Birth Sex Ratio and Determinants of Fecundity in Female Timber Elephants of Myanmar

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Abstract. I assessed the reproductive patterns of captive-born and wild-caught Asian elephants managed by the Myanmar Timber Enterprise. Calving among all female elephants was seasonal with higher births in cool months (October to February) and late monsoon (September). Captive-born mothers have significantly higher fecundity rates with lower inter-birth intervals than wild-caught mothers, likely due to harsh capture and breaking procedures, and inadequate nutrition due to unfamiliarity of foraging grounds and fettering during night foraging. Fecundity peaks between 22 and 25 years, levels out between 25 and 39 years and gradually declines after 40 years in both wild-caught and captive-born females. Complete reproductive cessation is not observed until age 60 in wild-caught mothers and at least age 49 in captive-born mothers, suggesting reproductive senescence is not likely in either captive-born or wild-caught females. Offspring sex ratio is not different from unity and not influenced by birth order of calves, mother's birth origin or age.

Introduction

Large, long-lived mammals fall into the category of 'K-selected' species that exhibit slow life histories- characterised by slow metabolism and development, delayed reproduction with low levels of fecundity, delayed attainment of puberty (Rachlow & Berger 1998), long period of infant dependency and increased mortality especially during the first year of life (Clubb *et al*. 2009). The reproductive success in these species may be determined by a number of factors including seasonal availability of food resources, predation, adult survival rate, population density, social factors, group sex ratio, ecological, psychological and physiological stress or insult during early development, confinement-related stress, and capture-related trauma and stress or a combination of these factors (Clutton-Brock 1984; Saether 1997; Rachlow & Berger 1998; Gaillard *et al*. 2000; Coulson *et al*. 2001; Shanks 2002; Lummaa & Tremblay 2003; Wielebnowski 2003; Archie *et al*. 2006; Loveridge *et al*. 2006). In captive females, additionally, inadequate space, housing and enrichment, adverse environmental conditions, failure to provide compatible breeding pairs or social groups, frequent changes in group composition, inability to train animals properly and poor diet can limit reproductive success (Shepherdson 1989; Schulte 2000; Wielebnowski 2003; Allen & Ullrey 2004).

Like non-human primates, marine mammals and some human tribes, African and Asian elephants living in the wild are composed of highly-related matrilineal family groups. They have complex social societies with multi-levelled, fission–fusion social structures (Vidya & Sukumar 2005; Wittemyer *et al*. 2005; Archie *et al*. 2006; Couzin 2006). Hierarchy (rank) is determined by age (Douglas-Hamilton 1972; Vidya & Sukumar 2005). In natural free–ranging environments, older, larger female African elephants consistently dominate smaller, younger females (Archie *et al*. 2006a; Couzin 2006). In captivity, such forces are relaxed or eliminated (Schulte 2000; Vidya & Sukumar 2005).

The past four or five decades have witnessed the accumulation of basic descriptions of life-history strategies for an increasingly large number of terrestrial mammals. This accumulation has fuelled a rich body of research in which evolutionary hypotheses are examined through a comparative approach (Harvey & Zammuto 1985; Hutchins & Kreger 2006). A few studies have explicitly compared within-species differences in life history strategies by comparing habitats, social groups or keeping systems, such as wild versus captive-born, farm versus zoo populations or zoo versus native populations (Kurt & Mar 1996; Snyder *et al*. 1996; Taylor & Poole 1998; Thévenon *et al*. 2003).

For elephants in particular, a few reports have been published on the differences of survival and reproductive patterns of captive elephants between zoo populations and those in the range states (Kurt & Mar 1996; Taylor & Poole 1998; Schmid 1998). Hutchins and Kreger (2006) argued that making direct comparisons between wild and zoo population is not appropriate, because there are too many differences in feeding ecology and diet, social organization and behaviour, reproductive biology and so forth between native habitats and zoo settings.

Some recent studies have compared reproductive endocrinology, ultrasonography, anatomy, disease outbreaks and drug efficiencies in Asian and African elephants from zoos (eg. Hildebrandt *et al*. 2006; Brown *et al*. 2004).

