Yangon, BG - Bago, RK- Rakhine, and TN- Tanintharyi, CH- Chin, SH-Shan, MG- Magway, MD- Mandalay. Points are scaled residuals, red lines are loess (localised regression) smoothers.

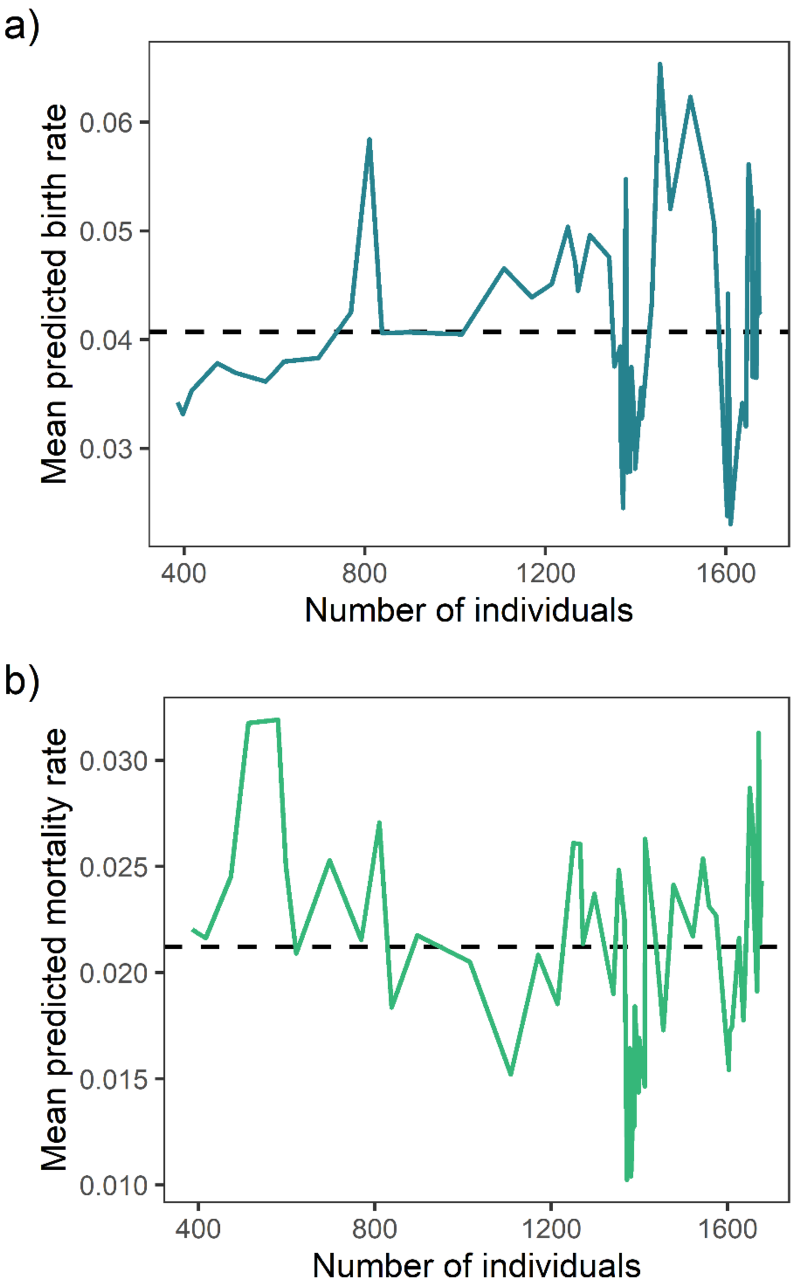

Figure S2.4 Mean model predicted values for the best-fit birth (a) and mortality (b) models with respect to population size. Solid lines are mean predicted vital rates, dashed lines are the mean birth and mortality rates across the study period. We found no clear relationship between population size and age-specific vital rates, and no further explanatory power when population size was included in the model (table S2.1).

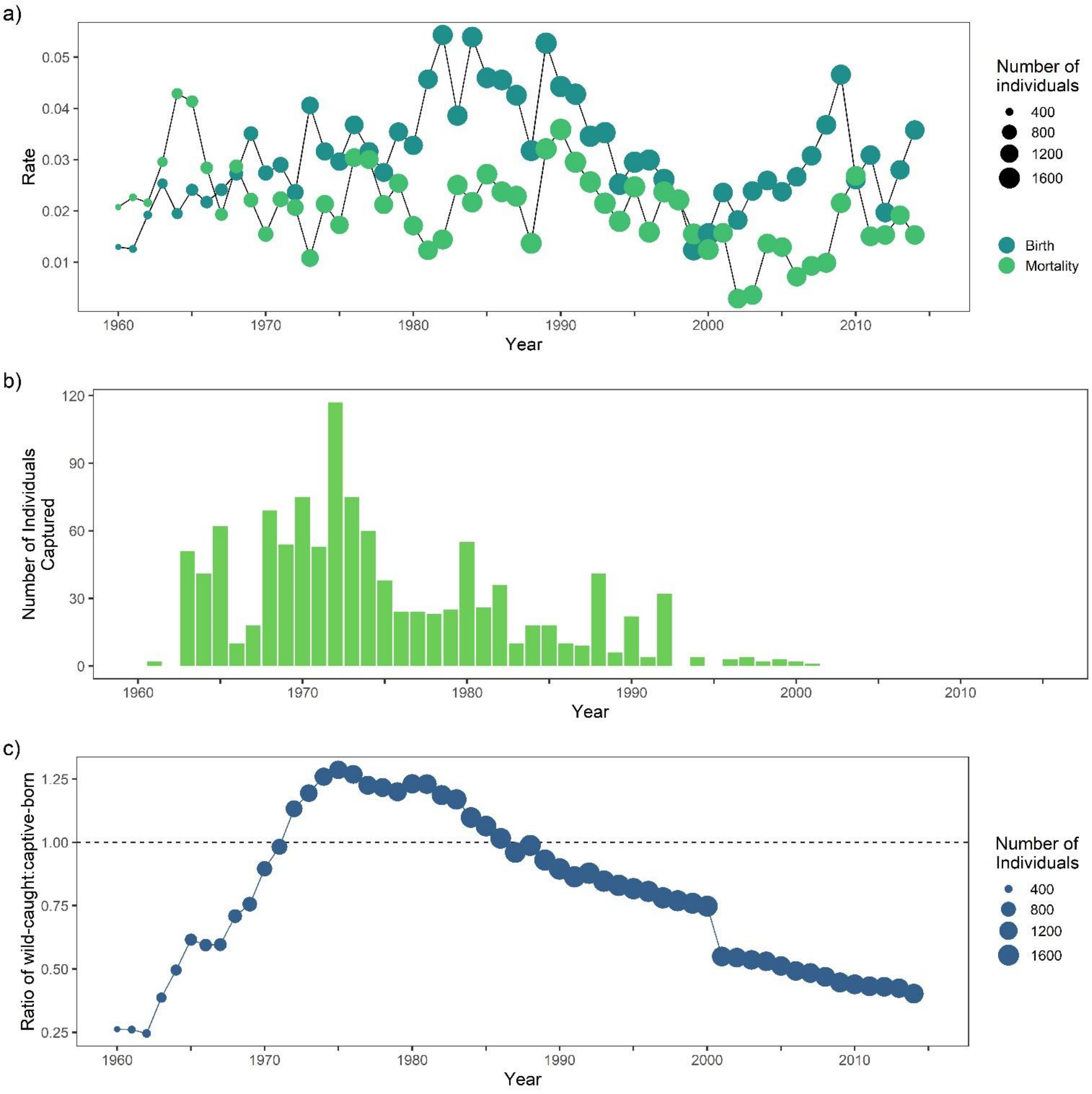

Figure S2.5 Population trends in female timber elephants between 1960 and 2014. a) Raw annual birth and mortality rates for female timber elephants. The size of the points indicates the population size in each year (range = 385 - 1677). b) Annual capture rate estimates of wild female Asian elephants under the age of 25 in Myanmar between 1960 and 2014. c) The ratio of wild-caught females to captive-born females, where the size of the point indicates the population size (range = 385-1677).

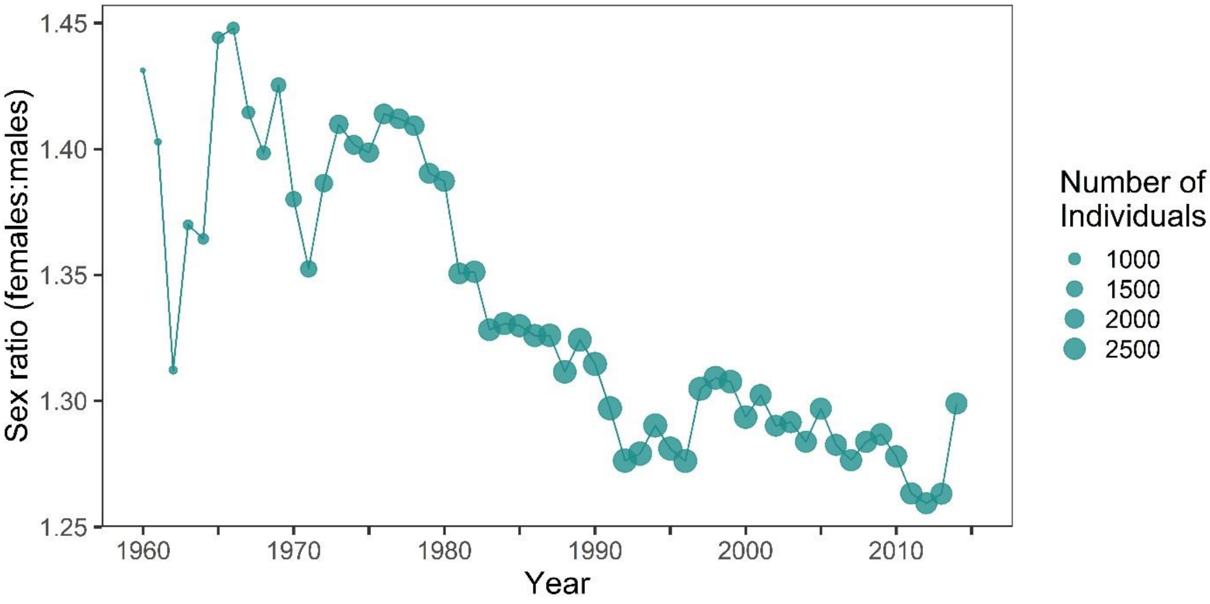

Figure S2.6 Temporal trend in the sex ratio of timber elephants between 1960 and 2014. The size of the points indicates the population size (range = 654-2991).

