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Climatic variation and age-specific survival in Asian elephants from Myanmar

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Abstract. Concern about climate change has intensified interest in understanding how climatic variability affects animal life histories. Despite such effects being potentially most dramatic in large, long-lived, and slowly reproducing terrestrial mammals, little is known of the effects of climatic variation on survival in those species. Asian elephants (*Elephas maximus*) are endangered across their distribution, and inhabit regions characterized by high seasonality of temperature and rainfall. We investigated the effects of monthly climatic variation on survival and causes of death in Asian elephants using a unique demographic data set of 1024 semi-captive, longitudinally monitored elephants from four sites in Myanmar between 1965 and 2000. Temperature had a significant effect on survival in both sexes and across all ages. For elephants between 1 month and 17 years of age, maximal survival was reached at ~24°C, and any departures from this temperature increased mortality, whereas neonates and mature elephants had maximal survival at even lower temperatures. Although males experienced higher mortality overall, sex differences in these optimal temperatures were small. Because the elephants spent more time during a year in temperatures above 24°C than in temperatures below it, most deaths occurred at hot (temperatures >24°C) rather than cold periods. Decreased survival at higher temperatures resulted partially from increased deaths from infectious disease and heat stroke, whereas the lower survival in the coldest months was associated with an increase in noninfectious diseases and poor health in general. Survival was also related to rainfall, with the highest survival rates during the wettest months for all ages and sexes. Our results show that even the normal-range monsoon variation in climate can exert a large impact on elephant survival in Myanmar, leading to extensive absolute differences in mortality; switching from favorable to unfavorable climatic conditions within average years doubled the odds for mortality. The persistence of a long-term trend toward higher global temperatures, combined with the possibility of higher variation in temperature between seasons, may pose a challenge to the survival of species such as Asian elephants.

Key words: Asian elephant; climate change; Elephas maximus; *mortality; Myanmar; rainfall; seasonality; semi-captive animals; temperature; timber elephants.*

Introduction

Evidence of changing climate patterns across the world (McCarthy et al. 2001), coupled with the possibility of increasing frequency of extreme climatic events (Easterling 2000), has intensified interest in understanding how climatic variability affects animal life histories (Parmesan and Yohe 2003, Loarie et al. 2009). Climatic variability is a form of ecological stress with both immediate and longer term effects on body mass (Loison et al. 1999), reproduction (Nussey et al. 2007, Bouwhuis et al. 2010), and mortality schedules (Moore et al. 1999) in various species of birds and mammals including humans (Munoz-Tuduri and Garcia-Moro 2008). For example, seasonal variation in climatic factors has been shown to influence infant survival through body mass in red deer (*Cervus elaphus*), with snow depth in winter explaining ~20% of the variability in body mass of calves born in the following spring (Albon et al. 1983), and in Alaskan caribou (*Rangifer tarandus*), in which 15% of variation in birth mass is explained by snowfall during gestation (Adams 2005). In mountain goats (*Oreamnos americanus*), winter climate was shown to affect survival across age groups, with mortality of older adults being more sensitive to extreme low temperature and snow depth than that of young adults (White et al. 2011). Survival of males is more affected by climate variability in various species, including the wild house mouse *Mus musculus* (Meikle and Westberg 2001) and red deer (Kruuk et al. 1999, Forchhammer et al. 2001), in agreement with the hypothesis that in mammals, males are more sensitive

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to environmental conditions during their development (Clutton-Brock et al. 1985, Clutton-Brock 1991, Lindström 1999).

Mostly for practical reasons, the large majority of studies of climate stress and survival have focused on short- to mid-lived species (Pounds 2001, Stireman et al. 2005, Umina et al. 2005, Schmidt et al. 2008). How survival of long-lived mammals, which take up to two decades to reach sexual maturity, have long gestations, and often provide extended parental care, is affected by climatic variation across seasons or over years has been less frequently investigated. The longest living extant terrestrial mammals include humans and the two species of elephants that can reach ages beyond 80 years (Wiese and Willis 2004), but extensive data on climatic effects on survival have only been published on humans. In a study of rural Bangladeshi children, individuals born in the monsoon ("hungry") season showed higher infant mortality (6.5%) than those born in the hot and dry ("harvest") season (4.5%; Moore et al. 2004). Limited evidence suggests that similar effects of climate on demography might also occur in the African elephant (*Loxodonta africana*) in Tanzania (Foley et al. 2008) and Kenya (Lee et al. 2011). Both studies refer only to the immediate effects of climate on survival in calves. Foley et al. (2008) revealed reduced survival in response to low rainfall in calves (particularly males) aged up to 8 years, but comparisons are based on a single severe drought in 1993. Lee et al. (2011) showed that rates of calf survival to age two in Amboseli (Kenya) were lowest in drought years. Unfortunately, the study presented no data on immediate effects of climate on adult survival. Studies of Asian elephants (*Elephas maximus*) are even rarer. Sukumar (1989) analyzed a sample of 88 captured elephants from India and found no association between annual rainfall and fertility rates during the years 1981–1983, and effects on survival were not reported.