On the other hand, there are no previous studies on Asian or African elephants that directly compare the reproductive patterns of captive-born and wild-caught individuals. It is worthwhile to conduct such a comparison as most elephants kept in captivity, such as zoos, tourist camps, logging camps etc. are originally derived from wild-caught animals. Here, I present the reproductive pattern of captive-born and wild-caught Asian elephants (*Elephas maximus*) of Myanmar, living in the same predation-free ecological environment, in an extensively management system.

A female elephant, which can live well beyond the age of 60 years, has the longest reproductive life span among any terrestrial mammal. During her lifetime, she has the potential to produce up to 12 calves (Sukumar 2003). In captive elephants, work-related stress is likely to impose some constraints on reproductive patterns, depending on how well individuals adapt to captive conditions.

Based on the yearly birth and death data of Myanmar elephants, I will present the seasonality of calving and mortality rate. Then, I will focus on the following key questions, in an attempt to explore variability in components of reproductive tactics of captive-born and wild-caught female timber elephants of Myanmar.

1. How is female reproductive potential impacted by birth origin (wild-caught versus captive-born)? In this context, I explored potential fecundity differences between these two groups, including (a) age at first breeding, (b) age-specific reproductive rates, and (c) interbirth intervals.

2. Do captive-born or wild-caught elephant females adapt offspring sex ratio? Also, for either group, does maternal age, maternal birth origin or birth order have a significant impact on the production of male versus female calves?

Materials and methods

Study population

The original data set is from the timber elephant studbook of Myanmar Timber Enterprise, containing 5213 elephants (female = 3050, male = 2259, unknown sex = 4), including 3230 calves born to 1340 females.

For captive-born animals, ages were known precisely. For wild-born animals, age at capture was estimated by experienced elephant handlers based on shoulder height and other indicators, such as folding patterns of the earflap and dentition. This study is based on a subset of these records, involving females (n = 2841) with full survival histories (i.e., known ages at entry and departure from the population) and complete calving information. Elephants captured before 1950 are excluded because capture dates are recorded only to the nearest decade.

Individual working elephants have a log book, which is maintained and updated by local veterinarians and regional extraction managers at least bi-monthly to check the health condition and ability of each elephant to work, and to correct any entry errors made by previous officers. The multiple sources of data recorded by the Myanmar Timber Enterprise (annual extraction reports and end of the year reports from each region) allow effective cross-checking of any apparent errors. Between-individual variation in workload or rest periods is limited by law: all state-owned elephants are subject to the same regulations set by the central government for hours of work per week, working days per year, and tonnage to extract per elephant. For example, all mature elephants (>17-55 y) work 3-5 days a week (depending on weather and forage availability) 5-6 h a day (maximum 8 h) with a break at noon. The maximum tonnage of logs allowed to be dragged in a year per elephant was 400 in 2010.

The elephants live in forest camps, where they are used during the day as riding, transport, logging and draft animals. At night the elephants forage unsupervised in the forest as groups (an average 12 h, range 10-14 h per day) where they find food and encounter tame and wild conspecifics. Most calves are thought to be sired by wild bulls, and calves born in captivity are cared for by their biological mothers and allo-mothers, and suckled until lactation no longer supports their demands. All elephants finish their work season by mid-February each year, and work resumes around mid-June depending on the arrival of monsoon.

The ages of captive-born elephants are exact because precise dates of birth are recorded, and this study concentrates only on the records of captive-born mothers and their offspring in order to have accurate data on maternal age and previous reproductive history, which are incomplete for most wild-captured mothers. Dates of matings are recorded by the mahouts when they notice the mounting marks on the back of female elephants. In humans, parity is defined as the number of previous pregnancies of greater than 20 weeks gestation, which is about half term of a normal pregnancy (Bai *et al*. 2002) or the number of children a woman has already had (Hinde 1998). The term "primipara" is used to characterize mothers with a single previous pregnancy while "multiparity" refers to multiple pregnancies or births, and "birth order" refers to children in the order they are born (first births, second births and so on) (Hinde 1998). Sex ratio is the ratio of female to male (female/male) offspring. It is not always possible to know when an elephant is pregnant, at least in the early to mid-periods. Therefore, in this study, I use first born calving records and later born calving records, so that there are only "primiparous" mothers (with a single pregnancy) and "multiparous" mothers (with more than one pregnancy). All other terms are used similar to women.