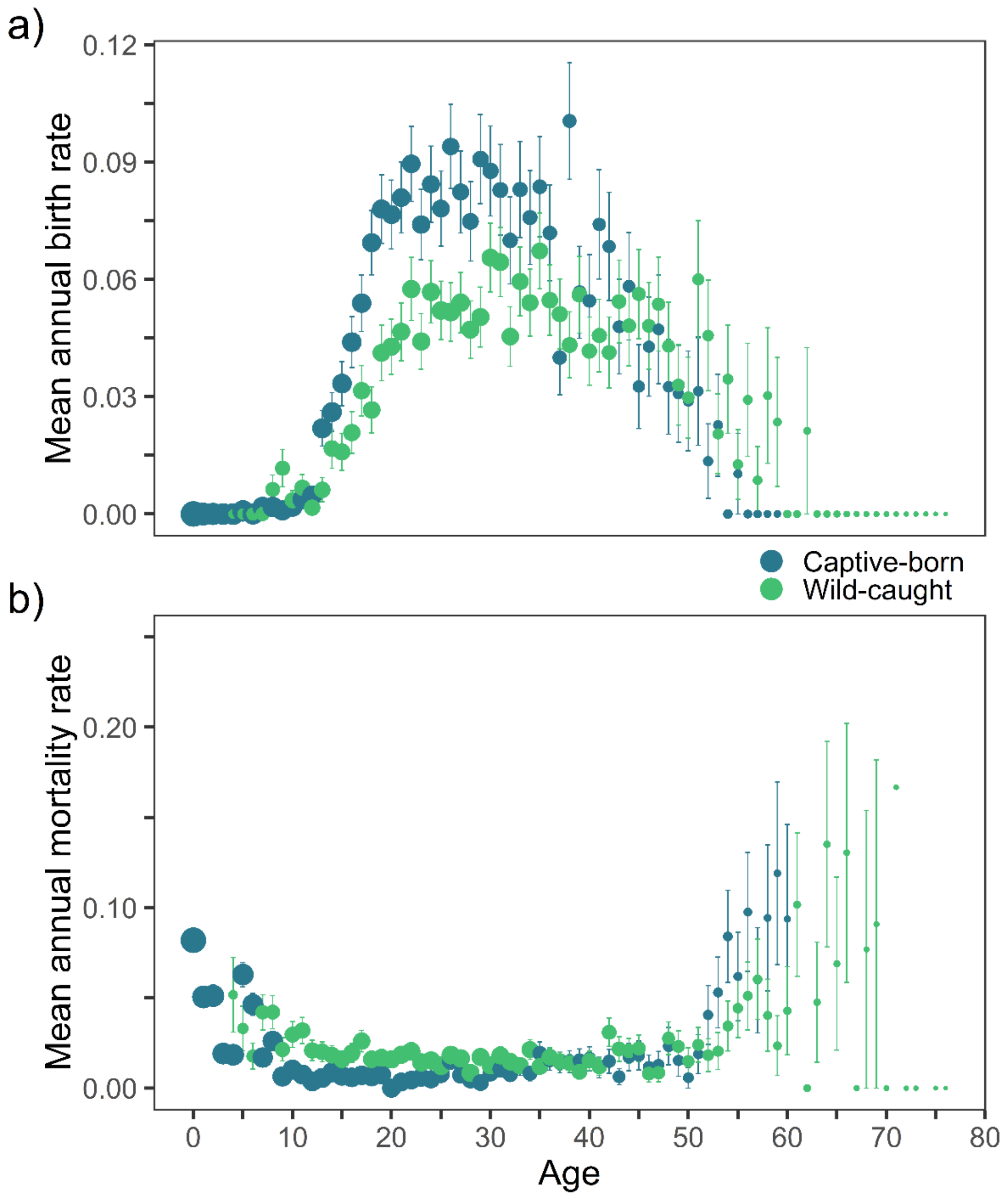

Figure S2.7 Mean age-specific birth (a) and mortality (b) rates in captive-born and wild-caught female timber elephants between 1960 and 2014. Points are mean annual age-specific birth rates across all years and regional divisions in Myanmar, with standard error bars. The size of the points indicates the sample size for a given age (range = 1-1965).

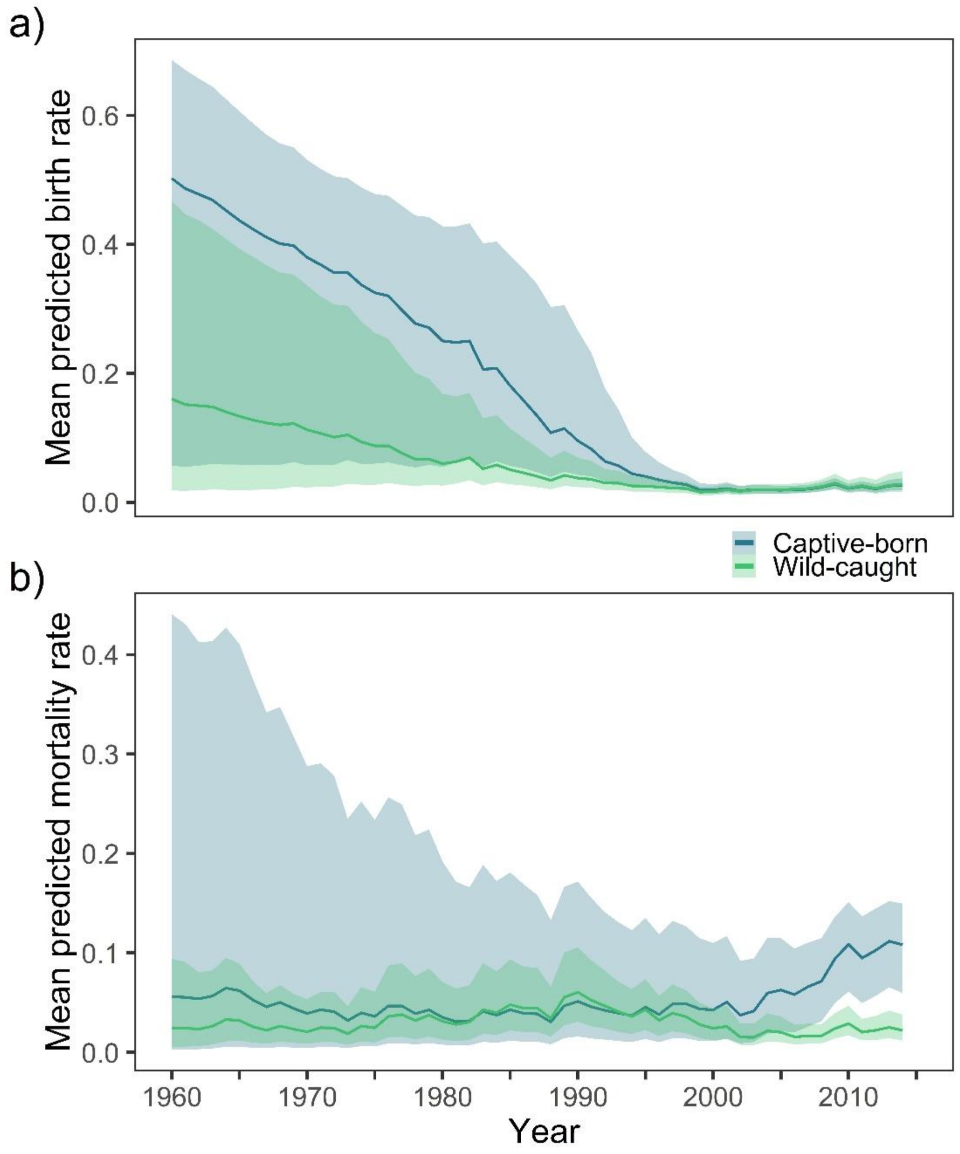

Figure S2.8 Change in the mean predicted birth (a) and mortality (b) rates between 1960 and 2014 for captive-born and wild-caught females. Lines are mean model predicted values over 1000 posterior simulations with 95% confidence intervals.

S2.3 Formulation of the stochastic individual-based model

Description of the individual-based model using the ODD protocol described by Grimm et al. 2006.

1 Purpose

The purpose of the model is to understand the long-term population dynamics of captive female elephants in Myanmar in a scenario where wild-capture is no longer practised. Here we present only the formation of the first age-specific projection model, which incorporated only demographic stochasticity and the mean age-specific birth/mortality probabilities across study years (1995-2014) for each birth origin.

2 State variables and scales

The model is formed at the level of each individual female. Individuals are characterised by two state variables: Their age (a, integer between 0 and 70 in years) and their birth origin (captive-born C, or wild-caught W). The population is characterised by the number of individuals in a given year (at each age and of each birth origin).

3 Process overview and scheduling

The model proceeds in annual time steps. Within each year or time step, 2 phases are processed in the following order: birth and mortality. This order was selected in order to allow females to reproduce and die in the same year. In each year, based on their age and birth-origin, females had a given probability of reproduction or mortality. An overview of the life-cycle and transition probabilities is given in figure S2.9.

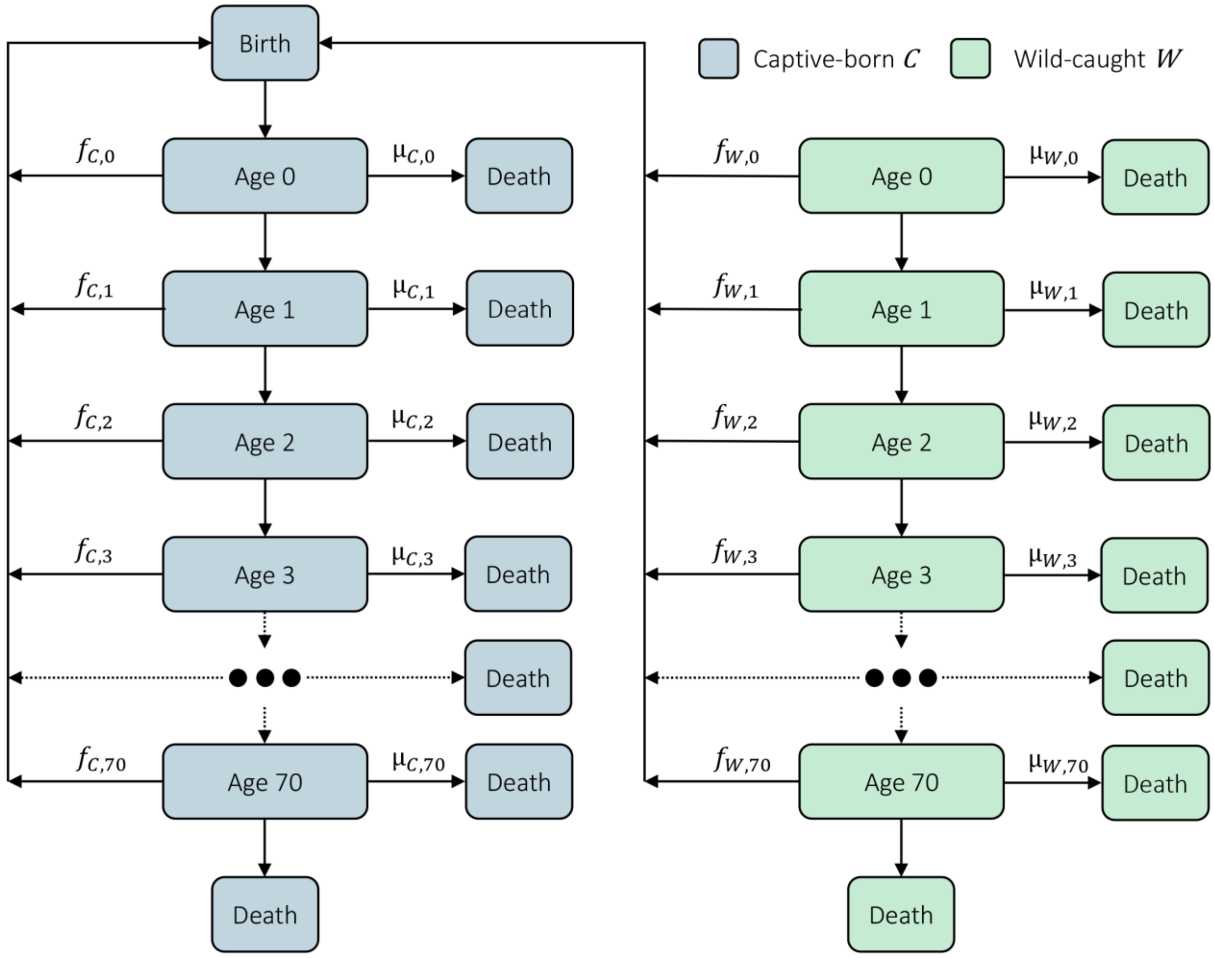

Figure S2.9 A schematic of the life-cycle for the individual-based stochastic projection model for female timber elephants without wild-capture. Colour denotes birth origin. Each individual at each age (a) had mean annual predicted birth probabilities of $f_{C,a}$ (captive-born) and $f_{W,a}$ (wild-caught), and mean annual predicted mortality probabilities of $\mu_{C,a}$ (captive-born) and $\mu_{W,a}$ (wild-caught). All individuals born were captive-born females at age 0. Individuals living past the age of 70 were removed from the analysis.

