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Survey of reproduction and calf rearing in Asian and African elephants in European zoos

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Abstract

Acyclicity, conception failure, abortion, stillbirth, dystocia, infanticide and neonatal mortality have all been reported as causes of reproductive failure in captive elephants. These events are often recorded in single case reports or in specific studies focused on a particular stage in the reproductive process. In North America wider surveys of reproduction in the captive elephant population have been completed and repeated to provide data over a number of years. This study is the largest and most comprehensive study of reproduction in the European captive elephant population to date. Two questionnaires collected data from throughout the reproductive process, from assessing cyclicity to independence of the calf at five years old. Information was collected regarding 189 birth events. Many causative and contributing factors of reproductive failure such as obesity, infectious disease, husbandry, facilities, stress, behaviour, herd size and social grouping have been proposed. The importance of these was assessed and possible associations were verified by statistical analyses. For African elephants, this study found that age, obesity, reproductive pathology and dominance, identified as important risk factors for failure to conceive in the American captive elephant population, were of low importance. The most significant cause in Europe was lack of physical access to a compatible bull. In Asian elephants, reproductive failure was much less common, but when it did occur, age and reproductive pathologies were significant factors as found in previous studies. Previous studies have found that age, obesity and infanticide were considered as the most important risk factors in the period from birth to rearing. In this survey it was found that herd stability and compatibility, allomothering or maternal experience and management at parturition can significantly influence reproductive success. Elephant endotheliotropic herpes virus was confirmed as the biggest cause of calf mortality. This work provides evidence that elephant management in European zoos that encourages the development of social and affiliative herd behaviours will improve reproductive success.

Introduction

Reproductive and breeding problems ranging from abnormal ovarian cycles to infanticide have been reported in zoo elephants (Brown et al. 2004, Taylor and Poole, 1998). These have been attributed to physical, physiological, social and management factors such as dystocia, infectious disease and group size. Studies have been undertaken on many of these specific issues in zoos (Flugger et al. 2001; Rees, 2009).

Much of the previous work on zoo elephant reproduction has been conducted in North America. There are some important differences in the elephant population in North American zoos when compared to the European elephant population, including an older mean age, smaller mean herd size, a lower reproductive rate and management limitations caused by diagnosis with tuberculosis, making direct extrapolation inaccurate. Only two elephant reproductive surveys have been undertaken in Europe to date. Prahl (2010) studied gestation, parturition and rearing in Asian elephants and found a high incidence of dystocia, stillbirth and calf mortality, with causative factors being infanticide, unsuccessful hand-rearing and infectious disease. Meijer (2010) investigated cyclicity and reproductive success in both Asian and African elephants in 15 zoos, finding that acyclicity was not a common problem in either species but that dystocia and infectious disease were important in Asian elephants.

Broader studies comparing reproductive data between zoos and timber camp elephants (Schmidt and Mar 1996; Hayward et al. 2014) and wild elephants (Clubb et al. 2008) have also been completed. Clubb and Mason (2002) conducted a study

using statistical analysis of studbook data, which included data on reproductive failure, and proposed some causative factors including obesity and chronic stress. Clubb and Mason (2002) did not collect information on elephant management and therefore were unable to link these findings to husbandry practices or make conclusions regarding specific risk factors.

This survey builds on previous work by utilising studbook interrogation to obtain indicators of reproductive performance and compile individual elephants' life histories to assess their previous social, reproductive and maternal experience. These were then used in conjunction with the structured collection of elephant management information focused on both general husbandry and specific animals and events most relevant to the study. The overall aim of the study was to identify risk factors associated with reproductive failure. Unrivalled access to information directly from the zoos allowed a wider range of risk factors to be investigated than has been possible in other studies. This study therefore provides the most comprehensive survey of reproductive activity in zoo elephants in Europe to date.

Methods

The reproductive process was separated into two phases: puberty to conception and conception to successful rearing of the calf to five years. A questionnaire was developed for each phase.

The first questionnaire collected data on individuals that had failed to reproduce. Reproductive failure was defined as not producing a calf within the last five years, so all elephants that had become pregnant in the last five years were excluded from this questionnaire. Three groups of elephants of interest were identified through studbook interrogation. The first comprised those elephants that had bred previously but not in the last five years, the second elephants that had never bred despite being housed with a proven bull for a period of at least two years, and the third elephants that had never had access to a proven bull in their lifetime. This resulted in a potential sample of 145 Asian and 93 African elephants for the first questionnaire. The zoos were sent a questionnaire for each of these individuals. The questionnaire is provided in the supplementary materials.