Age-specific fecundity (m_x) is the average number of female offspring produced by an individual female aged x, calculated as the number of female live births (b_f) to the mid-year population of mothers at age x (M_x) and x-1 (M_{x+1}). The total number of female calves born alive from captive-born mothers and wild-caught mothers were 526 and 499, respectively.

$$m_x = \left(\frac{b_f}{M_x + M_{x+1}} \right) \text{x } 0.5$$

Studbook data shows that the youngest age a female gave birth was 5.3 years. This was known because she was born in captivity. Sukumar (2003) stated that " There are reports of cows mating as early as 7-9 years old; even if these are exceptional, a mean age of maturity of 10-12 years old is likely here. In Southern India's Biligirirangans, I estimated the mean age of first calving in female (wild) elephants during 1981-1983 to be about 17-18 years". Based on this information, wild-caught females captured at ≤10 years of age are included in the analyses of calculating age-specific fecundity, assuming they are not likely to reproduce prior to capture. Those wild-caught females captured over 10 are excluded from analyses because it is impossible to trace the past breeding history before capture. The number of calves remaining for analysis of interbirth interval is 1378 (captive-born mothers = 999, wild-caught mothers = 379).

Methods

To explore the relationship between mothers' birth origin, mother's age at birth and birth order to sex ratio of calves, I conduct a binomial generalized linear model (GLM) using R-software (R version 2.8.1, released 22.12.2008). Significant main effects and interactions are included in the GLM using a stepwise procedure (Dalgaard 2002; Crawley 2003). For each regression analysis, a full model containing explanatory variables and first-order interaction terms are initially fitted. I then carry out model simplification with standard methodology through stepwise deletion (Dalgaard 2002; Crawley 2003). Significance is evaluated at the 5% error level using the likelihood ratio chi-square test.

Cox proportional hazard model is the most general of the regression models because it is not based on any assumptions concerning the nature or shape of the underlying survival distribution. The model assumes that the underlying hazard rate (rather than survival time) is a function of the independent variables (covariates); no assumptions are made about the nature or shape of the hazard function. In this paper, Cox regression analysis is used to test the effects of explanatory variables on age-specific reproductive rate and interbirth interval, using R-software (R version 2.8.1). In the case of reproductive rate, mothers' age at calving, entry to and departure from the population were analysed with histories split at calving (the event of interest), and censored at population departure. In the case of interbirth interval, time to event is measured by the difference in the age of mother between two consecutive live births of calves.

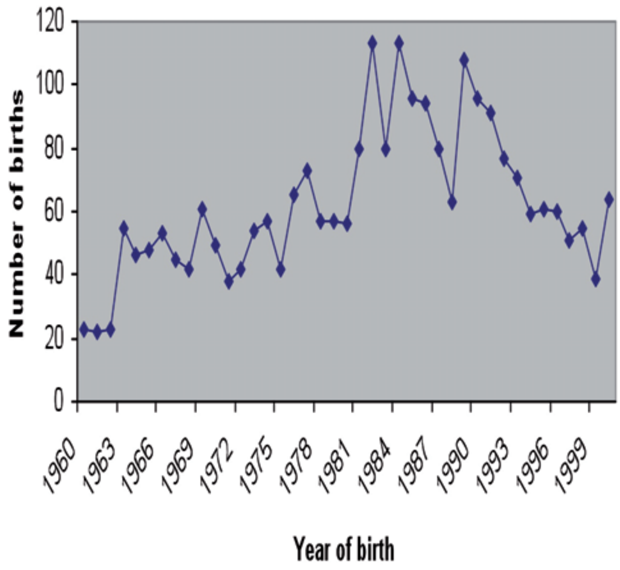

Figure 1. Yearly births between 1960 and 1999.