4 Design concepts

Stochasticity: Birth and mortality are interpreted as binary events drawn from the Bernoulli distribution for each individual from each birth origin, with a probability from the mean age-specific probability from the best-fit birth and mortality models. Observation: For model analysis, we recorded the population-level variable of $\ln population\ size$.

5 Initialization and input

We began the projection with the age-structure present in 2014 (N = 1369), which had 976 captive-born females and 393 wild-caught females. The starting age-structure is given in figure S11. Demographic stochasticity was incorporated by performing 500 iterations of the projection model. We projected forward 250 years, which captured long-term trends over 10-12.5 generations. For this projection, age-specific birth and mortality probabilities were averaged across the study period (1995-2014) from the best-fit model predictions. Furthermore, the projection was run on predicted values from the Kachin regional division. Explicitly, the mean age-specific predicted birth probability, $p(birth)$, is given by the following binomial additive model

$$p(birth) = \left[1 + e^{-(\beta_0 + g(a,\ C) + g(a,\ W))}\right]^{-1}$$

Where β_0 is the intercept, and the function $g()$ describes a tensor product interaction smoothing term fit with a thin plate regression spline for an individual at age a, and separately for captive-born, C, and wild-caught, W, females, but averaged across years 1995-2014, rather than incorporating an observation year effect (table S1). The mean age-specific predicted mortality probability, $p(mort)$, is given by the following binomial additive model

$$p(mort) = \left[1 + e^{-(\beta_0 + g(a,\ C) + g(a,\ W))}\right]^{-1}.$$

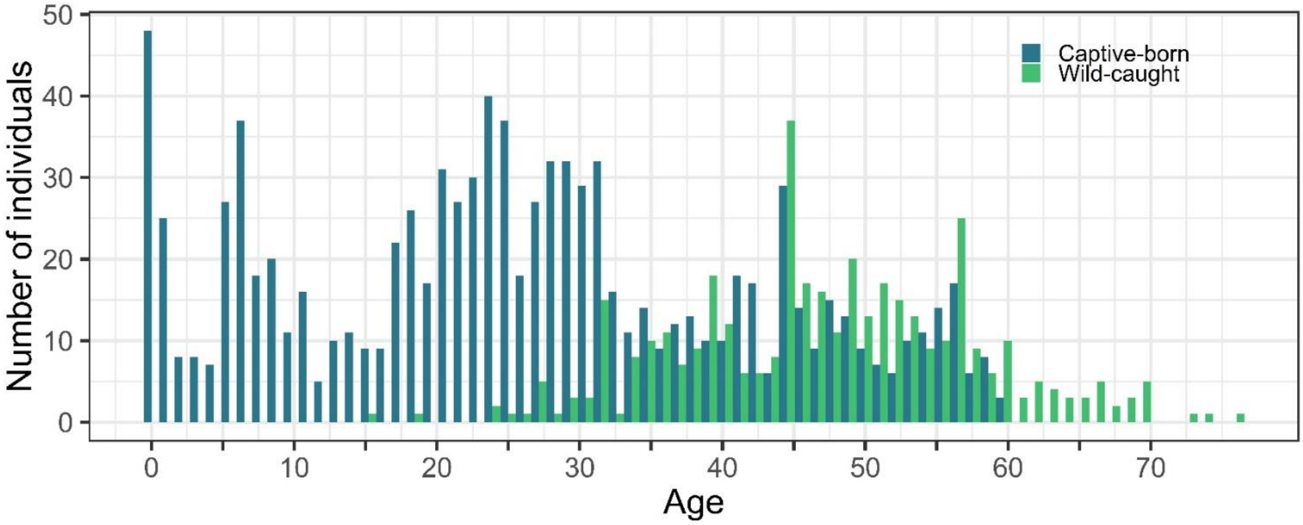

Figure S2.10 A histogram of the starting age-structure for stochastic, individual-based population projections, which was the age-structure present in 2014 (N = 1369). Ages are in 1-year bins. Colour denotes the birth origin.

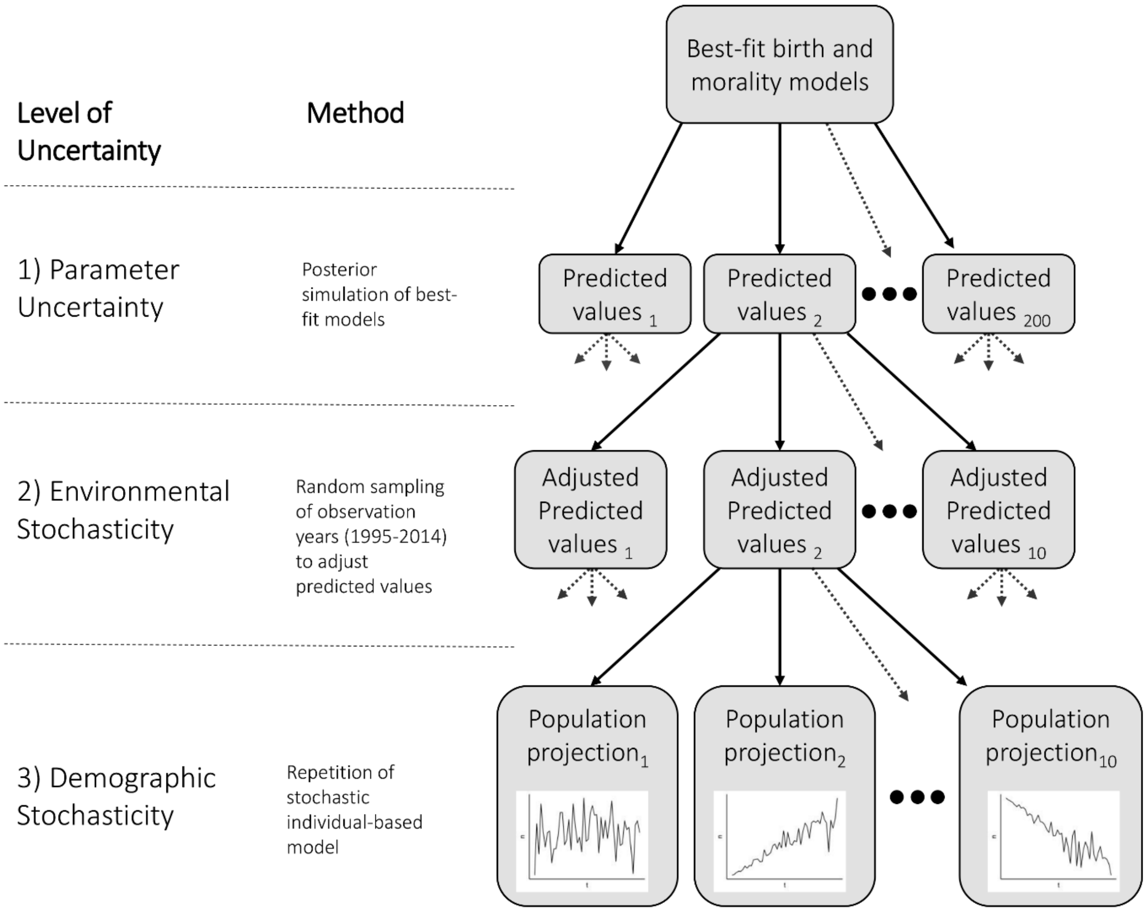

Figure S2.11 A schematic of the simulation framework for implementing the hierarchical population viability analysis under different levels of uncertainty. Starting from the best-fit birth and mortality models, 1) parameter uncertainty was incorporated through posterior simulation, generating 200 sets of predicted values. 2) Environmental stochasticity was incorporated by randomly sampling 10 sets of years (1995-2014) and adjusting predicted values based on observed variation in those years. 3) Demographic stochasticity was incorporated by repeating each population projection 10 times. When partitioning the variance in $\ln population\ size$ to these three levels of uncertainty, for each year we incorporated the hierarchical framework of demographic stochasticity within environmental stochasticity within parameter uncertainty using nested intercept-only random effects.

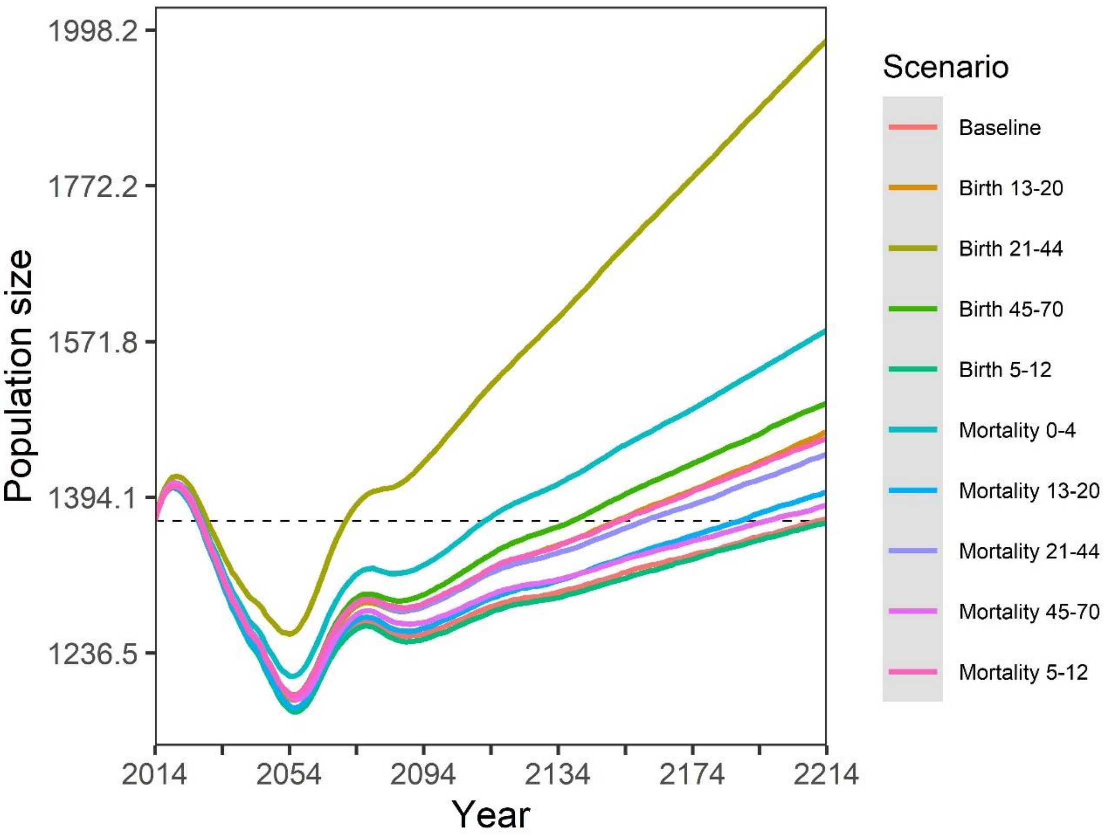

Figure S2.12 All scenarios of demographic change and their influence on population viability over 200 years. Each line represents either the baseline, average scenario of long-term viability or a scenario with a 10% increase (birth rates) or 10% decrease (mortality rates) for specific age classes. Population size axis on the natural logarithmic scale, dashed line represents starting population size.