As a consequence, we currently know little of how climate affects survival in the long-lived Asian elephant, or how effects are modulated by factors such as sex and age (Mar 2007). Although heat stress is a well-documented cause of death in Asian elephants (Fowler and Mikota 2006), which inhabit monsoon areas of extreme climatic variation, the effect of temperature on survival has not been studied. Thermoregulation presents a challenge to elephants because of their extremely small surface-to-volume ratio, high energetic costs of body cooling (Weissenbock et al. 2011), and lack of sweat glands and panting to dissipate heat (Hiley 1975). Asian elephants must respond to high temperature by tolerating heat storage in the day and decreasing heat storage in the night (Weissenbock et al. 2011), but it is unknown whether there is a cost in terms of mortality to this heterothermic strategy. The possibility that extremes of rainfall (including months without any rain) in monsoon areas may affect survival of Asian elephants also remains untested. Additionally, temperature and rainfall may also affect survival indirectly, for example by modulating forage availability, forage quality, and presence of disease vectors, among others.

Here we investigate the effects of monthly climatic variation on survival in Asian elephants of all ages and both sexes. We use a unique demographic data set of 1024 semi-captive Asian elephants from Myanmar (Burma) born between 1948 and 1999. Data include individual longevity from newborn to 52 years of age (Clubb et al. 2008, Mar et al. 2012, Robinson et al. 2012). This data set has several advantages. First, it includes repeated measures of temperature and rainfall over the whole life span of individuals (total of 176 100 elephant-months or 15 388 elephant-year observations). Consequently, rather than single events such as drought, or binary comparisons between hot vs. cold or wet vs. dry season, this study utilizes data covering a continuum of climatic conditions. Second, the data set accurately records survival from newborn to adult, in addition to data on stillbirths that are often missed out in field studies. Our Myanmar database allows us to investigate the immediate effects of climatic stress on elephant survival, and the interactions between climatic stress, age, and sex. Finally, our data set also includes records on the cause of death for nearly all deceased individuals as determined by local veterinarians. Analysis of underlying causes of death allows the rare opportunity to investigate the ways in which variation in climate, and by extension long-term climate change, may modify mortality patterns in Asian elephants. Those ways may include direct mechanisms such as heat stroke (Fowler and Mikota 2006), or indirect effects such as plant abundance and forage quality (Ruggiero 1992, Forchhammer et al. 2001, Campos-Arceiz et al. 2008), or prevalence patterns of parasites and pathogens (Altizer et al. 2006).

Methods

Study population

Asian elephants are distributed discontinuously across 13 range countries, and are classified as Endangered on the International Union for Conservation of Nature (IUCN) Red List of threatened species (IUCN 2012). The Union of Myanmar has the second-largest population of Asian elephants in the world after India, with ~5000 wild and 5000 semi-captive elephants (Mar et al. 2012), but these numbers are still debated, particularly concerning the wild population (Leimgruber et al. 2003). Over half of the semi-captive population are owned by the Myanmar Government and are employed in the timber industry (Aung and Nyunt 2001). Between-individual variation in workload and rest periods are set by law: 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. There is seasonal variation in the work undertaken by elephants (Toke Gale 1974). At the beginning of the monsoon in June to August, the main work of elephants is *aunging*, or the pushing of measured logs using their foreheads. Later in the rainy season and in the cool months (September to October), logs often form jams in the rivers, which can only be cleared by elephants through *yelaiking*, an operation that may cause occupational injuries such as leg fractures and joint dislocation. In the cold months of November to February, elephants drag logs left behind along the river banks. Taming of young elephants usually takes place in November. Elephants spend the dry season from March to May at resting camps (Mar 2007).

Throughout the year, elephants are not provisioned; they forage unsupervised in the forest at night (Toke Gale 1974). There is no selective breeding and most reproduction takes place at night in the forest, where wild bulls have access to estrus females (Mar 2007). For this reason, Myanmar timber elephants are characterized as semi-captive. Pregnant females are given a rest period from mid-pregnancy (around 11 months into gestation) until the calf is one year old (Toke Gale 1974). Thereafter, the mothers are used for light work but are kept with their calves that suckle on demand. Weaning age is around four years; at around five years, calves are separated from the maternal herd, tamed, and given a name, logbook number, and a mahout (individual caretaker and rider). The elephants are then trained and used for light work duties until the age of 17 years, when they are put in the workforce as mature logging elephants until retirement at the age of 55 (Mar 2007).

The Extraction Department, Myanma Timber Enterprise, collects and maintains records of all individual elephants owned by the state. This comprehensive countrywide system is unique to Myanmar and is the equivalent to studbooks kept by Western zoos. Data for each individual include registration number, sex, maternal identity, birth and death dates, place of birth, origin (wild-caught or captive-born), capture method (if applicable), year of capture, year or age of taming, birth dates and identities of calves, and cause of death. Births of captive-born elephants are recorded precisely, whereas an estimated date of birth is assigned to wild-caught elephants.