Results

In this subset of data, the youngest and oldest captive-born and wild-caught mothers are recorded as 5.30 y and 53.00 y (median = 24.73 y) and 6.44 y and 60.84 y (median = 29.25 y), respectively. The maximum number of calves that a single mother has given birth to, is ten.

Seasonality of births and calving rate

The yearly number of births between 1960 and 1999 is presented in Figure 1. Twenty-five percent of today's living population of timber elephants in Myanmar were born in captivity before 1974. During the last four decades, the highest calving rate occurred in 1982 and 1984 with 113 calves per year. After 1990, the calving rate declined to an average of 53 calves/year.

Although births are recorded in each month of the year, a lower rate is found in the late summer months (May and June) and early (wet) monsoon season (July and August) (Fig. 2). Timber elephants prefer to give birth the cool season between December and March. Taking account of the mean gestation period of Myanmar elephants as 20-22 months (Hundley 1922; Flower 1943; Anghi 1962), the peak mating and conception is likely to have occurred in the summer rest period, one year previously.

Age-specific fecundity rate

Age-specific fecundity rate is calculated on the subset of studbook data containing 2841 females with full survival histories (i.e., known ages at entry and departure from the population) and complete calving information. Cox regression analysis showed that age-specific fecundity of captive-born mothers is significantly higher than that of wild-caught mothers (Fig. 3, test statistic χ^2 = -11.9, P<0.001), with significant non-proportionality (Cox proportional hazards

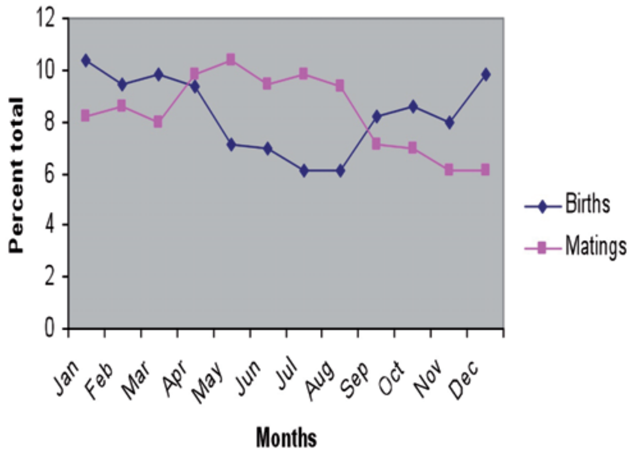

Figure 2. Births compared with matings by month.

test statistic $\chi^2 = 0.37$, $p = 0.54$). The first peak of fecundity is at age 22 and 25 y in captive-born and wild-caught females, respectively, with fecundity rate differing by half (m_x of captive-born = 0.083 vs. m_x of wild-caught = 0.041).

Although age-specific fecundity (m_x) varies from year to year the highest (m_x) value occured between 38 and 40 y for both captive-born and wild-caught female elephants. There are no reported births after age 50 in captive-born females. However, the oldest captive-born female elephant in my data set is 53 y old, and she is still alive at the end of the study period. So, there are no comparable records for fecundity of captive-born females beyond age 53. Evidence of calving until age 49 in captive-born females and until 61 y of age in wild-caught females indicates that complete reproductive cessation or menopause seems not to exist in captive Asian elephants

Interbirth interval

The number of calves remaining for analysis of interbirth interval is 1378 (captive-born mothers = 999, wild-caught mothers = 379). The shortest and the longest interbirth intervals are recorded as 1.52 and 21.44 y (median = 4.93 y) for captive-born mothers and 1.71 and 19.29 y (median = 5.28 y) for wild-caught mothers, respectively (Table 1). There are two females, with registration number recorded as 1804 and 1833, have given birth their second and fourth live-born calves at 1.52 and 1.62 y, respectively, after the birth of previous calves, indicating that (1) female elephants are capable of conceiving immediately after parturition and (2) the interbirth-interval period can be shortened to a minimum of 18 months. However, these inter-birth intervals are very short considering normal gestation length is 20-22 months.