S3. Supplementary information for chapter 4

Long-term fluctuation in demographic structure is a key determinant of population growth in a long-lived mammal

References included in chapter 4

S3.1 Grouping spatial divisions

For models examining age-specific and temporal trends in birth and mortality rates, we also included a random effect smoothing term of spatial division group in Myanmar, penalized with a ridge penalty (Wood 2008). We had life history records from 11 out of 14 spatial divisions (Ayeyarwady = 1520, Bago = 4968, Chin = 55, Kachin = 1112, Magway = 9587, Mandalay = 3890, Nay Pyi Taw = 2153, Rakhine = 222, Sagaing = 17707, Shan = 2633, Tanintharyi = 9, Yangon = 122, Unknown= 864). In the analyses, to make sample sizes more comparable we grouped divisions by proximity and elevation: Ayeyarwady, Yangon, Bago, Rakhine, and Tanintharyi regions were all grouped together because of low sample size and their coastal locations. Chin and Shan regions were grouped together because of their similar elevation and low sample sizes. Finally, Magway, Mandalay and Nay Pyi Taw regions were grouped together because of similar altitude, proximity and low sample size.

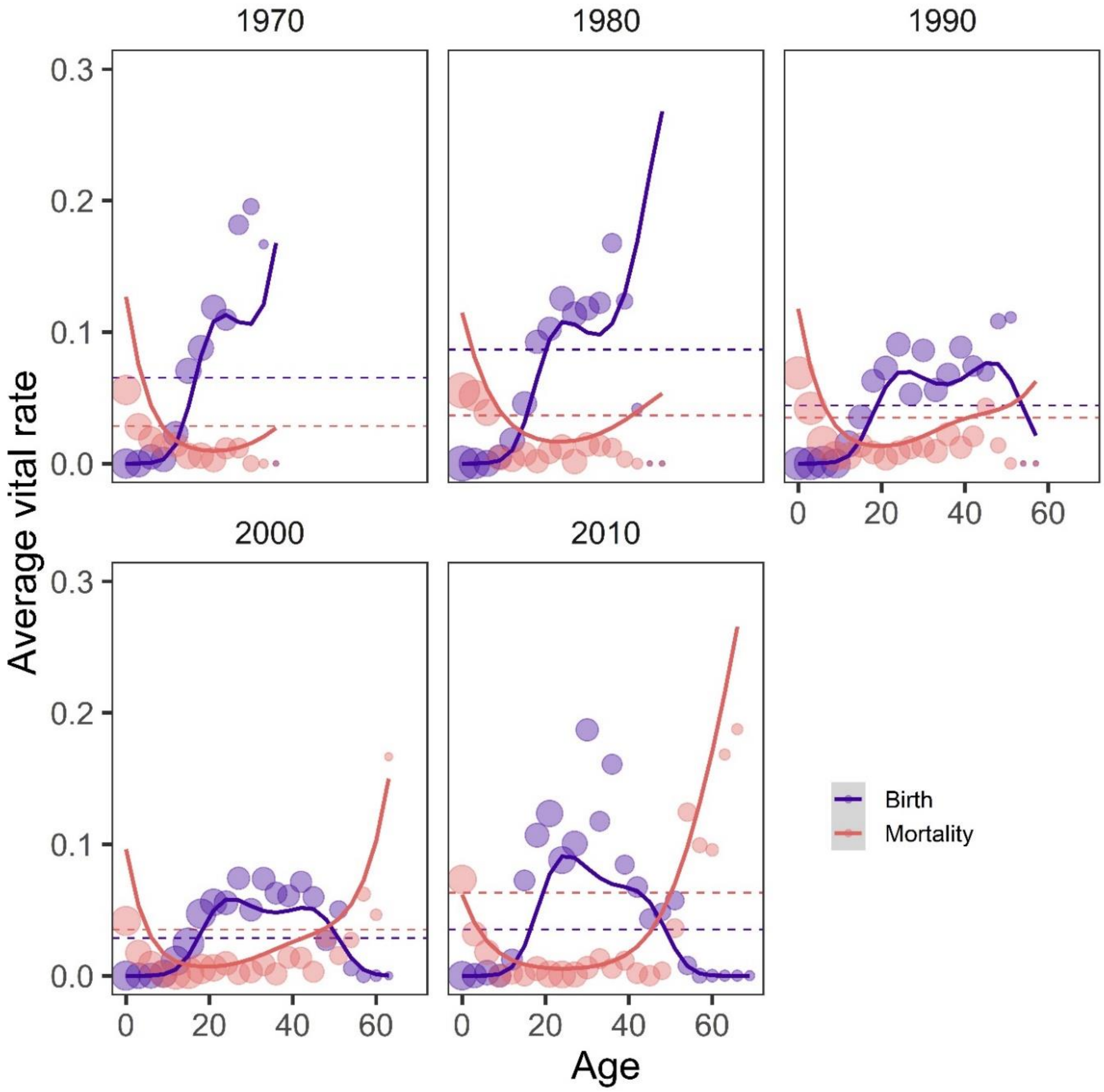

Figure S3.1. Average age-specific birth and mortality rates in captive-born females in each decade between 1970 and 2014. Points are mean observed age-specific vital rates in each decade, and the size of the points indicates the mean sample size for a given age in a given decade (range = 1-40). Lines are mean predicted values from additive models across each decade and regional divisions. Dashed lines are the mean vital rate values across ages for each decade.

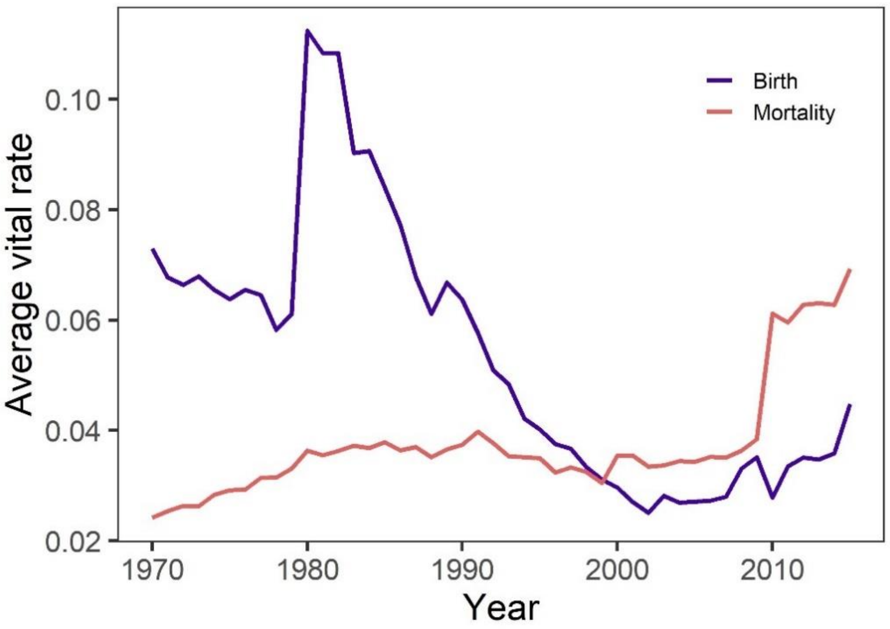

Figure S3.2. Annual trends in mean predicted vital rates between 1970-2014. Mean predicted birth (purple) and mortality (pink) rates in each year averaged across ages and regional divisions.

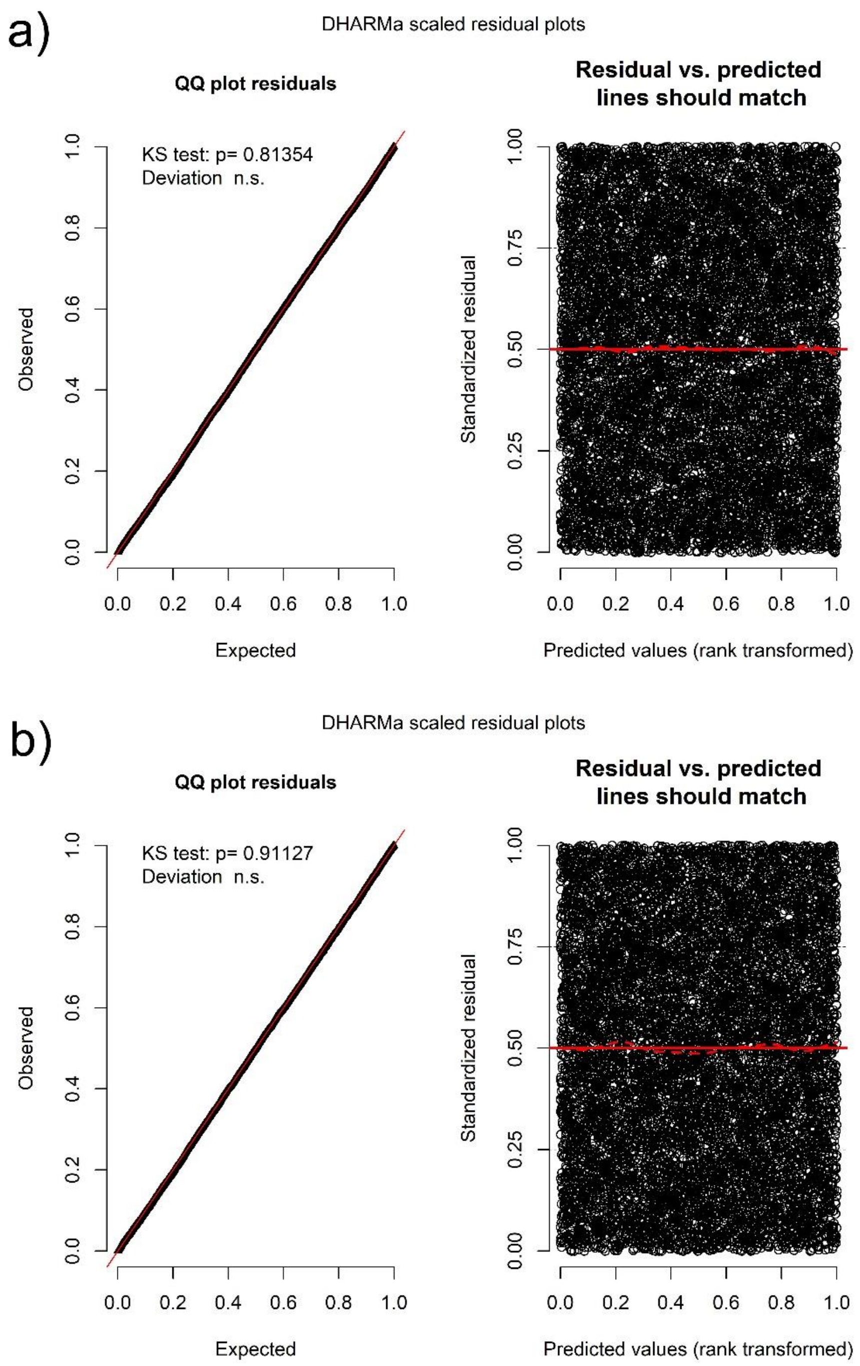

Figure S3.3. Scaled model residual diagnostics for the best-fit birth (a) and mortality (b) models over 1000 simulations. In neither birth nor mortality models was their evidence for deviation from uniformity in the residuals (left), or a relationship between predicted values and residuals (right).