The second questionnaire collected data on each pregnancy event. For African elephants all pregnancies recorded in the studbook were included (1982–2013). For Asian elephants all pregnancies from 1992 to 2013 were included. The questionnaire is provided in the supplementary materials. Three additional criteria were attached to the second questionnaire return: age of elephant at the birth, if the cow was primiparous or multiparous and the cow's previous experience of calves (defined as a calf being born in the cow's herd previously), as these were considered as potential risk factors in previous studies (Clubb et al. 2008; Dale et al. 2010)..

The questionnaires collected data on husbandry, management practices, veterinary interventions and social interactions and behaviours. Each zoo was asked to rate the hierarchical position of the cow on a five-point scale (1 being least dominant to 5 being most dominant). For questionnaire two, birth events were separated into five categories: abortions, stillbirths, dystocia, failure to accept calf and failure to rear calf to five years. The results within each outcome were compared to identify potential common factors.

The results were collated and analysed using SPSS 22 (IBM Corporation). All means are presented with standard deviations where appropriate. Continuous data were tested for normality using the Kolmogorov-Smirnov test. Where there were sufficient data, Student's *t*-tests (normally distributed data) or Mann-Whitney *U*-tests (data which could not be transformed to a normal distribution) were used to compare means and Pearson's chi-square analyses were used to test for association. It was not possible to combine all terms into a single model for most outcomes due to a lack of data representation for some category combinations; for this reason we corrected for multiple testing by applying a sequential Bonferroni correction to all *P*-values for tests on the same outcome variable (Rice 1989).

Table 1. Summary results for questionnaire 1.

Factor	African	Asian
Hormones monitored	65.5% (28/43)	59.5% (22/37)
Reproductive tract pathology	25.5% (11/43)	43.2% (16/37)
Normal reproductive cycle	67.4% (29/43)	51.4% (19/37)
Acyclic	4.7% (2/43)	13.5% (5/37)
Unknown reproductive cycle	27.9%(12/43)	32.4% (12/37)
Mean age at puberty	9.5±1.58 years (N =5)	5.6±1.03 years (N =4)
Other health issues	16.3% (7/43)	13.5% (5/37)
Unstable herd hierarchy	9.3% (4/43)	27.0% (10/37)
Changes to herd composition	67.4% (29/43)	48.6% (18/37)
Cow refuses to allow bull to mate her	44.7% (17/38)	21.4% (6/28)
Bull refuses to mate the cow	31.6% (12/38)	21.4% (6/28)
Cows only mixed with bull when in oestrus	21.0% (8/38)	25.0% (7/28)
Cow never mixed with bull housed at the same zoo	21.0% (8/38)	7.1% (2/28)
No bull housed at the zoo	11.6% (5/43)	24.3% (9/37)
Overnight access to the bull	5.2% (2/38)	25.0% (7/28)

Results

Questionnaire 1

For questionnaire 1 responses were received relating to 43 African and 37 Asian elephants. The summary results for the first questionnaire are shown in Table 1.

Acyclicity rates were 6.5% (2/31) for African elephants and 24% (6/25) for Asian elephants for the animals who were monitored.

Age of cow

For both species, acyclic animals were generally older (African: mean acyclic animals = 38.0±8.49 years, mean cycling animals = 22.7±9.69 years; Asian: mean acyclic animals = 35.5±7.56 years, mean cycling animals = 30.5±9.73 years). Acyclic elephants ranged from 32 to 44 years (African) and from 28 to 47 years (Asian). The mean difference in age between cyclic and acyclic individuals was not significant following a sequential Bonferroni correction for either African (t_{29} = 2.17, P = 0.038) or Asian (t_{23} = 1.15, P = 0.260) elephants.

Reproductive tract pathology

In this study, 25.5% (11/43) of non-reproductive African elephants had confirmed reproductive pathology, 16.2% (7/43) had endometrial cysts and 6.9% (3/43) had ovarian cysts, but all of these animals cycled normally. For the Asian elephants, 43.2% (16/37) of the non-reproductive elephants had confirmed

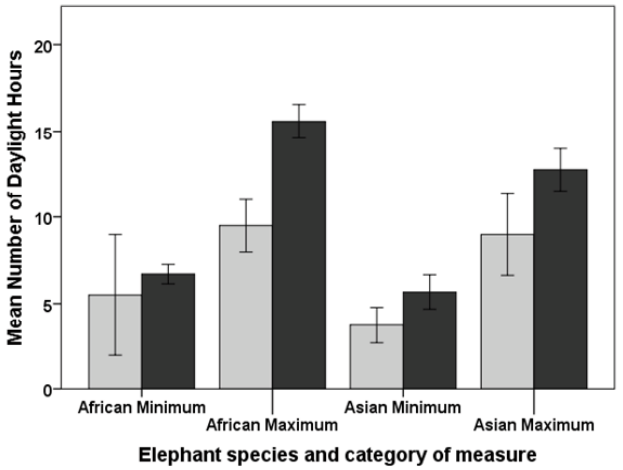

Figure 1. Minimum and maximum hours of access to daylight of elephants of each species by reproductive status. Pale grey bars are acyclic individuals whilst dark grey bars are individuals which are cycling normally. Data from 31 African and 16 Asian elephants are included. Error bars represent standard deviations.

reproductive pathology. 16.2% (6/37) of cows had been diagnosed with uterine leiomyomas and 13.5% (5/37) had ovarian cysts. Six of these animals were acyclic. However, there was no significant association between reproductive tract pathology and acyclicity in either species (African: $\chi^2_1 = 1.18$, $P = 0.278$; Asian: $\chi^2_1 = 3.28$, $P = 0.070$).