Using a survival analysis of all potential females exposed to the "risk" of a birth, Cox regression analysis is used to examine the independent effects of explanatory variables (birth order, sex, birth origins of mothers) on interbirth interval. After systematic model simplification, the minimum adequate model indicates that dam origin is the only variable that significantly determined the birth interval ($\chi^2 = -5.36$, $P< 0.001$, Cox proportional hazards test $\chi^2 = 0.30$, $p = 0.58$). There were no significant interactions between any of the main effects investigated. Wild-caught mothers show significant lower birth rates than captive-born mothers, with the possibility of a subsequent birth following an index calf 22% lower or longer than captive-born mothers (exponential coefficient = 0.78, 95% confidence interval 0.71-0.95).

Birth sex ratio (female/male)

One thousand nine hundred and twenty six calves with full information of maternal birth origin (captive-born = 387 and wild-caught = 464) and survival history are included in this analysis. In every birth order, captive-born and wild-caught mothers gave birth with a near even sex ratio, with the exception of a few male-skewed births in high parity (parity 8 and 9) in captive-born females. Birth sex ratio shows

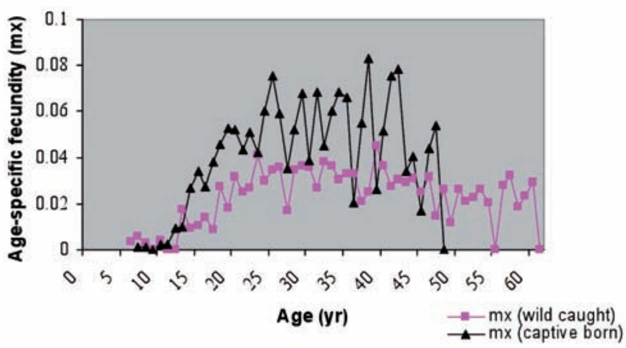

Figure 3. Age-specific fecundity rate of captive-born and wild-caught mothers.

Table 1. Birth intervals by parity.

Birth order	N	Min.	Max.	Median	Mean ± SE
1	877				
2	544	1.61	22.92	5.69	6.38 ± 0.15
3	315	1.52	17.08	5.25	5.80 ± 0.15
4	174	2.00	15.46	4.58	5.35 ± 0.20
5	88	1.88	11.20	4.50	5.14 ± 0.23
6	42	1.81	10.75	4.04	4.40 ± 0.30
7	21	1.84	9.79	5.35	5.30 ± 0.45
8	8	2.19	10.08	6.36	6.29 ± 0.96
9	3	3.00	4.59	3.03	3.54 ± 0,53
10	2	3.67	8.96	6.31	6.31 ± 2.65
Total	1378	1.52	22.92	5.21	5.89 ± 0.09

no significant difference between birth orders (binomial test statistics $\chi^2 = 0.418$, ns), between captive-born (n = 387) and wild-caught (n = 464) females (binomial test statistics $\chi^2 = 0.545$, ns), or between mothers' ages (binomial test statistics $\chi^2 = 0.785$, ns).

Discussion

Seasonality of births

Seasonal reproduction can happen in tropical animals, similar to temperate-zone animals and they display distinct seasonal peaks in reproductive activity if they do not reproduce year-round. In some cases, reproductive activity is spread out over weeks or months, but nonetheless is clearly seasonal rather than continuous (Bronson 1995; Aung *et al*. 2001). Even *Homo sapiens*, the archetypal example of a continuously breeding species, exhibit significant seasonality in births (Bronson 1995). Studies have shown that seasonal reproduction can be initiated by day length, temperature, rainfall and food supply or quality of habitats or interactions between these factors (Gaillard *et al*. 1993; Helm & Gwinner 2005; Perfito *et al*. 2005; Toigo *et al*. 2006).

Based on the supportive information from several studies, the reproductive output of timber elephants would correspond to the seasonal availability of good quality feed under the influence of rainfall. This was supported by the studbook data, where fewer calves were born during the summer months between May and August than the rainy and cold months. A similar calving pattern was reported by Sukumar (2003) where births peaked "towards the end of wet (rainy) season" and before the arrival of monsoon in both south India and Myanmar. Likewise, Moss (2001) identified a clear seasonality of conceptions in African elephants corresponding to rainfall.