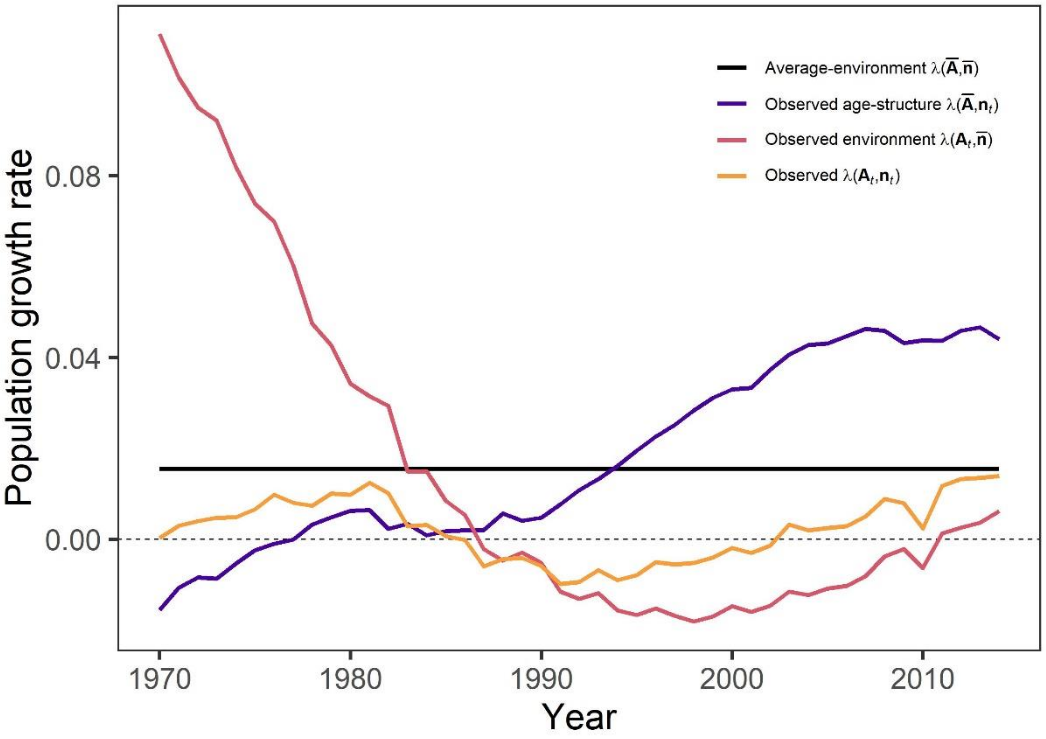

Figure S3.4. Annual natural log-transformed population growth rates from equations 3-6. The yellow line is the observed population growth rate $\lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$ from equation 3. The black line is the average environment population growth rate $\lambda(\bar{\boldsymbol{A}}, \bar{\boldsymbol{n}})$ from equation 4. The purple line is the population growth rate including the observed age-structure in each year, but holding the average environment projection matrix, $\lambda(\bar{\boldsymbol{A}}, \boldsymbol{n}_t)$ from equation 5. The pink line is the population growth rate including the observed environmental component in each year, but holding the average environment age-structure, $\lambda(\boldsymbol{A}_t, \bar{\boldsymbol{n}})$ from equation 6. The dashed line at $\ln \lambda = 0$ i.e. $\lambda = 1$, indicates replacement rate.

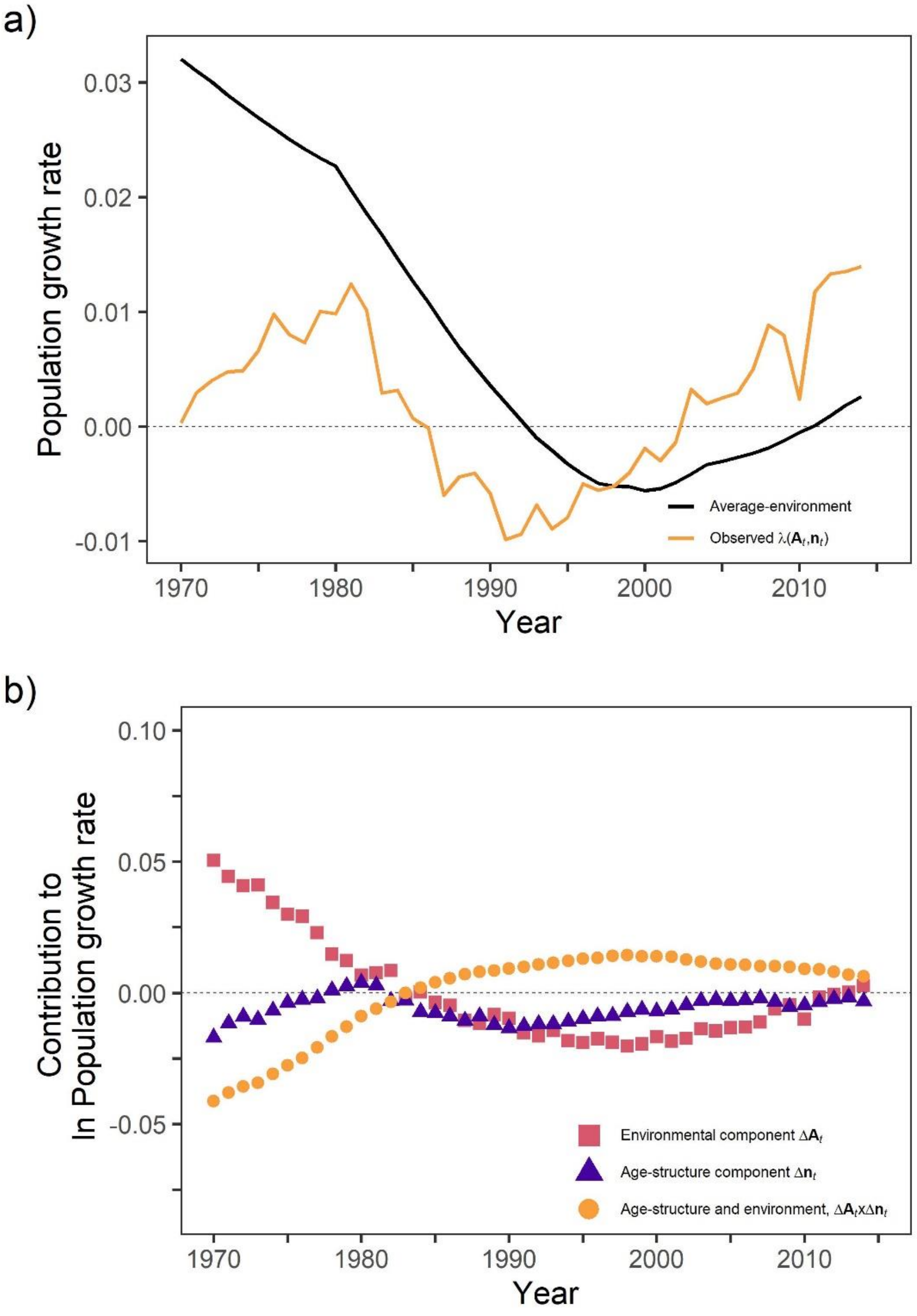

Figure S3.5 Repeating the variance decomposition with a time-varying average environment model. a) The observed log transformed short-term population growth rate (yellow line, $\ln\lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$ from equation 3) between 1970 and 2014, relative to a time-varying average-environment short-term population growth rate (solid black line). Average environment population growth rates were calculated for each year using the mean projection matrix over a sliding window of 20 years (10 years before and 10 years after). Dashed black line indicates a ln population growth rate of 0. b) The contribution of the age-structure component (purple triangles, $\Delta\boldsymbol{n}_t$) and environmental component (or age-specific vital rate component, pink squares, $\Delta\boldsymbol{A}_t$) to variation in annual log-transformed short-term population growth rates ($\ln\lambda(\boldsymbol{A}_t, \boldsymbol{n}_t)$) between 1970 and 2014. Yellow circles indicate non-additive contributions from both the age-structure and environmental components in a given year ($\Delta\boldsymbol{A}_t x \Delta\boldsymbol{n}_t$). 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. These results indicate that the predominant pattern of a strong negative contribution of age-structure and positive contribution of the environmental component early in the study period was maintained in this additional analysis. Thus, we conclude that the use of the average-environment population growth rate, $\ln \lambda(\overline{\boldsymbol{A}}, \overline{\boldsymbol{n}})$ from equation 4, across the study period was appropriate in the current study.

S4. Supplementary information for chapter 5

Identifying delayed climatic drivers of age-specific life-history in a long-lived mammal

References included in chapter 5

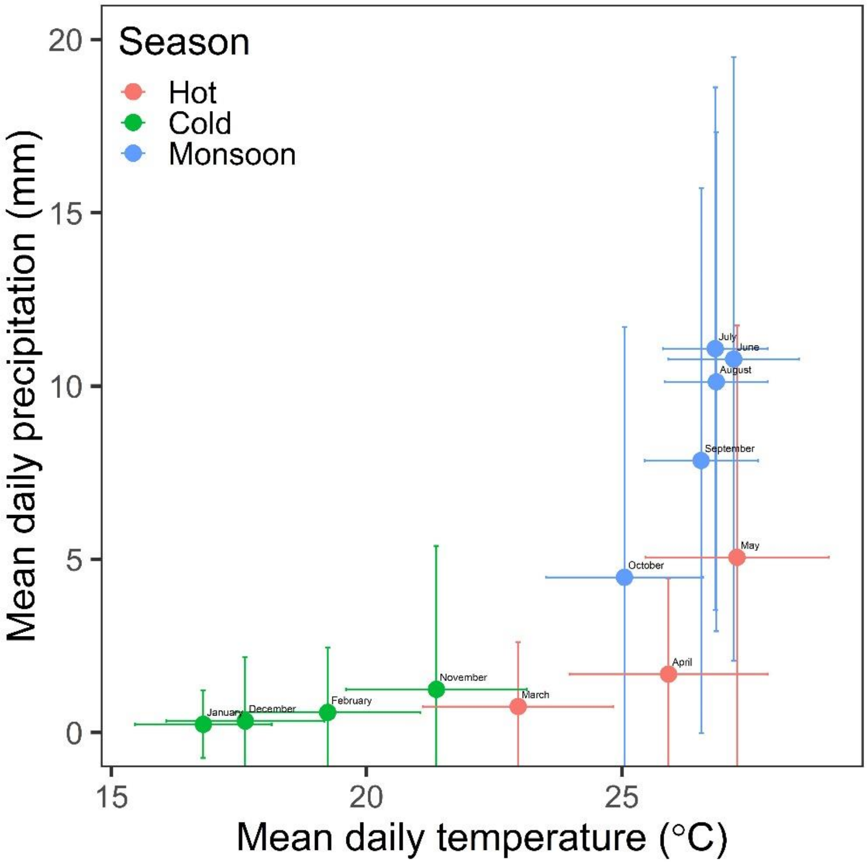

Figure S4.1 Daily average temperature and precipitation in each month for the deciduous forest area of Sagaing and Kachin regional divisions in Myanmar. Colour indicates season, points are mean daily climate values across the climate data period period (precipitation 1951-2007, temperature 1961-2007), with standard deviation for both temperature and precipitation.