Social ranking

A high proportion of the non-reproductive elephants in this study had a high social rank, with 64% (21/33) of the African and 60% of the Asian (21/35) elephants where social ranking was known being rated at 4 or 5 on a five-point scale. However, cyclic and acyclic animals did not significantly differ in their social rank where this was known (African: $n = 25$, $U = 7$, $P = 0.133$; Asian: $n = 25$, $U = 49.5$, $P = 0.642$).

Change in herd composition

There was no significant influence of the occurrence of changes in herd composition in the last six months on whether or not cows were acyclic for either species (African: $\chi^2_1 = 0.624$, $P = 0.430$; Asian: $\chi^2_1 = 0.146$, $P = 0.702$).

Exposure to daylight

In both species, the acyclic animals generally had less access to daylight (Fig. 1). However, these differences were not significant (African minimum: $t_{29} = -0.53$, $P = 0.600$; African maximum: $t_{29} = -1.61$, $P = 0.118$; Asian minimum: $t_{14} = -1.05$, $P = 0.311$; Asian maximum: $t_{14} = -1.48$, $P = 0.161$), perhaps since there were only two African and four Asian acyclic elephants for which hours of access to daylight were known.

In addition to the factors highlighted above which may influence the occurrence of acyclity, in this cohort of non-reproducing elephants the major cause was a failure to be mated with. 30.2% (13/43) of African and 29.7% (11/37) of Asian elephant cows either lived at a zoo which did not house a bull or were never mixed with a bull. A further 67.4% (29/43) of African and 32.4% (12/37) of Asian elephant cows were never mated due to behavioural incompatibility with the resident bull. This resulted in 97.6% (42/43) of African elephants and 89.1% (33/37) of Asian elephants not reproducing because they were not mated by a bull.

Questionnaire 2

For questionnaire 2 responses were returned for 67 African and 122 Asian elephants. The summary results from questionnaire 2 are shown in Tables 2 and 3.

Age of cow

In both species, the cow's age had no significant influence on the likelihood of abortion (Asian: $t_{119} = 0.405$, $P = 0.686$; African: $t_{64} = 0.661$, $P = 0.511$) or dystocia (Asian: $t_{114} = -0.760$, $P = 0.449$; African: $t_{58} = -0.661$, $P = 0.511$). The cow's age also had no significant influence on the likelihood of stillbirth in Asian elephants ($t_{114} = -0.884$, $P = 0.378$), but for African elephants, older cows were more likely to suffer from a stillbirth than younger cows (mean age (stillbirth) = 23.6 ±8.69 years, mean age (live birth) = 18.45 ±6.13 years, $t_{59} = -2.262$, $P = 0.027$), although this result was not significant following a Bonferroni correction.

Whilst there was no difference in the mean age of the cow at parturition on the likelihood of accepting the calf for African elephants ($t_{47} = -0.767$, $P = 0.447$), younger Asian elephants were more likely to reject the calf (accept: 21.0±7.42yrs, reject: 17.8±6.22yrs, $t_{100} = -2.041$, $P = 0.044$), although this result was not significant following a Bonferroni correction. There was no difference between the mean ages of cows and the likelihood their calf reached five years old for either species (Asian: $t_{100} = -0.404$, $P = 0.687$; African: $t_{49} = -0.477$, $P = 0.635$).

Primiparity, dystocia and stillbirth

In both species, primiparous cows were no more likely to abort than multiparous cows (Asian: $\chi^2_1 = 0.325$, $P = 0.569$; African: $\chi^2_1 = 0.013$, $P = 0.909$). However, the association between primiparity and dystocia differed between species. For Asian elephants, dystocia tended to be less prevalent in primiparous cows ($\chi^2_1 = 4.213$, $P = 0.040$), but this result was non-significant following

Table 2. Summary results for population level data in questionnaire 2.