Mean gestation period for Myanmar elephants is estimated as 20-21 months (Hundley 1922; Flower 1943; Anghi 1962) to recalculate the mating season in timber elephants. I report that peak mating and conception coincided with the summer resting months (Fig. 2). According to the studies of reproductive strategies of polygynous endemic tropical deer (*Cervis eldi thamin*) in central Myanmar, reproduction is seasonal, with mating seasons occurring during the hot-dry season and parturition in cool months in November-December (Aung *et al*. 2001). Elephants in my study show similar breeding pattern of tropical long-lived mammals living in similar habitats.

Age-specific fecundity rate

Wild-caught and captive-born mothers showed similar fecundity patterns, peaking between 38 and 40 years. However, the maximum fecundity of wild-born mothers was half that of captive-born mothers (Fig. 3). This may be due to a reduced availability of food, capture/training stress or a combination of the two. Resource availability affects the life history patterns of growth, maintenance and reproduction (Isaac 2005). Food deprivation or restricted food intake can suppress ovulation, oestrus behaviour and mothering ability in various mammals (Wade & Schneider 1992) including humans (Lummaa & Tremblay 2003).

Although no study has been conducted on feeding ecology of captive elephants, it is expected that captive-born and wild-caught elephants may differ in their abilities to extract high quality resources from their foraging environment.

Having been born in the area in which they live and forage, captive-born elephants are more likely to have knowledge of high quality resources. Wild-caught elephants, removed at a young age from their mothers and natal home are more likely to experience lower nutrition in the early post-capture period due to the unfamiliarity with good foraging areas. In addition, they may have difficulty competing with resident captive-born elephants for the best forage sites. This may be partly due to a restricted ability to move and walk because their front feet are fettered when they are released into the forest at night to forage. Captive-born calves are trained to forage alongside their mothers, and they are not fettered until they are weaned at or around taming age at around 4.5 years of age. Some captive-born calves continue suckling until 7 or 8 years, many years after taming, or as long as the mothers allow, or until the mothers are pregnant again. Fettering is practiced in both captive-born and wild- caught elephants only after taming. It is assumed that captive-born calves have more mobile in early ages, have enough opportunity to follow their mothers and aunts, and can more easily learn the better foraging patches and terrains.

Based on studies of ruminants and other livestock animals, it is well known that proper nutrition and dietary husbandry are fundamental to reproductive success (Allen & Ullrey 2004), and limited food availability is associated with infertility in humans (Wade & Schneider 1992). The same likely applies to wild-caught elephants used for work in the timber industry.

Wild-caught elephants also are more likely to suffer from stress than captive-born animals because they are selectively removed from their natal herd, usually (≈70%) at around 10 years of age. Here in this study, only wild elephants capture under ten is used. Research has shown that maternal separation and early life environmental stress predisposed to various pathologies (Lummaa & Clutton-Brock 2002; Shanks 2002). Growth, survival, and breeding success of individuals could be influenced by the environmental conditions that individuals experience during their early development and such effect had a permanent effect on reproductive success late in their life. The earlier an individual's development was disturbed, the stronger were the effects (Lummaa & Clutton-Brock 2002). As taming/breaking follows immediately after capture, the psychological and physical trauma sustained during the early days in captivity, compounded with restricted movement and living under the dominance of humans and residence captive-born elephants, could have a cumulative effect to suppress future fecundity.

Wild-caught females take some years to recover from the stress of capture and/or taming so that their reported age of first calving in captivity is older than captive-born females. For captive-born calves, breaking normally takes only a few days, whereas the breaking period for wild-caught animals lasts a minimum of 2 weeks to a maximum of 8 weeks depending on temperament. The longer the taming process, the harsher the punishments and more unpleasant the process generally is.

Interbirth interval

In general, it is widely accepted that a minimum intercalving interval is ≈ 2 years (Gee 1955; Yin 1962; Sukumar 2003), taking account of the average gestation period as 640-660 (±14) days (Schmidt 2006). However, earlier reports documented that the range of gestation period as 17 months 17 days to 24 months 13 days (Burne 1943). The shortest and the longest interbirth intervals in timber elephants are recorded as 1.52 and 21.44 y (median = 4.93 y) for captive-born mothers and 1.71 and 19.29 y (median = 5.28 y) for wild-caught mothers, respectively. Moreover, I provide evidence that in working elephants, mothers' birth origin was the main variable that governed the length of the intercalving interval. Wild-caught females tended to have fewer births than captive- born females, with longer birth intervals.