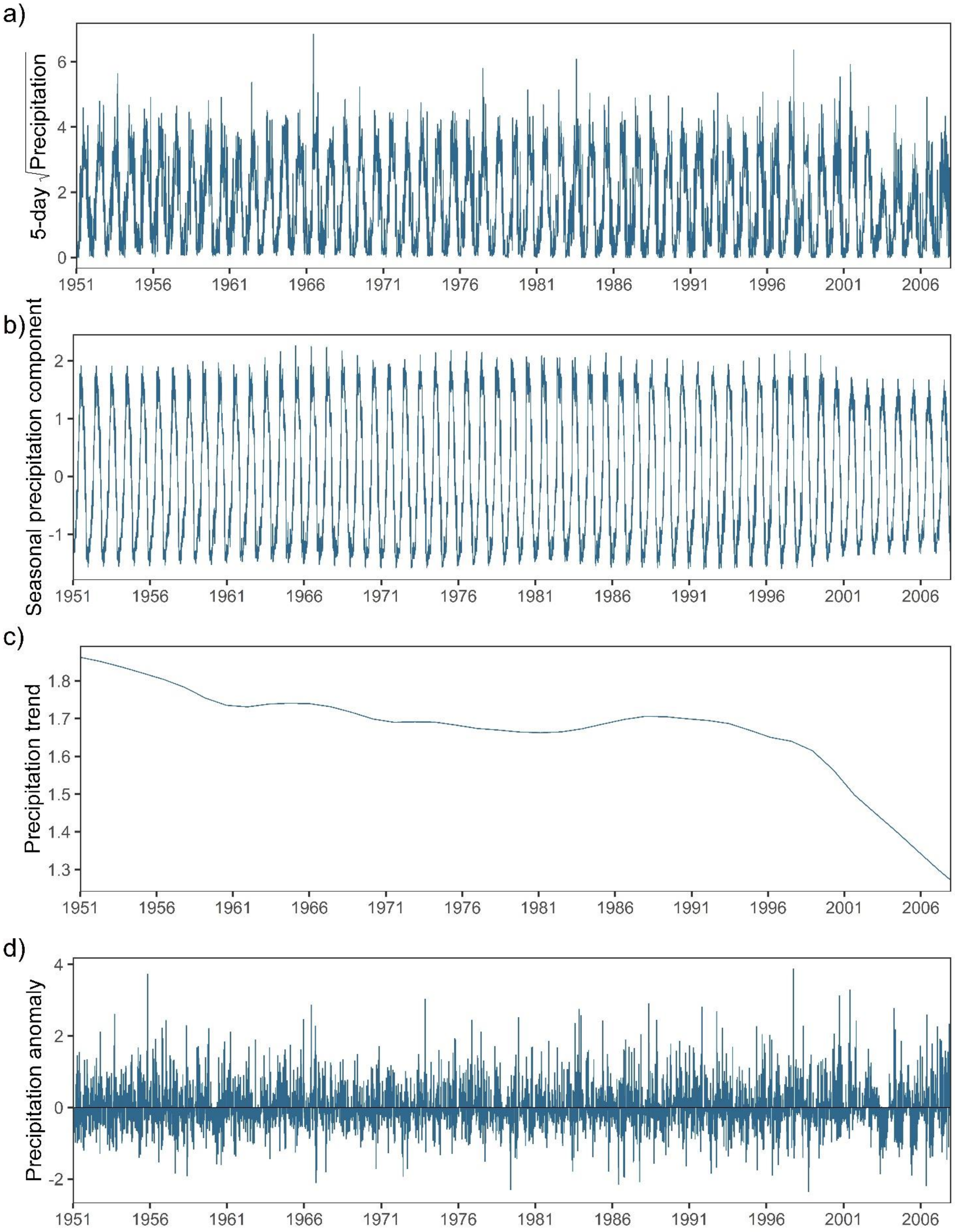

Figure S4.2 Additive decomposition of 5-day square root transformed precipitation data. a) Raw 5-day square root transformed precipitation data. b) Seasonal component of precipitation using a 15-year window. c) Trend component of precipitation using 1000 5-day increments as the window. d) Remainder, or Anomaly, component of precipitation.

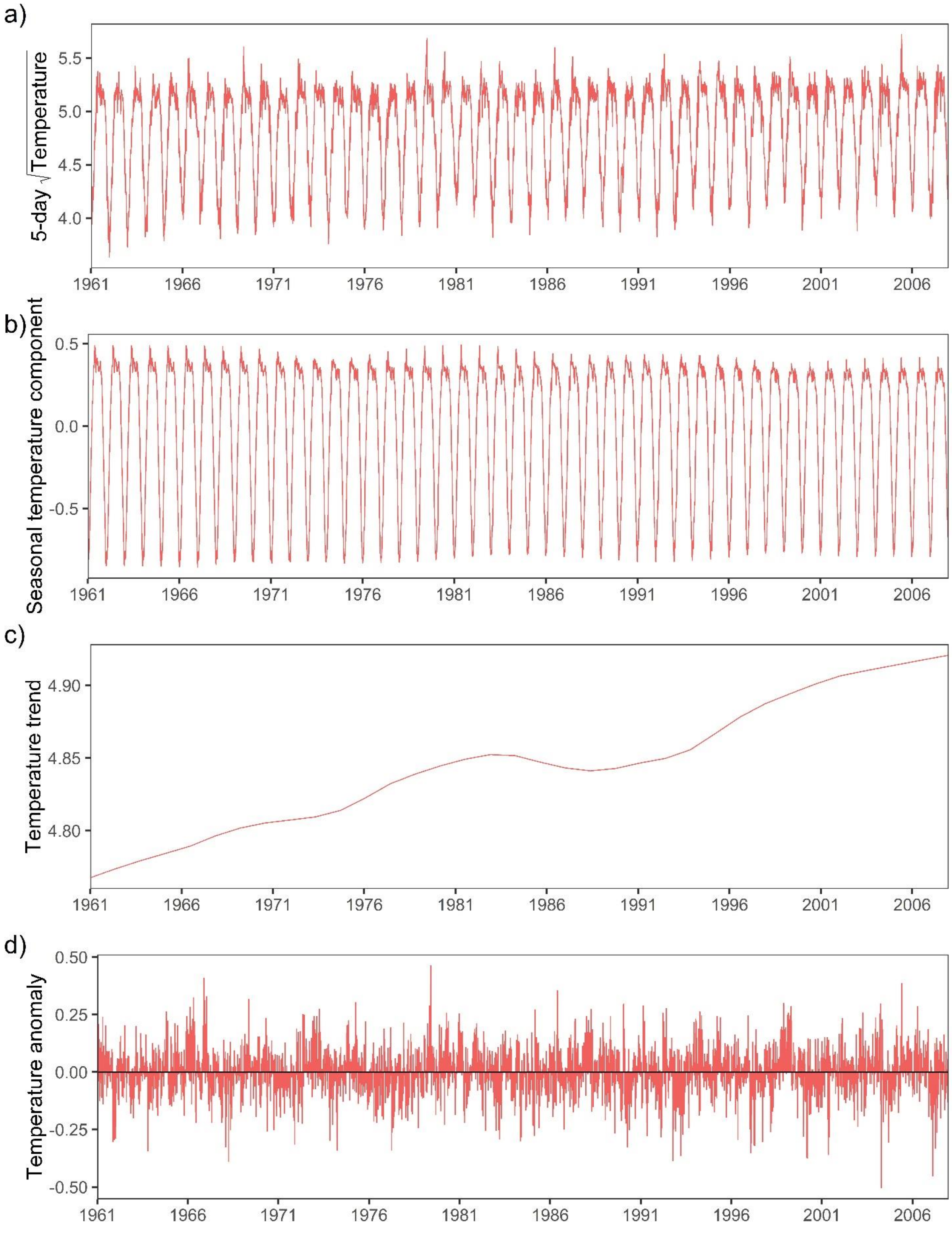

Figure S4.3 Additive decomposition of 5-day square root transformed temperature data. a) Raw 5-day square root transformed temperature data. b) Seasonal component of temperature using a 15-year window. c) Trend component of temperature using 1000 5-day increments as the window. d) Remainder, or Anomaly, component of temperature.

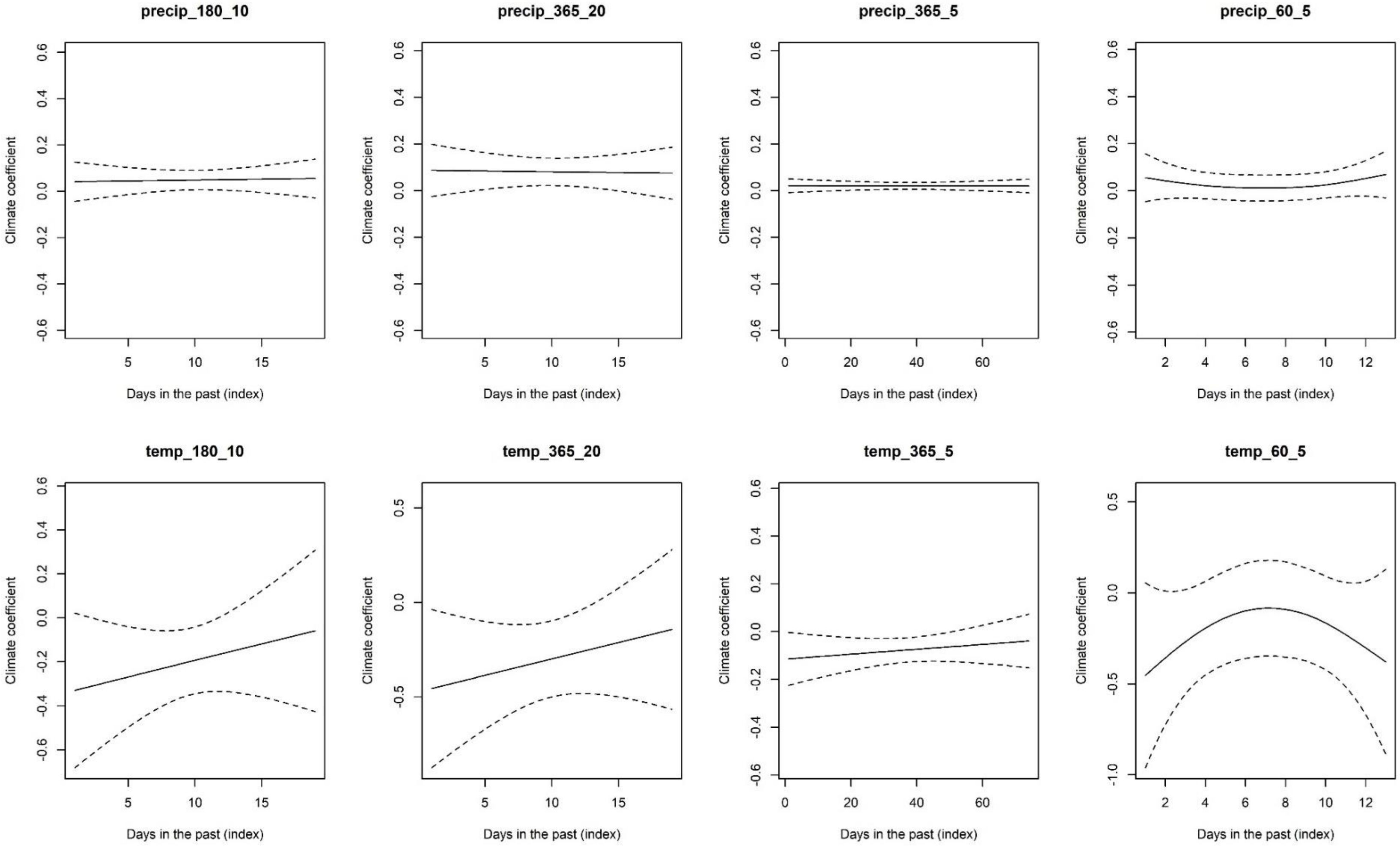

Figure S4.4 Past climate effects from *continuous* models of delayed climatic drivers on juvenile mortality. Each panel shows the weighted climate effect in the past, with the title of each panel denoting the climate variable (temp = Temperature, precip = Precipitation) and the climate window (e.g. 180_10 indicates a 180 by 10 day climate window). Solid lines are the mean climate smoothing effect from the model, dashed lines are standard errors.