Our complete data set collected from the records of the Myanma Timber Enterprise contains details of 8006 elephants born or captured from the wild between 1925 and 2000 (Clubb et al. 2008, Mar et al. 2012, Robinson et al. 2012). The sample analyzed in this study is a subset of 1024 elephants (488 males, 531 females, 5 of unknown sex) born between 1948 and 1999, designed to match the years (1965–2000) and locations (Mawlaik, Shwebo, Gangaw, and Katha) for which monthly average temperature and total rainfall data were available from the Department of Meteorology and Hydrology of Myanmar. The climatic data were recorded separately for each of the four regions. We restricted our sample to captive-born elephants born or alive during at least one month between 1965 and 2000, with known birth dates and status (dead or alive) until death or exiting the population, and living in the Mawlaik ($N = 361$ elephants), Shwebo ($N = 176$), Gangaw ($N = 220$), or Katha ($N = 267$) regions.

Statistical analyses of climatic influence on survival

We examined elephant survival in each month using logistic regression models that were implemented as generalized linear mixed-effect models to predict the probability of survival per month based on the survival status (binary) for each elephant-month observation across the 35-year study period. Odds for survival was calculated as odds $= s/(1 - s)$, with s being the monthly survival probability. Each discrete time unit (here months) for each individual was considered as a separate observation following Allison (1982).

The model with all potentially relevant fixed effects considered includes: elephant age (five categories), sex (two categories), location (four categories), temperature (continuous), and rainfall (continuous). Alternative models were all derived from this global one and we performed the analysis using an information theory approach of multimodel inference that calculates AIC for each competing model (Akaike 1973). Pairwise comparisons between models were performed using evidence ratio (i.e., the ratio between AIC weights) to determine which model best fitted the data. For a detailed presentation of this framework, refer to Burnham and Anderson (2002).

We restricted our data set to individuals for which all five variables were available, leading to a total of 118 891 elephant-month observations from 834 elephants (417 males, 417 females), among which 253 death events were recorded. Age was modeled as a categorical factor because we expect survival to be strongly dependent on age, but we have little a priori information about the precise shape of their relationship. Specifically, we defined five age categories based on the life history of the elephants (Mar 2007): 0 months (neonate including stillbirths, $N = 793$ elephants); 1–36 months (0–3 years old, infant, $N = 727$); 37–72 months (3–6 years old, weaning age, $N = 633$); 73–204 months (6–17 years old, young trainee working elephants, $N = 536$); >204 months (>17 years old, mature, fully grown logging elephants, $N = 231$). The number of deaths observed in each age category was 39, 67, 79, 50, and 18, respectively. The temperature and rainfall covariates provide, respectively, the average and total values over the month, recorded in the region where a given elephant lives. These two continuous covariates were modeled using both a linear and a quadratic term, providing a straightforward characterization of the optimum conditions for survival.

In model 1, the most general model, we included the interaction between age and the climatic variables because age-dependent characteristics such as body size are likely to mediate the effect of climate on elephant survival. We included the interaction between sex and the climatic variables, because, in several species of

TABLE 1. Set of the seven candidate models used to model the survival of Asian elephants (*Elephas maximus*) from Myanmar during 1965–2000.

Effect	Model number 1	2	3	4	5	6	7	No. parameters
Intercept	1	1	1	1	1	1	1	1
Temperature	1	1	1	1	1	0	0	1
Temperature^2	1	1	1	1	1	0	0	1
Rain	1	1	1	1	0	1	0	1
Rain^2	1	1	1	1	0	1	0	1
Age	1	1	1	1	1	1	1	4
Sex	1	1	1	1	1	1	1	1
Location	1	1	1	1	1	1	1	3
Age × Temperature^2	1	1	0	0	0	0	0	4
Age × Rain^2	1	1	0	0	0	0	0	4
Sex × Temperature^2	1	0	1	0	0	0	0	1
Sex × Rain^2	1	0	1	0	0	0	0	1
Year	1	1	1	1	1	1	1	1
Mother ID	1	1	1	1	1	1	1	1
K	25	23	17	15	13	13	11	

Notes: For each of the seven a priori models, a column of binary indexes indicates which effects are included (1) or omitted (0) in the model. Interaction effects are symbolized with "×." The row "*K*" indicates the number of parameters considered by each model. This number is obtained by multiplying the number of parameters associated with each effect (last column) with the binary indexes of each model. Note that the effects "Year" and "Mother ID" are factorial and are modeled as random effects.

mammals, males have been shown to be more sensitive than females to environmental fluctuation (Clutton-Brock et al. 1985, Lee and Moss 1986, Clutton-Brock 1991). In the interactions, we allowed the characteristics of elephants to modify only the quadratic coefficient of the climatic effects, not the linear term. This meant that the number parameter estimates was reduced by 10, and that both the extremum and the curvature of the quadratic effect could vary as a function of the interaction terms. More complex model structures are conceivable (e.g., triple interaction among age, sex, and climate), but we could not find an a priori reason to justify inclusion of additional parameters. We also included two random effects to deal with the heterogeneity in the baseline death rate caused by year effects (36 categories) and by sibship effects (458 categories when mother identity is used), because 73% of the elephants had at least one sibling present in the data set.