Factor	African	Asian
Abortion rate	7.5% (5/67)	3.2% (4/122)
Twinning rate	1.4% (1/67)	1.6% (2/122)
Dystocia rate	11.9% (8/67)	16.4% (20/122)
Stillbirth rate	11.9% (8/67)	12.3% (15/122)
Cow failed to immediately accept calf and allow to feed	13.4% (9/67)	22.9% (28/122)
Cow failed to immediately accept calf but went on to rear it successfully	7.5% (5/67)	14.8% (18/122)
Dam aggressive to calf	4.4% (3/67)	9% (11/122)
Infanticide by mother	1.5% (1/67)	2.5% (3/122)
Killed by another herd member	0% (0/67)	1.6% (2/122)
Number of calves attempted to be handraised	5.9% (4/67)	3.3% (4/122)
Number of calves handraised successfully	1.5% (1/67)	0% (0/122)
Survival rate overall (including abortions and stillbirths)	71.6 % (48/67)	68.0% (83/122)
Survival rate of live births	81.3% (48/59)	81.4% (83/102)
Mortality rate to infectious disease	2.9% (2/59)	9.8% (10/102)

Table 3. Summary results for individual health, social and husbandry management at time of parturition from questionnaire 2.

Factor	African	Asian
Reproductive tract pathology diagnosed	0% (0/67)	7% (4/57)
Hormones monitored during pregnancy	26.8% (18/67)	41.8% (51/122)
Cow developed ventral oedema during pregnancy	16.4% (11/67)	7.4% (9/122)
Cow in free contact at birth	38% (26/67)	38.5% (47/122)
Cow in protected contact at birth	13.4% (9/67)	29.5% (36/122)
Cow in no contact at birth	47.7% (32/67)	0% (0/122)
Changes in herd composition in preceding 6 months	26.9% (18/67)	48% (59/122)
Cow in unstable herd	23.8% (16/67)	24.5% (30/122)
Other health issues	13.4% (9/67)	3.3% (4/122)
No contact with other elephants at time of birth	1.5% (1/67)	4.1% (5/122)
Visual contact with other elephants at time of birth	25.4% (17/67)	38.5% (47/122)
With selected other elephant at time of birth	11.9% (8/67)	27.0% (33/122)
In whole herd at time of birth	11.9% (8/67)	29.5% (36/122)
Unknown contact with other elephants	49.2% (33/67)	4.1% (5/122)
Cow chained for birth	11.9% (8/67)	33% (41/122)

a Bonferroni correction. For African elephants, dystocia was significantly more prevalent in primiparous cows (χ^2_1 = 12.453, P < 0.001, Fig. 2). There was no association between stillbirth incidence and primiparity in African elephants (χ^2_1 = 0.266, P = 0.606), whereas for Asian elephants, primiparous cows were significantly more likely to suffer a stillbirth (χ^2_1 = 9.564, P = 0.002, Fig. 3). In both species dystocia was significantly associated with stillbirth with 50% (5/10) of stillbirths in African elephants and 86% (12/14) in Asian elephants being associated with dystocia (African: χ^2_1 = 13.962, P < 0.001; Asian: χ^2_1 = 56.432, P < 0.001).

A number of additional associations with dystocia and calf survival were identified in Asian elephants, where the sample size was much larger than that of African elephants. The mean body weight of calves (both live and stillborn) from cows which experienced dystocia was 132.3±26.10kg compared with a weight of 108.3±22.4kg from cows without dystocia. Dystocia is therefore associated with a significantly larger calf birth weight (N = 60, U = 0.00, P < 0.001). The position of the calf was also found to be associated with dystocia: 71% (25/35) were born hind limbs first and 29% (10/35) front limbs and head first; no calves were reported to have been born in the breach position. 60% (6/10) of calves born headfirst experienced dystocia compared to 16% (4/25) born hind limb first; dystocia was significantly associated with headfirst birth (χ^2_1 = 6.776, P = 0.009). 40% (4/10) of the calves born headfirst were stillborn compared to 12% (3/25) born hind limb first; stillbirth appeared to be linked to calving position but this difference was not statistically significant (χ^2_1 = 3.500, P = 0.061).

There was a significantly higher incidence of dystocia in free versus protected management systems in Asian elephants (χ^2_1 = 6.658, P = 0.010, Fig. 4) and in free versus no contact management systems in African elephants (χ^2_1 = 7.877, P = 0.005, Fig. 5).

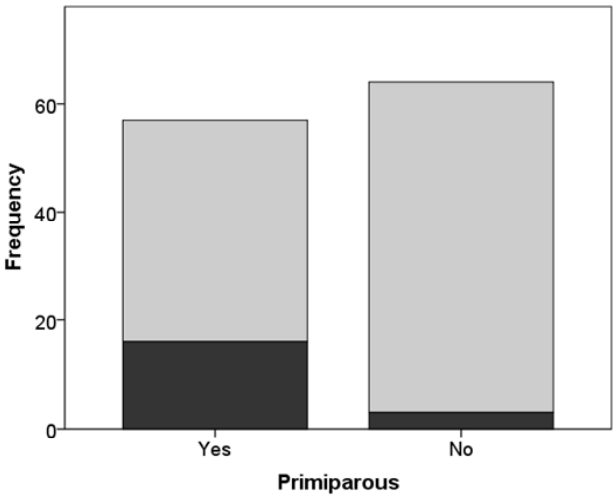

Figure 2. Primiparous African elephants were significantly more likely to suffer from dystocia (N = 121). Dark grey indicates presence of dystocia whilst light grey indicates a lack of dystocia.