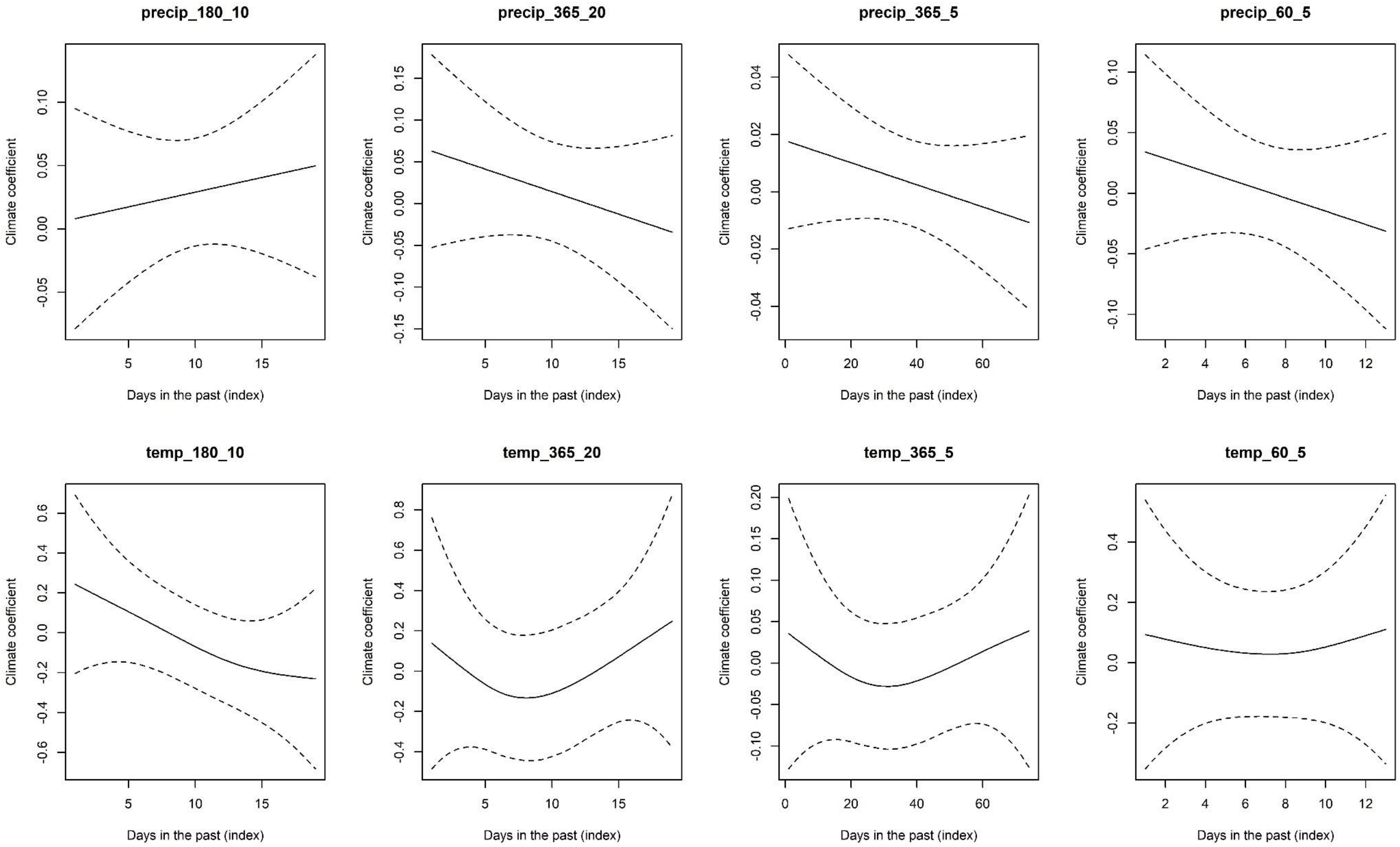

Figure S4.5 Past climate effects from *continuous* models of delayed climatic drivers on peak-age conception. Each panel shows the weighted climate effect in the past, with the title of each panel denoting the climate variable (temp = Temperature, precip = Precipitation) and the climate window (e.g. 180_10 indicates a 180 by 10 day climate window). Solid lines are the mean climate smoothing effect from the model, dashed lines are standard errors.

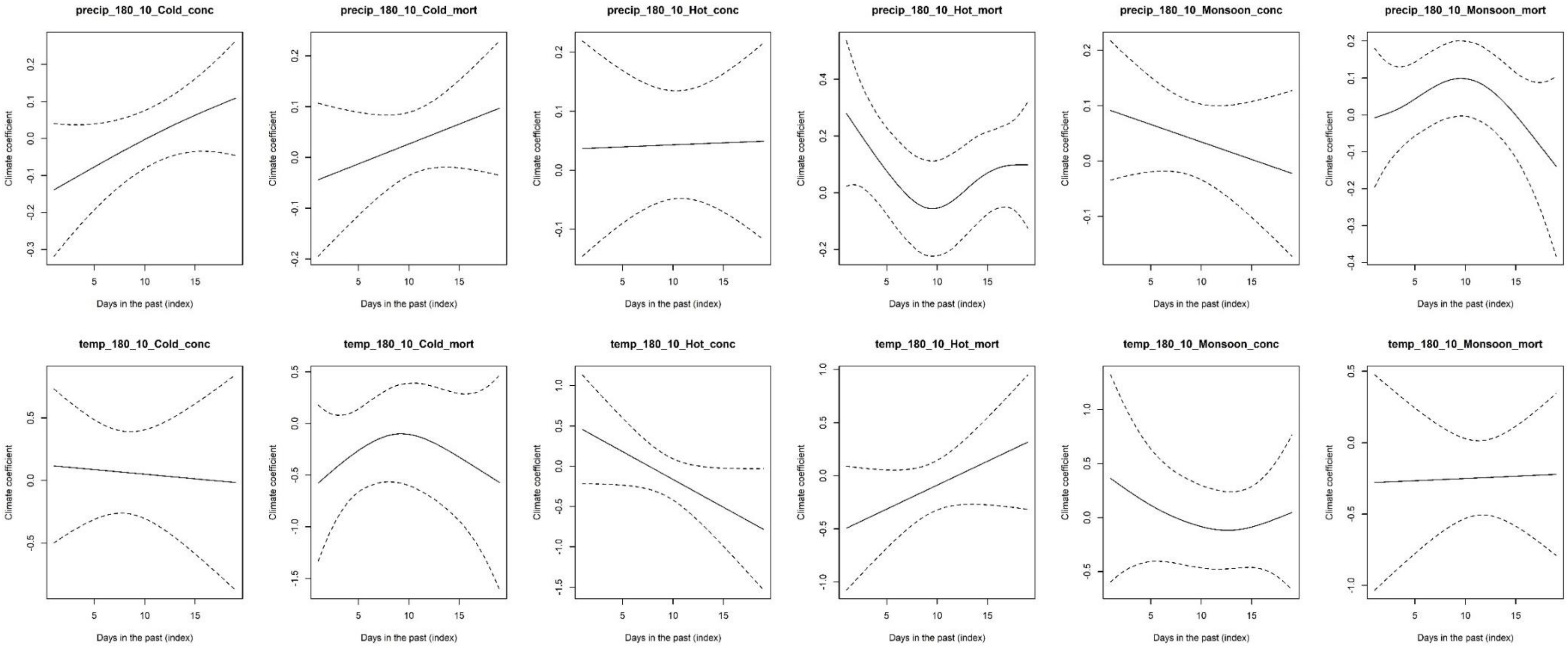

Figure S4.6 Seasonal past climate effects from *continuous* models of delayed climatic drivers on vital rates. Each panel shows the weighted climate effect in the past, with the title of each panel denoting the climate variable (temp = Temperature, precip = Precipitation) and the climate window (e.g. 180_10 indicates a 180 by 10 day climate window), the season (Hot, Cold and Monsoon), and the response variable (mort = juvenile mortality, conc = peak-age conception). Solid lines are the mean climate smoothing effect from the model, dashed lines are standard errors.

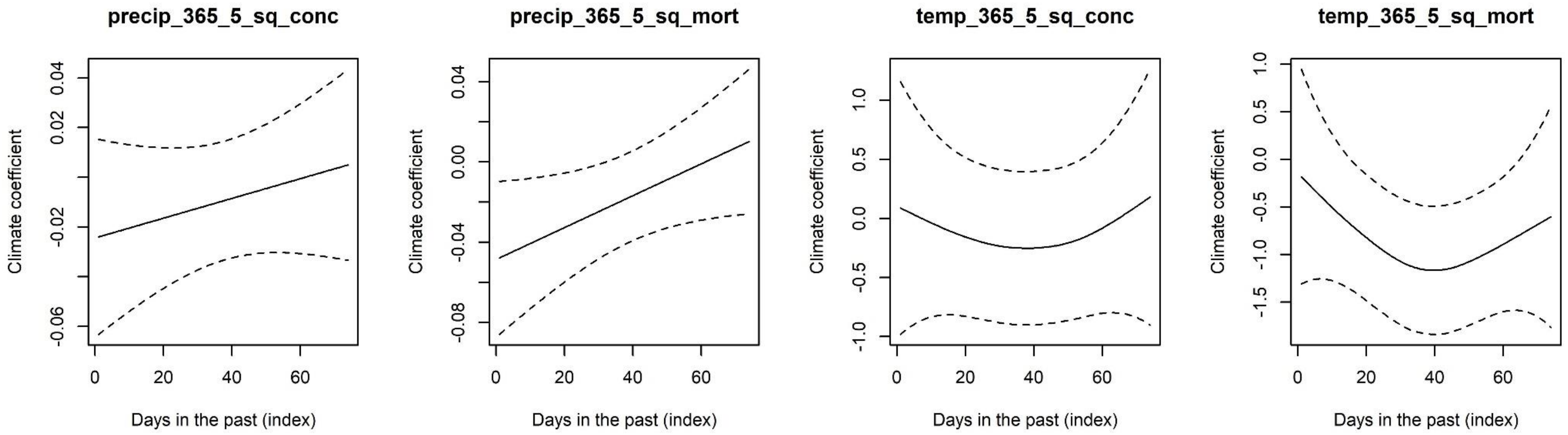

Figure S4.7 Past effect of variance in climate anomaly from *continuous* models of delayed climatic drivers on vital rates. Each panel shows the weighted climate effect in the past, with the title of each panel denoting the climate variable (temp = Temperature, precip = Precipitation) and the climate window (e.g. 365_5 indicates a 365 by 5 day climate window), and the response variable (mort = juvenile mortality, conc = peak-age conception). Solid lines are the mean climate smoothing effect from the model, dashed lines are standard errors.