From model 1 (Table 1), we derived six other models with alternative and simpler fixed effect parameterizations to provide reliable estimates of climatic effects on survival as well as insights into underlying biological processes. Age, sex, and location are known to substantially influence the survival rate of Myanmar elephants (Mar et al. 2012, Robinson et al. 2012), so these effects were included in all a priori models. In contrast, all candidate models contain different parameterizations of the effects of climate on survival (Table 1). Models 2 and 3 correspond to situations where, respectively, either sex or age does not interact with the effect of climate. In model 4, neither sex nor age interacts with climatic effects. From model 4 (i.e., no interactions), three simpler models were then derived: model 5 and 6 omit entirely either the effect of rain or temperature on survival; and model 7 neglects both climatic effects on survival.

Models were ranked by decreasing parsimony from the one with the lowest AIC (the best approximating model) to the largest (the poorest fit to data); see Table 2. All AIC were compared to the AIC of the best-approximating model. From that we calculated the AIC weight of each model, which represents their relative likelihood or relative strength of evidence, given the data and the candidate model set (Burnham and Anderson 2002). We then performed a multimodel inference of parameter estimates and their unconditional standard errors using model-averaging (for details, see Burnham and Anderson 2002). Because the models including interactions were worse than the best-approximating model excluding them, our data may be too limited to draw precise inference on the interaction effects. Rather than performing a classic model-averaging technique that would bias upward the importance of interactions and rely on imprecise estimates (Burnham and Anderson 2002), we draw inferences on the effect of temperature and rainfall on elephant survival from the *shrinked* model averaging technique (Table 3). The only drawback of the approach is that it prevents exploration of the unconditional confidence intervals around parameter estimates; results from alternative methods are therefore provided in Appendix A: Table A1. Models were fitted using the function *glmer* from the package *lme4* (Bates et al. 2011) version 0.999999-0, and the multiple-model inference was performed using the package *MuMIn* (Barton 2012) version 1.17.11 with R version 2.15.1 (R Development Core Team 2011).

Causes of death

We analyzed data on the causes of death among the Myanmar elephants as classified by local veterinarians through necropsies. Of the total of 315 deaths in our sample, cause of death was known for 288 cases. Both the cause of death and average temperature in month of

TABLE 2. Summary of the candidate models.

Model	*K*	Log-likelihood	AIC	ΔAIC	*w*
4	15	−1644.78	3319.6	0.00	0.45
2	23	−1637.26	3320.5	0.97	0.28
3	17	−1644.41	3322.8	3.27	0.09
5	13	−1648.60	3323.2	3.63	0.07
1	25	−1636.80	3323.6	4.04	0.06
6	13	−1648.91	3323.8	4.27	0.05
7	11	−1653.10	3328.2	8.65	0.01

Notes: All models were fitted using 118 891 elephant-month observations from 834 elephants and included a total of 253 deaths. Terms are: *K*, the number of parameters; AIC, the Akaike information criterion; ΔAIC, the difference in AIC between the best approximating model (model 4) and the alternative models; and *w*, the AIC weight representing the relative strength of evidence for each model.

death were known for 270 cases; both the cause of death and total rainfall in month of death were known for 272 elephants. The 72 causes originally listed by the veterinarians were grouped into five major categories: accidents (the single largest category, responsible for 97, or 34%, of the 288 deaths, including attacks by snakes, tigers, and other elephants, as well as work-related injuries); infectious disease (including anthrax, lung infections, and diarrheal disease, causing 24% of fatalities); noninfectious disease (18% of deaths, mostly cases of "general weakness," constipation, and sudden death); birth-related (20%, or 58 deaths, of which 56 were perinatal deaths and infant death by maternal agalactia [absent or faulty secretion of breast milk], and only 2 maternal deaths); and heat stroke (4%, or 12 deaths). To investigate the association between temperature and rainfall with cause of death, we divided the deaths into quartiles according to temperature and rainfall at the month of death. Quartile boundaries were calculated as 21.9°C, 27.4°C, and 29.1°C for temperature, and 5.5 mm, 59.0 mm, and 165.5 mm for rainfall. We used Fisher's exact tests to assess whether causes of death were dependent on the quartiles for rainfall or on the quartiles for temperature. The Fisher's exact test is an alternative to the chi-squared test that is particularly well-suited when expected values in the contingency table are small, as is the case here for heat stroke.

Results

Climatic and death seasonality

Average temperature, rainfall, and death events fluctuated through the 35-year study period (Fig. 1A, B). Although little year-to-year variation exists, climate follows a strong tropical monsoon pattern within each year (Fig. 2A, B). Monthly temperature varied from 14°C to 34°C (25° ± 3.7°C, mean ± SD), and monthly total rainfall varied from 0 mm to 906 mm (111.4 ± 102.6 mm, mean ± SD). Temperatures peak in April, immediately before the onset of monsoon rains (May to September), and minima are observed from October to January, overlapping partially with the dry season (December to May). The number of deaths for all ages and timber sites combined also varied between months ($N = 315$ elephants, $\chi^2_{11} = 23$, $P = 0.018$), with 33, 26, 21, 37, 36, 32, 29, 13, 24, 21, 18 and 25 death events per month recorded from January to December, respectively.