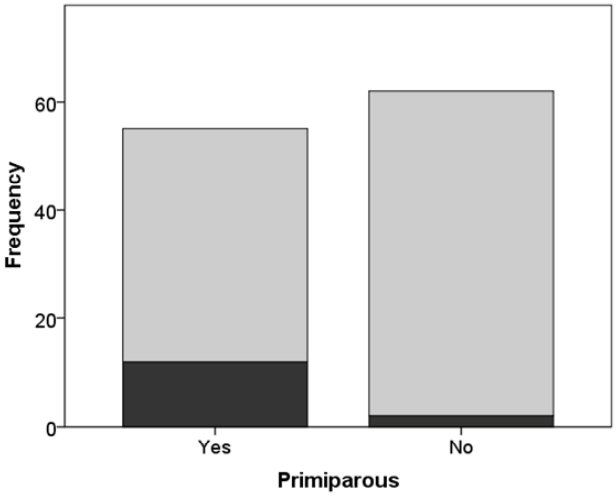

Figure 3. Primiparous Asian elephants were more likely to suffer a stillbirth (N = 117). Dark grey indicates a stillbirth whilst light grey indicates a live birth.

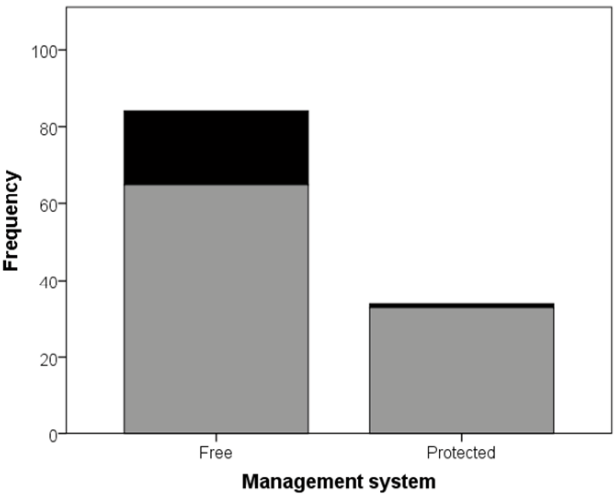

Figure 4. Asian elephants were more likely to suffer dystocia if managed in a free contact system versus a protected contact system (N = 118). Dark grey indicates the occurrence of dystocia whilst light grey indicates a normal birth.

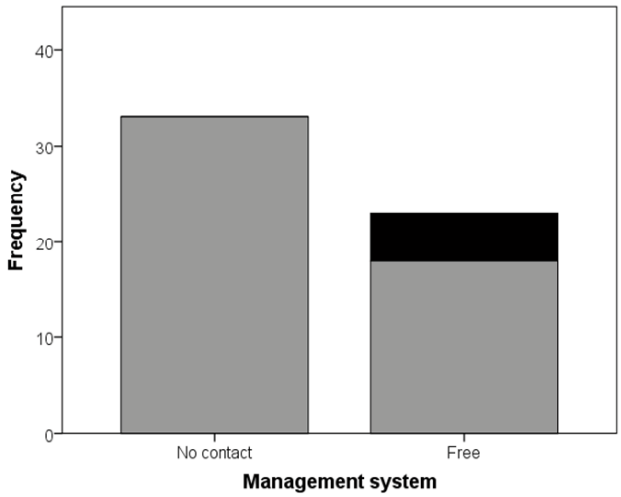

Figure 5. African elephants were more likely to suffer dystocia if managed in a free contact system versus a no contact system (N = 56). Dark grey indicates the occurrence of dystocia whilst light grey indicates a normal birth.

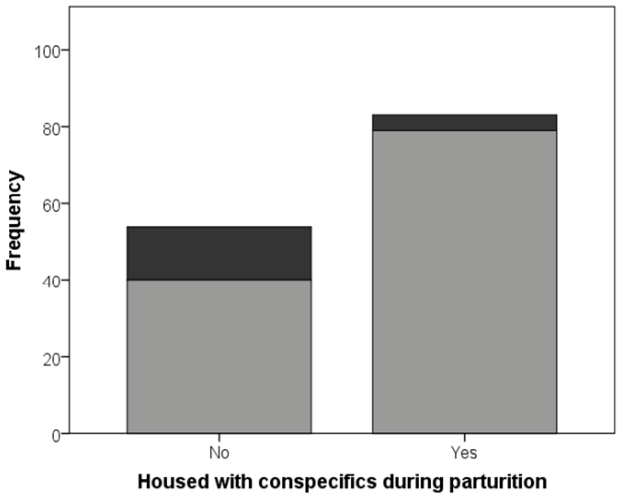

Figure 6. Asian elephants were more likely to suffer dystocia if they were physically separated from conspecifics during parturition (N = 137). Dark grey indicates the occurrence of dystocia whilst light grey indicates a normal birth.