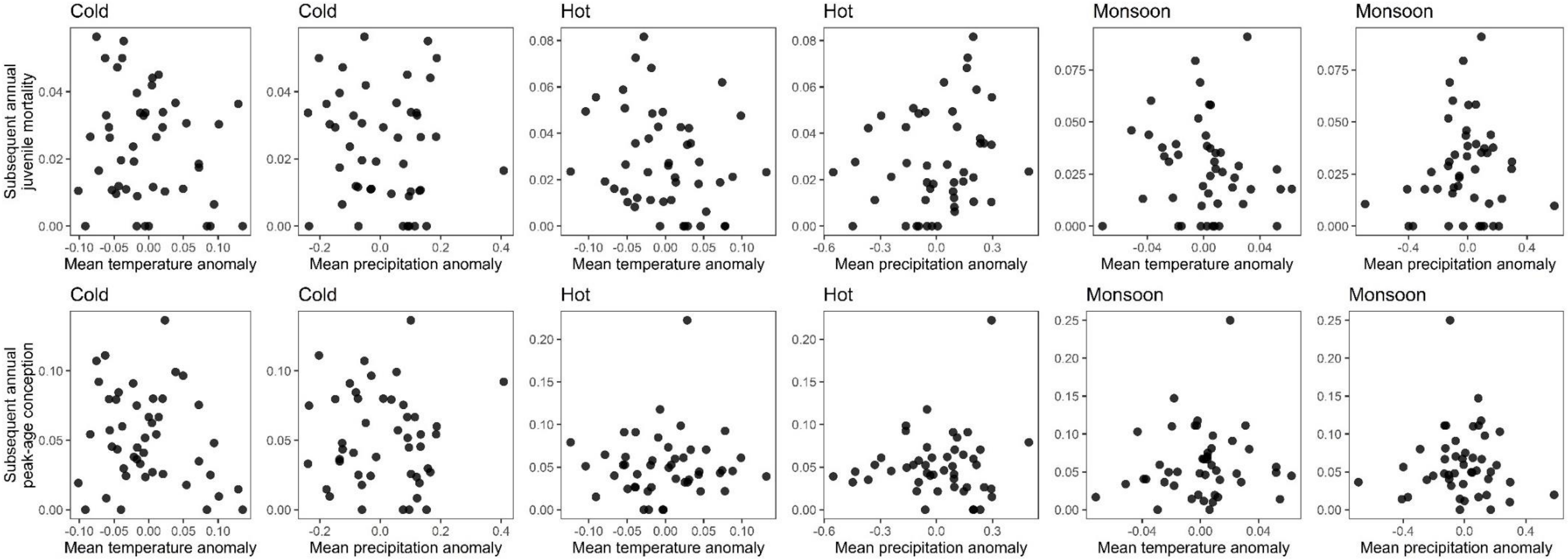

Figure S4.8 Past seasonal climate effects on subsequent juvenile mortality (top) and peak-age reproduction (bottom) from *frailty* models of delayed climatic drivers. Panels display the mean temperature and precipitation anomaly in the focal season (title) between 1961-2007 (a proxy for the weighted climate effect in the focal season) and its effect on subsequent annual vital rates.

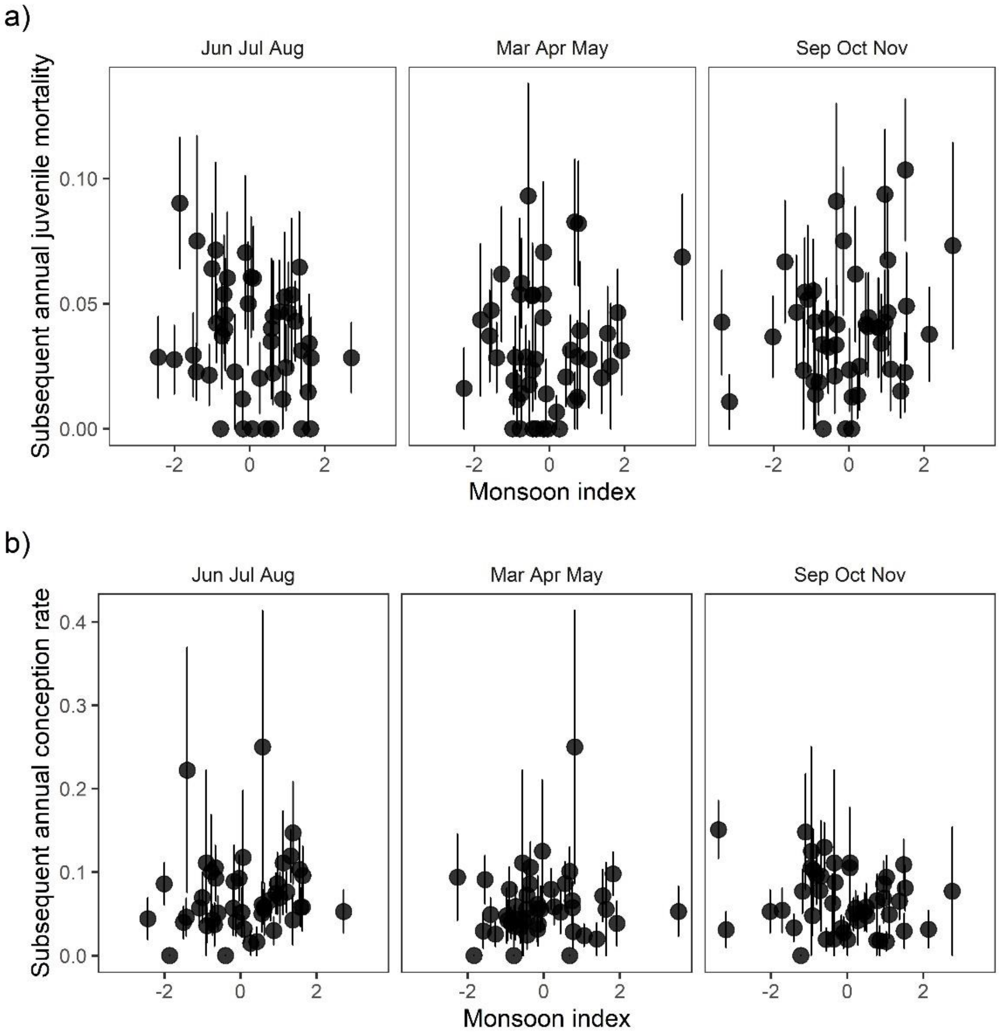

Figure S4.9 Past monsoon index effects on subsequent juvenile mortality (a) and peak-age reproduction (b) from *frailty* models of delayed climatic drivers. Panels display the Monsoon indices from the three periods from Tsai et al. (2015) (title) and subsequent annual vital rates.

Table S4.1 Cross validation results for *continuous* FLM models. For Model, numeric values indicate the climate window used in the focal model, or the response variable/season in additional analysis (Seasonal FLMs and Climate anomaly variance). All Seasonal FLM models were run with a 180 by 10 day climate window, and all Climate anomaly variance models were run with a 365 by 5 day climate window. $\Delta\, log\ loss$ and ΔBIC indicate the difference between the test model (with the climate variable) and the base model (without the climate variable in $log\ loss$, the cross-validation metric, and Schwarz's Bayesian information criterion (BIC), respectively. $\Delta\, log\ loss$ values of less than -2 are highlighted in bold, indicating cross validation support for the model.

Analysis	Climate variable	Model	$\Delta \log loss$	ΔBIC
Juvenile mortality	Precipitation	180 by 10 days	-0.8	21.7
		365 by 20 days	-0.6	18.8
		365 by 5 days	-0.6	18.6
		60 by 5 days	1.5	35.7
	Temperature	180 by 10 days	-0.8	17.0
		365 by 20 days	**-2.0**	15.4
		365 by 5 days	**-2.0**	15.6
		60 by 5 days	0.2	26.9
Peak-age reproduction	Precipitation	180 by 10 days	0.9	22.7
		365 by 20 days	1.6	21.8
		365 by 5 days	1.5	21.2
		60 by 5 days	1.7	24.6
	Temperature	180 by 10 days	4.2	28.8
		365 by 20 days	4.6	35.1
		365 by 5 days	4.8	35.0
		60 by 5 days	3.3	27.3
Seasonal FLMs	Precipitation	Cold season peak reproduction	0.0	21.8
		Cold season juvenile mortality	0.4	21.2
		Hot season peak-age reproduction	3.0	21.3
		Hot season juvenile mortality	1.7	36.4
		Monsoon season peak-age reproduction	0.8	20.7
		Monsoon season juvenile mortality	-0.1	37.1
	Temperature	Cold season peak-age reproduction	2.0	22.5
		Cold season juvenile mortality	0.3	29.7
		Hot season peak-age reproduction	-0.7	17.6
		Hot season juvenile mortality	1.4	20.1
		Monsoon season peak-age reproduction	5.1	30.8
		Monsoon season juvenile mortality	0.7	20.4
Climate anomaly variance	Precipitation	Peak-age reproduction	1.5	23.5
		Juvenile mortality	**-3.1**	19.2
	Temperature	Peak-age reproduction	2.8	34.3
		Juvenile mortality	**-5.4**	28.0

Table S4.2 Cross validation results for *frailty* models. All seasonal weighted climate effect models were run using FLM models with 10 day increments across the focal season, and all Monsoon index models were run using GLMs. FLM knots indicates the number of knots used in the seasonal weighted effects models. $\Delta\, log\, loss$ and ΔBIC indicate the difference between the test model (with the climate variable) and the base model (without the climate variable) in $log\, loss$, the cross-validation metric, and Schwarz's Bayesian information criterion (BIC), respectively. $\Delta\, log\, loss$ values of less than -2 are highlighted in bold, indicating cross validation support for the model.

Analysis	Response variable	Climate variable	Focal season	FLM knots	$\Delta \log loss$	ΔBIC
Seasonal weighted climate effect	Juvenile mortality	Temperature	Cold	4	5.7	26.5
			Hot	3	3.1	17.5
			Monsoon	6	7.2	20.7
		Precipitation	Cold	4	**-2.5**	9.1
			Hot	3	6.6	20.8
			Monsoon	6	11.9	22.8
	Peak-age conception	Temperature	Cold	4	6.6	21.0
			Hot	3	3.4	19.8
			Monsoon	6	3.0	16.9
		Precipitation	Cold	4	9.1	24.5
			Hot	3	1.3	17.3
			Monsoon	6	1.5	21.7
	Mortality, all ages	Temperature	Cold	4	5.9	18.7
			Hot	3	11.2	23.0
			Monsoon	6	7.1	21.8
		Precipitation	Cold	4	-0.6	13.9
			Hot	3	10.9	17.1
			Monsoon	6	13.2	18.8
	Conception, all ages	Temperature	Cold	4	8.7	26.0
			Hot	3	2.9	18.3
			Monsoon	6	11.5	20.4
		Precipitation	Cold	4	**-2.8**	15.8
			Hot	3	3.0	21.0
			Monsoon	6	5.0	27.1
Monsoon index	Juvenile mortality	Single index	March April May		0.9	7.7
			June July August		0.3	6.3
			September October November		0.5	6.5
	Peak-age conception		March April May		1.3	7.4
			June July August		0.9	7.0
			September October November		1.9	4.4
	Mortality, all ages		March April May		1.6	7.6
			June July August		2.0	10.0
			September October November		0.9	9.9
	Conception, all ages		March April May		**-2.2**	6.9
			June July August		8.6	10.1
			September October November		1.5	1.0