Climatic influence on survival

The best model considering both temperature and rainfall (model 4) had an evidence ratio 76 times higher than the model without climate, although the two models only differ by four parameters (temperature, temperature^2, rainfall, rainfall^2). In addition, the three best models (4, 2, and 3) indicate that both temperature and rain influence elephant survival. Temperature had a pronounced effect on elephant survival, with the lowest predicted survival occurring during the hottest and coldest months (Fig. 3). On average, elephants experienced temperatures higher than the optimal for survival (mean 25.7°C, median 27.2°C) and spent 2.03 times longer in temperatures higher than 24.0°C. The frequency of hot and cold temperatures experienced by elephants, combined with the higher survival cost triggered by high temperatures compared to low ones, led to a majority of all deaths occurring during the hot (>24.0°C) rather than the cold (<24.0°C) range of temperatures (Fig. 1A).

The weakest effect of temperature was observed in neonate elephants (0.66% of observations, 39 deaths; see Appendices B and C): the odds for monthly survival

Table 3. Regression parameter estimates of the multimodel inference (MMI) based on the seven candidate models.

Variables	β	Model number
Intercept	−3.23	{1234567}
Temperature	0.16	{12345}
Temperature^2	0.10	{12345}
Rain	0.02	{12346}
Rain^2	−0.11	{12346}
Age		
0 months (ref)	0	{1234567}
0–3 years	−2.80	{1234567}
3–6 years	−2.59	{1234567}
6–17 years	−3.92	{1234567}
>17 years	−4.04	{1234567}
Sex		
Females (ref)	0	{1234567}
Males	0.30	{1234567}
Location		
Gangaw (ref)	0	{1234567}
Katha	0.04	{1234567}
Mawlaik	−0.60	{1234567}
Shwebo	−0.19	{1234567}
Age × Temperature^2		
0 months (ref)	0	{12}
0–3 years	0.07	{12}
3–6 years	0.09	{12}
6–17 years	0.15	{12}
>17 years	−0.06	{12}
Age × Rain^2		
0 months (ref)	0	{12}
0–3 years	−0.10	{12}
3–6 years	0.01	{12}
6–17 years	−0.09	{12}
>17 years	−0.12	{12}
Sex × Temperature^2		
Females (ref)	0	{13}
Males	−0.01	{13}
Sex × Rain^2		
Females (ref)	0	{13}
Males	0.00	{13}

Notes: Model-averaging was based on all models and aims at reducing the bias away from zero in estimates (MMI). The estimates are expressed on the logit scale. The variables "Temperature" and "Rain" were fitted as *z*-scores. For each categorical variable, the level of reference is indicated by "(ref)." Variance estimates for mother identity and for the year random effects were, respectively, 0.66 and 0.16 in model 1 and were not computed for the MMI.

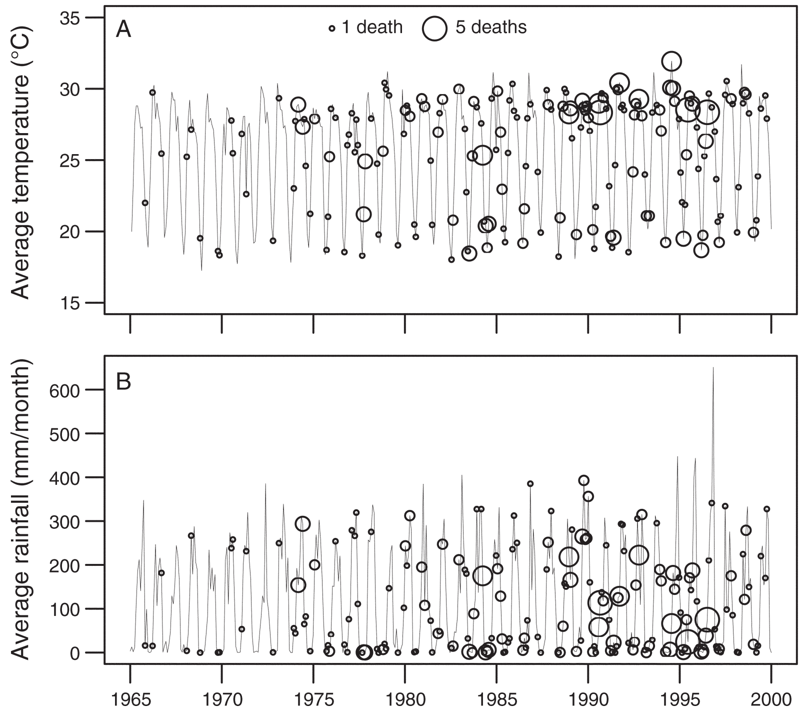

FIG. 1. Monthly climatic variation and elephant deaths in longitudinally monitored Asian elephants from Myanmar, 1965–2000. (A) Monthly average temperature and (B) total rainfall, represented by the black curves, are averaged across the four Myanmar timber elephant sites. Circles show the timing of all the 315 death events over the total of 176 100 elephant-month observations from 1024 elephants. The diameter of the circles is proportional to the number of deaths occurring within the same month.