Numerous physiological and behavioural mechanisms link reproduction and energy metabolism. A complete reproductive cycle of ovulation, conception, pregnancy, lactation and offspring care is one of the most energetically expensive activities that a female mammal can undertake. In other large mammals such as African elephants (*Loxodonta africana*) (Laws *et al*. 1975) and white rhinoceros (*Ceratotherium simum*) (Rachlow & Berger 1998), females in high-density populations exhibit longer intervals between births than those in lower-density areas, suggesting that food competition among individuals in high-density population affected body condition and thus affected the reproductive potential. Moss (2001) stated that median intercalving interval in African elephants in Amboseli was extended by about 1.3 years if the previous calf survived for more than 2 years.

Working animals need additional energy. High energy demands coupled with limited feed supply could easily deplete the body reserves of wild-caught females more than captive-born (resident) females, which should have better opportunity to enjoy a more reliable source of food. A reproductive attempt at a time when calories are not sufficiently available can result in a reduced return on the maternal energetic investment, maternal reproductive output (Osrin & de L' Costello 2000; Knackstedt *et al*. 2005). Wild-caught females may optimize long-term reproductive success by delaying pregnancies until energy supplies can be replenished and energy demands are less severe.

Birth sex ratio

In this study, I provide the first evidence that the offspring sex ratio of Myanmar timber elephants is not different from unity and is not influenced by birth order of calves, mother's birth origin and age. Similar findings were reported in captive Indian elephant (Sukumar 2003) and other large land mammals such as African elephant (Moss 2001). According to Sheldon and West (2004), in polygynous ungulate mammals, there was a weak but significant correlation between maternal condition and sex ratio. They also claimed that such a relationship was stronger when sexual size dimorphism was more male biased and when gestation periods are longer. Under the influence of work-related and capture/taming-related stress, timber elephants living in an extensive keeping system were presumed to adjust sex ratio differently in wild-caught and captive-born mothers. Having a better survival (Mar 2007, Clubb *et al*. 2009) and reproductive rate than wild-caught elephants, captive-born females were previously assumed to produce male-skewed sex ratio similar to other studies (Clutton-Brock 1984). Wild-caught females, due to their early stressful life combined with work-related stress and pressure of living under human and dominance of resident captive-born herd mates, would be more likely to produce female-biased offspring sex ratio (Rivers & Crawford 1974; Kojola 1997). Referring to the maternal investment in polygynous large mammals, namely elk (*Cervus elaphus*), Kohlmann (1999) stated that "if females in populations suffer from generally low body condition, intrauterine and neonatal mortality may further reduce the number of sons produced and produce a significant bias toward daughters". These findings are at variance with the findings in my study. The findings of the study demonstrate that Asian elephant females in Myanmar timber camps do not adapt offspring sex ratio regardless of body condition or in relation to social context or resource availability.

Conclusions

- In this sub-set of data, fewer calves are born during the late summer months between May and June, and in early monsoon season (July and August), indicating peak mating and conception coincide with summer.
- Captive-born mothers have significantly higher birth rates than wild-caught mothers, with fecundity rate differing by half.
- Wild-caught mothers exhibit a significantly lower birth rate than captive-born mothers.
- Fecundity peaks between 38 and 40 years in both wild-caught and captive-born females.
- Reproductive senescence is not likely to occur in female Asian elephants.
- The shortest and the longest interbirth intervals are found to be 1.52 and 21.44 y (median = 4.93 y) for captive-born mothers and 1.71 and 19.29 y (median = 5.28 y) for wild-caught mothers, respectively.
- In sum, evidence suggests that fecundity is greater among captive-born females. Given this, and the negative consequences of capturing and training wild-born females,

the most humane and efficient way to sustain working populations of Asian elephants is through well-planned and far-sighted captive breeding efforts.

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