19/84 (23%) of Asian elephants in free contact systems suffered dystocia compared to 1/34 (3%) of Asian elephants in protected management systems; 5/23 (22%) of African elephants in free contact systems suffered dystocia compared to 0/33 (0%) of African elephants in no contact management systems.

Female Asian elephants which were housed with conspecifics during parturition showed a significantly lower incidence of dystocia than those either separated from other elephants, or allowed to see or touch conspecifics ($\chi^2_1 = 12.771$, $P < 0.001$, Fig. 6). 14/54 (26%) of females isolated from conspecifics showed dystocia compared to 4/83 (5%) of those housed with conspecifics. There was no significant association found between the incidence of dystocia and being housed with conspecifics during parturition in African elephants ($\chi^2_1 = 1.488$, $P = 0.223$). There was no significant association found between the frequency of calf rejection and being housed with conspecifics during parturition in either Asian ($\chi^2_1 = 0.452$, $P = 0.501$) or African elephants ($\chi^2_1 = 0.080$, $P = 0.777$).

Previous maternal experience of calves

In this study 77% (7/9) of the African elephant cows that initially rejected the calf had either had a calf themselves previously or else had been in a herd where another cow had reared a calf successfully. In contrast, 57% (16/28) of the Asian elephant cows that initially rejected their calves were primiparous or had failed to rear a calf before and had also not been in a herd where another cow had reared a calf, meaning they had no prior experience of calves. This finding was supported statistically, with those Asian cows having no maternal experience being more likely to reject their calves initially ($\chi^2_1 = 9.96$, $P = 0.002$).

Primiparous Asian cows were more likely to demonstrate poor maternal skills initially; 61% (17/28) of the cows that failed to accept their calves were primiparous and there was a significant association between primiparity and acceptance of a calf ($\chi^2_1 = 5.451$, $P = 0.020$). For African cows, although 63% (5/8) of cows which failed to accept their calf were primiparous, there was not a significant association between primiparity and acceptance ($\chi^2_1 = 1.861$, $P = 0.173$). There was no association between primiparity and the likelihood a calf reached five years old (Asian: $\chi^2_1 = 0.695$, $P = 0.404$; African: $\chi^2_1 = 0.811$, $P = 0.368$).

In African elephants, 86% (38/44) of the cows that successfully reared their calf to five years had had their own calves or had direct experience of calves in the herd previously. However, there was no significant association between experience of calves and successful rearing to five years ($\chi^2_1 = 0.148$, $P = 0.700$). In Asian elephants, in 86% (71/83) of successful rearings, the cow had had her own calf or had direct experience of calves in the herd previously. 47% (9/19) of the calves that died before reaching five had a dam with no experience of calf rearing. This association between maternal experience and successful calf rearing was supported statistically ($\chi^2_1 = 24.56$, $P < 0.001$).

Finally, in Asian elephants, herd stability is also important for the successful rearing of calves. Of those calves born into stable herds, 86% (69/80) reached five years of age, compared to 61% (14/23) born into unstable herds. There was therefore a significant association between herd stability and calf survivorship ($\chi^2_1 = 7.354$, $P = 0.007$).

Discussion

The key findings from this study are shown in Table 4.

Acyclicity and reproductive failure

Acyclicity has previously been identified as an important cause of reproductive failure in elephants (Brown et al. 2004; Freeman et al. 2009; Hildebrandt et al. 2011). In this study reproductive hormones were monitored in over 60% of elephants but acyclicity was only reported in 14.5%. Other factors are therefore contributing to reproductive failure in European captive elephants.

In previous studies, the average age of acyclic cows of both species was greater than for cycling cows (Brown et al. 2004; Proctor et al. 2010). In this study, although there tended to be an association between acyclicity and older age in African elephants, this result was not statistically significant. No such association was found in Asian elephants.

Table 4. Summary of associations between various factors and reproductive outcomes identified by this study. The "Significant results" column displays results remaining significant at $\alpha = 0.05$ following a Bonferroni correction; those which approached significance or showed a potential relationship are reported in the "Trends" column. Result applies to both species unless indicated in parentheses.