decreased by a factor of 1.2 (females) and 1.11 (males) from 22.5°C (the optimum) to the mean minimal temperature across years (18.0°C), and by a factor of 1.7 (females) and 1.62 (males) from 22.5°C to the mean maximal temperature across years (31.4°C). The strongest effects were observed for elephants between 6 and 17 years of age, for which corresponding odds for females and males were 2.0 and 1.9 from 24.0°C (the optimum) to 18.0°C, and were 2.2 and 2.1 from 24.0°C to 31.4°C. However, because overall mortality was highest among calves (~26% in total during the first 6 years), the absolute differences in survival caused by temperature variation were also greatest in this age group, with variation in temperature across months leading to 0.57% of all calves dying during the hottest month each year, as compared to 0.23% dying during the months with an average temperature closest to 23.4°C (i.e., the optimal value for survival averaged across the three first age categories and both sexes). Over the years, such monthly differences accumulate and result in considerable variation in mortality risk. In contrast, among the mature logging elephants with high overall survival rate (20.3% of observations, 18 deaths), 0.18% died in the hottest month each year in comparison to 0.09% in the coolest months. Except for this last age category, the effect of temperature on survival was similar in both sexes, with the optimal temperature for females only shifting by 0.1°C to 0.5°C positively,

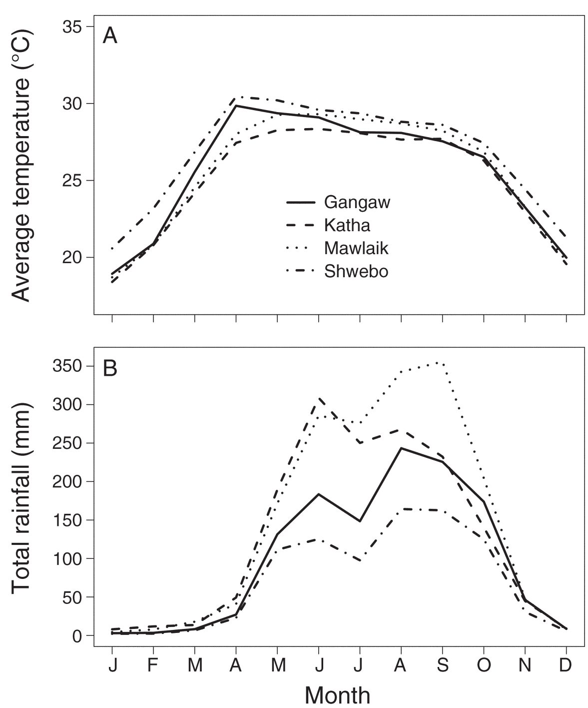

FIG. 2. Within-year climatic variation for the four Myanmar timber elephant sites. (A) Monthly average temperature and (B) total rainfall are averaged across years (1965–2000).

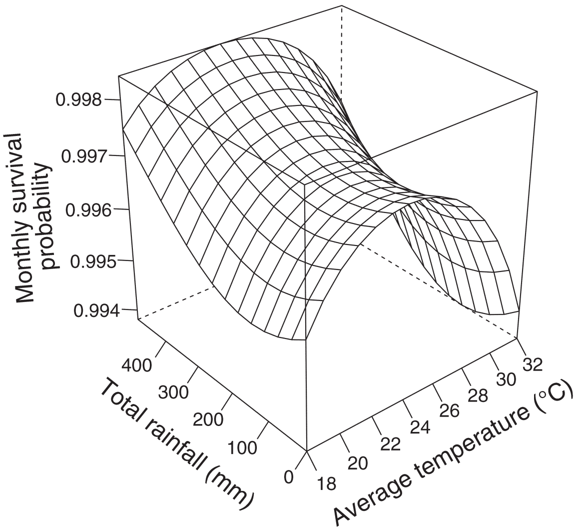

FIG. 3. Monthly survival of Asian elephants as a function of temperature and rainfall in Myanmar during 1965–2000. Predicted probabilities for monthly survival were obtained from the multimodel inference (see Table 3 for details) and are given for a female aged 37–72 months living in the region of Gangaw. For other age groups, see Appendix C.

depending on the age category (see Appendix B for details). Because the result for old ages is based on only 18 deaths, whether or not the large sex difference in the effect of temperature on survival of mature elephants applies to the population is yet to be confirmed.

Rainfall also influenced survival, with the highest survival rates occurring during the wettest months. Lowest survival was reached at ~135 mm of rainfall for all age categories and both sexes (minimal values for survival varied between 130.7 and 140.7 mm). The odds for monthly survival were predicted to slightly decrease from the complete absence of rainfall (i.e., the mean minimal rainfall across years) to 135 mm of monthly rainfall by a factor varying from 1.1 to 1.2, depending on age and sex (see Appendix B for details), and then to increase by 1.8 to 4.3 times from 135 mm to the mean maximal rainfall (490 mm). Contrary to the interaction between age and temperature, the effect of rainfall on survival depended little on age (Appendix B). However, once again the largest overall mortality among calves caused the lack of rainfall to reduce absolute survival rates most dramatically in this group, with 0.37% of all calves dying during the driest month each year compared to 0.28% dying during the months with the highest rainfall. In contrast, 0.08% of the mature logging elephants died in the driest month in comparison to a very similar value of 0.07% in the highest-rainfall month each year.

