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RESEARCH ARTICLE

Social Factors Influence Ovarian Acyclicity in Captive African Elephants (*Loxodonta africana*)

Elizabeth W. Freeman,[1,2]* Greg Guagnano,[2] Deborah Olson,[3] Mike Keele,[4] and Janine L. Brown[1]

[1]*Department of Reproductive Sciences, Conservation & Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia*
[2]*Department of Environmental Science and Policy, George Mason University, Fairfax, Virginia*
[3]*Department of Conservation and Science, Indianapolis Zoo, Indianapolis, Indiana*
[4]*Oregon Zoo, Portland, Oregon*

Nearly one-third of reproductive age African elephants in North America that are hormonally monitored fail to exhibit estrous cycle activity, which exacerbates the nonsustainability of the captive population. Three surveys were distributed to facilities housing female African elephants to determine how social and environmental variables contribute to cyclicity problems. Forty-six facilities returned all three surveys providing information on 90% of the SSP population and 106 elephants (64 cycling, 27 noncycling and 15 undetermined). Logistic analyses found that some physiological and social history variables were related to ovarian acyclicity. Females more likely to be acyclic had a larger body mass index and had resided longer at a facility with the same herdmates. Results suggest that controlling the weight of an elephant might be a first step to helping mitigate estrous cycle problems. Data further show that transferring females among facilities has no major impact on ovarian activity. Last, social status appears to impact cyclicity status; at 19 of 21 facilities that housed both cycling and noncycling elephants, the dominant female was acyclic. Further studies on how social and environmental dynamics affect hormone levels in free-living,

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*Correspondence to: Elizabeth W. Freeman, Department of Reproductive Sciences, Conservation & Research Center, National Zoological Park, Smithsonian Institution, Front Royal, VA 22630.
E-mail: freemane@si.edu

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cycling elephants are needed to determine whether acyclicity is strictly a captivity-related phenomenon. Zoo Biol 28:1–15, 2009.

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INTRODUCTION

Although enhanced breeding efforts have led to increased pregnancy and birth rates among captive African elephants (*Loxodonta africana*), the North American population is still not self-sustaining [Olson and Wiese, 2000]. With restrictions and political concerns associated with importation, zoos must enhance breeding success of elephants to maintain the captive population. Reproductive rates of captive elephants are low owing in part to a lack of available bulls for breeding and occasional behavioral incompatibilities between the sexes. However, the main concern is the high rates of ovarian cyclicity problems that eliminate over one-third of females from the breeding pool [Brown, 2000; Brown et al., 2004b; Olson and Wiese, 2000].

It is not known what causes acyclicity or whether it is exclusively a captivity-mediated phenomenon. Noninvasive fecal hormone monitoring of free-ranging elephants has recently provided evidence that prolonged periods of anestrous are related to reduced availability of quality browse [Wittemyer et al., 2007a]. However, an analogous effect of altered nutritional status is not likely to occur in most zoo settings. In fact, it is highly unlikely that any single factor is responsible for the high rates of ovarian acyclicity observed among captive individuals [Brown et al., 2004a], but rather both physiological and psychological conditions probably are involved. Husbandry or management practices are not the sole contributing factors to acyclicity; otherwise, all females at a given facility would have the same ovarian status. Only 4% of North American facilities exclusively house noncycling females, whereas 52% house both cycling and noncycling cows [Brown et al., 2004b]. Thus, captivity-related factors probably mediate acyclicity only indirectly [Brown et al., 2004a]. We propose that ovarian activity is related to social rank, physical conditions and/or climate [Schulte et al., 2000], because both social [Schulte, 2000] and environmental factors differ between captive and free-living elephants.

Failure of ex situ populations to reproduce at levels comparable with the wild can be caused by a lack of species-appropriate socio-environmental conditions [Lindburg and Fitch-Synder, 1994]. Thus, captive managers need detailed knowledge of the life history traits and social organization of each species to ensure successful propagation in captivity [Wielebnowski, 1998]. Systematic, cross-institutional evaluations of the captive environment that integrate behavior and husbandry research can identify causes of poor breeding success and contribute to the creation of self-sustaining ex situ populations [Kleiman, 1994; Lindburg and Fitch-Synder, 1994; Mellen, 1994; Wielebnowski, 1998]. Data can be collected in person; however, written surveys are commonly used because of logistical and cost considerations associated with direct interviews [Carlstead et al., 1999b; Mellen, 1994; Wielebnowski, 1998, 1999]. Surveys rely on the familiarity of humans with the animals in their care, which enables them to filter and integrate individual traits based on a variety of situations over long periods of time [Line, 1987]. This intimate knowledge of individual animals relative to their cohorts can provide insight into variables that contribute to overall health and reproduction [Carlstead et al., 1999b; Wielebnowski, 1999].