Outcome	Significant results	Trends
Acyclicity		Older age (African)
		Reduced access to daylight
Dystocia and stillbirth	Dystocia and stillbirth	Older age and stillbirth (African)
	Primiparity and dystocia (African)	Primiparity and dystocia (Asian)
	Calf weight and dystocia (Asian)	
	Calf position and dystocia (Asian)	
	Management system and dystocia	
	Social contact during birth and dystocia (Asian)	
	Primiparity and stillbirth (Asian)	
Calf rejection	Previous experience of calves (Asian)	Primiparity (Asian)
		Younger age (Asian)
Calf survival	Previous experience of calves (Asian)	
	Herd stability (Asian)	

In African elephants, it has been demonstrated that dominant matriarchs, particularly those with a large body mass and a long history with the same conspecifics, are the most likely to be acyclic (Freeman et al. 2004, 2010; Proctor et al. 2010). This result was not supported in this study, with no association being found between acyclicity and either social rank or herd stability. This may have been due to an inaccurate reporting of social hierarchy position. Although body condition scores (a proxy for unknown body mass) were collected, these data were not analysed statistically due to a poor response rate to this question.

Reproductive tract pathology has been identified as a potential cause of reproductive failure in zoo elephants (Hermes et al. 2004; Hildebrandt et al. 2011). We found no association between acyclicity and reproductive pathologies in the sample for which both factors were recorded; indeed the majority of the elephants that were suffering from reproductive pathology were cycling normally. However, Lueders et al. (2010) associated foetal loss and resorption with the presence of a uterine leiomyoma and endometrial cysts, suggesting that these elephants may not be reproducing because their reproductive pathologies prevent them from conceiving, rather than because of a lack of cycling.

The amount of exposure to daylight has been reported as positively influencing reproductive cycles (Schulte 2000), but this result has been disputed by others (Brown and Lehnhardt 1997). In this study the acyclic animals had at least 50% less access to daylight than cycling animals. Possibly due to the relatively small sample size for which daylight exposure was reported, this association was not found to be significant, but the clear trend reported warrants further investigation and a recommendation to maximise access to daylight for captive elephants.

The main conclusion we can draw from this study is that although the incidence of acyclicity may be reduced by improving captive elephants' access to daylight, the major reason for captive European elephants failing to reproduce is actually likely to be a lack of physical access to a bull; this applied to 97.6% (42/43) of African elephants and 89.1% (33/37) of Asian elephants.

Stillbirth and dystocia

In this study 16.4% (20/122) of Asian elephants experienced dystocia. This incidence rate is significantly lower than that reported in a previous study of 74 elephant parturitions in European zoos, where 36% of parturitions suffered from dystocia (Prahl 2009). The stillbirth rate of 11.9% (8/67) in African elephants and 12.3% (15/122) in Asian elephants in this study is higher than the 4% rate reported in Asian elephants in timber camps (Mar et al. 2012) but lower than previously reported in captive Asian elephants in Europe (16.2%, 12/74; Prahl 2009). A studbook analysis undertaken in 2002 similarly calculated a stillbirth rate of 16% (26/166; Stevenson 2004).

We found that stillbirth was significantly associated with dystocia in both species. Primiparous African elephants were more likely to suffer dystocia and primiparous Asian elephants were more likely to suffer stillbirth. We can therefore conclude that primiparity could be a key factor increasing the likelihood of calf mortality due to stillbirth in both species. Since primiparity may also have a possible link with increased likelihood of calf rejection for Asian elephants (although this result was not statistically significant), we suggest the close monitoring of primiparous elephants may improve rates of calf survival.

Dystocia was also significantly associated with larger calf weight and the headfirst birth position in Asian elephants in this study. These results are consistent with those found previously; stillborn Asian elephant calves were significantly heavier than live-born calves (Clubb et al. 2009; Dale 2010; Kurt and Mar 1996) and dystocia has been linked to both breach birth (Oosterhuis 1990) and headfirst birth (Wallace et al. 1992; Thitaram et al. 2006). Although not apparent from this study, age of cows has also previously been identified as a potential risk factor for dystocia and stillbirth. Doyle et al. (1999) found that the age of the cow can influence the likelihood of dystocia and stillbirth; Flugger et al. (2001) also reported that 75% of Asian elephant cows over 20 years of age at their first pregnancy suffered dystocia and lost their calves. These are therefore risk factors associated with

dystocia and stillbirth which could be identified during pregnancy; we would recommend closer monitoring of cows with these risk factors.

Abortion

We found no significant associations between the rates of abortion and either age or primiparity in either species which is consistent with other studies.

Social experience

Maternal aggression, particularly in primiparous mothers, has frequently been reported in European and American zoos (Murray et al. 1996). Three studies have reported infanticide rates in European zoo elephants. Taylor and Poole (1998) found a rate of 10% (12/121), Saragusty et al. (2009) a rate of 14.8% (8/54) and Prahl (2009) a rate of 3% (3/102). This study found lower rates of maternal aggression resulting in infanticide of 1.5% (1/67) in African elephants and 2.5% (2/122) in Asian elephants.