Of the non-climatic control variables, age exerted the strongest influence on monthly survival rate. Among the five age categories, survival was highest for mature logging elephants (those >17 years old) and lowest for neonates (see Appendix B). In comparison to mature logging elephants, the odds for survival in the other age categories (in increasing age order) decreased by ~60, 4, 5, and slightly >1 (each considered at its optimal climatic condition). The estimated values were very similar between sexes (Appendix B), although overall the odds for survival were 1.34 times higher in females than in males. Survival also varied between the four locations considered, with Mawlaik presenting the highest survival rate. Compared to Mawlaik, the odds for survival were 1.5 times lower in Shwebo, 1.8 times lower in Gangaw, and 1.9 times lower in Katha.

Causes of death

Our results show that variation in temperature has a general effect on the distribution of causes of death (Fisher's exact test, $P = 0.006$). Of the 12 reported heat stroke deaths, seven occurred in the hottest quartile (Table 4). In the hottest quartile, heat stroke caused 9.7% of all deaths, whereas the main cause of death was accidents (36%), followed by infectious disease (29.2%).

TABLE 4. Recorded cause of death grouped by quartile of temperature ($N = 270$ elephants) and rainfall ($N = 272$ elephants) in the month of death for Asian elephants from Myanmar during 1965–2000.

	Cause of death (no. elephants)					
Quartile	Accident	Perinatal	Infection	Noninfectious	Heat stroke	Total
Temperature						
Coldest	16	12	14	22	3	67
Medium cold	24	12	16	10	1	63
Medium hot	26	20	14	7	1	68
Hottest	26	7	21	11	7	72
Total	92	51	65	50	12	270
Rainfall						
Driest	16	12	18	18	3	67
Medium dry	26	11	11	16	3	67
Medium wet	28	9	17	11	4	69
Wettest	23	20	19	5	2	69
Total	93	52	65	50	12	272

Those two causes of death represent, respectively, only 23% and 20.5% of all deaths in the coldest quartile. In contrast, noninfectious diseases (32.8%) were the leading cause of death in the coolest months, in comparison to 15.8% or less in the other three temperature quartiles. The distribution of causes of death by rainfall quartile was also significant (Fisher's exact test, $P = 0.05$; see Table 4). Noninfectious disease deaths were highest in the driest quartile of months, causing 26.9% of deaths in comparison to 7.2% in the wettest quartile. Perinatal deaths were highest in the wettest quartile of months at 29.0%, in comparison to 17.9% or less in the other quartiles.

Discussion

Departures from optimal temperatures across the monsoon seasons lead to substantial increases in Asian elephant mortality, particularly among the neonates and infants whose baseline mortality is the highest. Our results have implications for predicting the way changes in the global climate might influence mortality of large terrestrial mammals such the endangered wild populations of Asian elephants, as well as for linking the currently observed high mortality rates of Asian elephants in zoos worldwide to potentially suboptimal climatic conditions for the species.

In the ecological setting of Myanmar, elephants experience unfavorably high temperatures more often than unfavorably low temperatures. Consequently, the two months that are usually the warmest (May and June) are also the two months for which most deaths have been recorded in our entire data set ($N = 8006$ elephants) covering the whole timber elephant population of Myanmar for more than 80 years. Although heat stroke is not the main source of mortality in hot months (accounting for ~10% of deaths), the proportion of deaths caused by heat stroke increased during these months (Table 4). This was also true for infectious diseases that accounted for ~30% of deaths, suggesting that high temperature could exert an indirect negative effect on elephant survival through an increase in disease prevalence. Indeed, temperature may be associated with seasonal fluctuation in the presence and numbers of vectors or carriers of infectious disease (Fisman 2007), whereas the seasonal occurrence of the tropical monsoon and higher rainfall may increase cases of waterborne disease (Lipp et al. 2002, Codeço et al. 2008). In colder months, we identified a higher number of deaths by noninfectious disease, which encompass cases of "general weakness," sudden death, or multiple chronic diseases. An explanation could be that the additional costs of thermoregulation due to larger differences between day and night temperatures during the cooler months could result in individuals with poor body condition dying from noninfectious causes, particularly general weakness. It is also possible that the seasonal nature of workload and work intensity (see *Methods*) could cause part of the increase in noninfectious disease deaths in the coolest months. However, this would not apply to calves, which are not engaged in work and yet have the lowest survival of all age groups.

As well as the reduced survival in temperatures deviating from ~24.0°C, rainfall had independent effects, with increased survival in the wettest months. Studies of African elephant calves have found a strong association between drought years and reduced survival (Foley et al. 2008, Lee et al. 2011). However, the climatic conditions faced by the two species differ; Asian elephants experience relatively predictable monsoon rainfall patterns, whereas the African elephants in the cited studies inhabit semiarid regions from Kenya and Tanzania. Our study includes elephants of all ages. Quantifying the effects of climatic variability on adult survival is important because, although mortality is higher in infants and juveniles (Mar et al. 2012), in a slowly reproducing species even small changes in adult survival can result in large consequences for population growth rates (Sæther and Bakke 2000, Leimgruber et al. 2008, Beston 2011).

Overall, switching from good to bad climatic conditions within an average year approximately doubled the odds for mortality. The other factors investigated (age, sex and region) also exerted an influence on mortality of the same order of magnitude, except for the specific case of neonates that had higher mortality. However, although males showed mortality rates ~34% higher than females, the effects of temperature and rainfall on survival were relatively similar in both sexes. This contrasts with Foley et al. (2008), who showed that mortality in male African elephant calves was more responsive to climatic variation. However, our study investigated the effect of a continuous distribution of monthly temperatures and rainfall experienced by elephants over 35 years, rather than the effect of a single severe drought event. The studies are thus not directly comparable, and it remains possible that males are more vulnerable to extreme conditions such as droughts (Loison et al. 1999, Coulson et al. 2001).

Our findings have important implications both for management of captive Asian elephants and for predicting future demographic trends in wild elephants in the context of global climate change. First, both in range and non-range countries, the number of captive elephants is decreasing (Sukumar 2006) and zoo populations may not be sustainable (Faust et al. 2006, Clubb et al. 2008). Supplementing captive populations with the capture of wild elephants has been legislated against in many range countries, including Myanmar, which limits capture of wild elephants to work in the timber industry (Mar 2007). Breeding of captive elephants has become increasingly important and one-quarter of all remaining Asian elephants now live in captivity in range countries in Asia, with a further 1000 in zoos around the world (Kurt et al. 2008), but such programs are challenged by the high rates of calf mortality, particularly in Western zoos (Clubb et al.

2008). The precise characterization of the relationship between survival and temperature should contribute to the establishment of health improvement strategies for calves as well as older elephants. Temperature has a significant effect on survival, particularly at the extreme values. The decrease in survival at low temperatures was not responsible for a large increase in deaths in the warm ecological settings of Myanmar, where elephants were more likely to encounter hot temperatures. However, low temperature effects could contribute to the low survival of elephants in captivity, including those in zoos, particularly in countries in which temperatures are, on average, equal to or lower than the coldest months in Myanmar. The possibility that elephants born in areas with lower temperatures could adapt to local conditions and therefore have a different optimal temperature range requires further investigation, but of the current European zoo population, 80.7% were born in range countries and have thus not lived all their lives in zoos (Clubb and Mason 2002).

Changes in global temperature predicted by models of climate change could have implications for the maintenance of the shrinking wild and captive Asian elephant populations in the range countries. Our data on average monthly temperatures in the four Myanmar sites reveal a statistically significant, but small, linear increase of 0.03°C per year, or an increase of ~1°C over the 35 years between 1965 and 2000. A 1°C increase across 35 years is a small effect in comparison to an average of ~12°C across a single year between cold and hot months, and for this reason, year was included as a random variable (control) in our models. However, if the trend toward increasing temperature persists over the decades, elephants may fail to quickly readapt to shifting average temperatures and may suffer an increasing cost of hot temperature. In Southeast Asia, temperature is predicted to increase by 0.1°C to 3°C during the next 30–40 years, with warming occurring more at night than daytime in all seasons, accompanied by higher total rainfall but declines in dry-season precipitation (Chotamonsak et al. 2011). In addition to these changes, atmospheric systems are projected to alter both the timing and location of the Southeast Asian monsoon, with earlier onset and high precipitation levels projected to shift northward through Myanmar (Kitoh 2006, Qing 2012). Elephants are long-lived, with a long generation time and therefore low maximum population growth rate, making them particularly vulnerable to climate change and potentially exposed to a higher extinction risk (Lebreton 2006). Worryingly, some models have predicted that extinction of wild Myanmar elephants could occur in as little as 30 years (Leimgruber et al. 2008). Increased extremes in temperature and rainfall (both within a year and between years) may therefore lead to significant increases in mortality of Myanmar elephants in the near future. Our results are likely to have direct relevance to wild elephants in addition to the semi-captive timber elephants, because the two populations live in the same forest, share diseases, forage and consume the same resources, maintain regular interactions, and reproduce together (Toke Gale 1974, Mar et al. 2012). Given the current lack of longitudinal data on wild Asian elephant populations, our results using the detailed life history data on timber elephants might thus provide us with the best available opportunity to estimate how survival in wild populations might respond to climate changes.

In summary, many studies on effects of climate change on long-lived species have focused on birds (van de Pol et al. 2010). However, the direct and indirect effects may be as great or even greater in long-lived terrestrial mammals that may have a limited potential to adapt to climate change due to their large body size and physiological constraints to thermoregulation (Weissenbock et al. 2011), their life history strategy characterized by low rates of population growth (Lebreton 2006), and the lower likelihood of successful range shifts as a response to habitat destruction (Leimgruber et al. 2003). There has been some debate as to whether tropical species will be more or less resilient to climate change than temperate species (Corlett 2012). Our results indicate that, even in a highly seasonal environment, modest deviations from optimal conditions have effects on Asian elephant survival.

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Supplemental Material

Appendix A

A table showing regression parameter estimates, standard errors, and absolute coefficient of variation from the global model and from the multimodel inference (MMI) based on the seven candidate models (*Ecological Archives* E094-101-A1).

Appendix B

A table of the influence of age and sex on survival (*Ecological Archives* E094-101-A2).

Appendix C

A figure of monthly survival of Asian elephants as a function of temperature and rainfall in Myanmar during 1965–2000 (*Ecological Archives* E094-101-A13).