In this study, 18.7% of African elephant calves and 18.6% of Asian elephant calves born alive failed to reach five years of age. This is a lower juvenile mortality rate than has been found by previous studies. Studbook analysis between 1986 and 2006 showed that 21% of African elephant calves in European zoos, 45% of African elephants in North American zoos and 42% of Asian elephants in Europe died before five years of age (Sargusty et al. 2009). A second analysis of European studbooks, using data up until 2005 and combining the two species, demonstrated an infant mortality rate of 25.6% (Clubb et al. 2008). In Myanmar, 25% of calves died before reaching five years old (Mar et al. 2012).

In elephant society, reproductively inactive females, including young prepubescent cows, play an important role in care giving through allomothering (Schulte 2000). Allomothers gain experience in calf rearing and may later receive aid with their own offspring from more experienced cows (Dublin 1983). Mar et al. (2012) reported that primiparous Asian elephant females had a four times greater risk of losing a live-born calf, as compared to their later calves. African elephants in zoos had a live-born infant mortality rate of 23.1% in primiparous dams and 0% in multiparous dams (Clubb et al. 2008). In this study, in 83.7% (31/37) of African elephant and in 86% (71/83) Asian elephant successful rearings, the cow had had her own calf or had direct experience of calves in the herd previously. In Asian elephants 71% (5/7) of the cows that failed to rear their calves were primiparous. The associations between a lack of experience of calves and both increased likelihood of calf rejection and failure for a calf to survive found in this study indicate that (a) primiparous cows should be housed in groups with reproductive elephants where possible to allow allomothering experience, and (b) those which lack this experience should be monitored closely from parturition to the first few years of motherhood. A lack of correlation between maternal age and either acceptance of calves or their survival to five years highlights that it is maternal experience, and not age, which significantly influences maternal behaviour.

Stress caused by isolation and restricted contact with herd members and chaining during birth have previously been suggested to cause stress-induced suppression of oxytocin production and therefore dystocia (Clubb et al. 2009; Mason and Veasey 2010). Two previous studies reported a significant reduction in maternal aggression in zoos where the cows could give birth unchained and in the herd (Flugger et al. 2001; Prahl 2009). Elephants demonstrate a strong need for proximity to and bodily contact with other elephants, especially in periods of stress or uncertainty (Adams and Berg 1980; Garai and Kurt 2006) and therefore to inhibit contact opportunities could be considered as an additional stress. No previous studies have collected data on the influence of social contact on the risk of dystocia and the significant association found here between reduced access to conspecifics during parturition and the higher rates of dystocia warrants further research. These results clearly indicate that reduced contact during parturition could significantly increase the likelihood of dystocia and this should therefore be avoided where possible.

Social stability, in terms of a stable herd composition, was found to be significantly associated with higher rates of calf survival to five years old. A further recommendation would therefore be that herd composition is changed as infrequently as possible during this sensitive period of juvenile development.

Management system

The significant association found here between management system and the incidence of dystocia in both species is a novel result which certainly requires further research. A link between more interventionist management and higher incidences of dystocia suggests that allowing elephants the ability to display social herd behaviour is beneficial. This provides further evidence to support our findings regarding the importance of herd stability and allomothering experience.

Conclusions

This study is the most comprehensive survey of reproduction in captive elephants in Europe to date. Unlike previous studies it collates data from the entire reproductive pathway and addresses the two elephant species separately. Acyclicity, dystocia, abortion, stillbirth and calf mortality rates were found to be lower in both species than in all previous studies; this is perhaps indicative of an improvement in our understanding of best management practices for captive elephants.

This study specifically focused on non-reproducing elephants of breeding age. Our findings indicate that social and behavioural factors are the primary cause of reproductive failure in European zoo elephants. Potential breeding animals need to be housed at a zoo with the facilities to accommodate a bull. Further work to investigate social interactions between cows and bulls and how to encourage positive reproductive behaviour in zoos is recommended.

Risk factors for dystocia and stillbirth were confirmed as being primiparity, larger calf weight and calf position during parturition. Cows showing signs of these risk factors must therefore be closely monitored during parturition in order to reduce incidences of stillbirth.

Our novel findings related to the impact of management regime and the extent of contact with other elephants at the time of parturition on dystocia indicate that allowing herd births may reduce the risk of dystocia. Further investigation of this is warranted.

The significance of alllomothering or previous maternal experience on calf rearing and mortality was strongly indicated in both species. This, in addition to the finding that herd stability had a significant influence on the survival of calves, suggests that zoo elephant groups should be managed to promote a multi-generational, family herd social structure which facilitates social learning and support.

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