For this study, three surveys were distributed to North American facilities housing female African elephants to determine what social traits and environmental conditions, if any, are shared by noncycling females. Additional life history information was gathered from the North American African Elephant Studbook [Olson, 2003]. Data on environmental parameters, including longitude, latitude, elevation, average annual precipitation and temperature of each facility, were acquired from the National Oceanic and Atmospheric Administration (NOAA). Survey, studbook and environmental data were analyzed to produce a mathematical model of variables associated with ovarian acyclicity. The goal was to enhance our understanding of the mechanisms that control estrous cycle activity so that mitigating strategies can be developed to create a self-sustaining captive population of African elephants.

MATERIALS AND METHODS

Determination of Ovarian Status

At least a year of current progestagen data was used to categorize the ovarian status of each elephant in the study. Serum progestagens were analyzed using a solid-phase progesterone radioimmunoassay (Siemens Medical Solutions Diagnostics, Inc., Los Angeles, CA) [Brown et al., 2004a]. Females were considered cyclic if they exhibited normal estrous cycle ranges with an overall length of 14–16 weeks, a luteal phase length of 8–12 weeks and a follicular phase length of 4–6 weeks [Plotka et al., 1988; Hodges, 1998; Brown, 2000]. Some elephants exhibited irregular cycles with periodic short luteal phases (<8 weeks in duration) or prolonged nonluteal phases (>6 weeks in duration). However, because these elephants demonstrated luteal activity, they were categorized as "cycling." Elephants that maintained continuous baseline progestagen concentrations (<0.1 ng/mL), i.e. no luteal activity, were categorized as "noncycling" [Brown et al., 2004b].

Surveys and Data Collection

Three surveys were distributed to facilities with adult, female African elephants listed in the African Elephant Studbook [Olson, 2003]. Keepers with at least 6 months experience working directly with the elephants were asked to complete a temperament survey on each female to determine whether noncycling females across facilities share common temperament traits. Respondents were asked to complete questions that ranked each elephant on a social scale (Table 2). The elephant manager or SSP liaison at each facility was also asked to complete health and socio-environmental surveys [Freeman, 2005]. The health survey was designed to determine how the general health of the elephant (i.e. body condition and medical history) related to ovarian status. The socio-environmental survey was designed to investigate the relationship between captivity-related variables and ovarian activity. It was composed of questions related to (1) facility design; (2) elephant management; (3) changes within the herd (births, deaths and transfers) in the last 5 years; (4) number and experience of keeper staff; and (5) makeup of the elephant diet [Freeman, 2005].

For each elephant, age, number of herdmates, transfers between facilities and the length of time spent at the current facility were obtained from the Studbook [Olson, 2003]. Location and climate data, including longitude, latitude and elevation were downloaded for each facility from the NOAA National Climatic Data Centre (NCDC) website http://www.ncdc.noaa.gov/oa/ncdc.html. The 30-year (1971–2001) annual means for temperature and precipitation for each location were acquired from the NCDC [National Oceanic and Atmospheric Administration, 2001]. We used the 30-year means for temperature and precipitation because they reflect the trends for each region, where most elephants have spent their adult lifetime, rather than focusing on a specific year(s).

Data Analyses

A model was designed to determine the relationship between the survey variables and the ovarian activity. Model variables (Tables 1 and 2) consisted of factors that were significant in preliminary analyses [Freeman, 2005] as well as those that are of particular interest to captive elephant managers (Elephant Taxon Advisory Committee/Species Survival Plan). To determine changes in the herd structure over the 5 years before our analyses, we created an index of herd changes (“changes”) by adding the births and transfers in, and subtracting the deaths and transfers out (Table 2). The number of respondents completing the temperament surveys varied among facilities (range, 1–10). The inter-rater reliability on all temperament survey questions was assessed for each elephant that had two or more raters using Kendall’s coefficient of concordance (W), which tests for the degree of association among multiple raters [Lehner, 1996]. Survey questions in which concordance coefficients failed to reach statistical significance at a level of $P < 0.05$ for inter-rater reliability on a given elephant were excluded from further analyses. The mean survey score among raters for each elephant was used in subsequent data analyses. Descriptive statistics were run on all the variables. Variables that were highly skewed or displayed extreme kurtosis were analyzed for outliers using stem and leaf plots; outliers were removed from further analyses.

Principal components analysis (PCA) [Martin and Bateson, 1993] was used to reduce related variables (such as temperament and social history) to a few underlying factor scores that could be used for subsequent analyses in our model. Components with eigenvalues > 1 were retained for interpretation and labeled according to the variables that showed the highest loadings [Stevenson-Hinde et al., 1980; Gold and Maple, 1994; Wielebnowski, 1999]. The factor scores generated by the PCA were used in subsequent analyses. Spearman rank order correlation was used to determine the relationships among the model variables. To test for multicollinearity we regressed each variable in turn against all other independent variables. Variables with an $r^2 > 0.80$ and a variance inflation factor (VIF) > 4.00 have a high degree of collinearity and were excluded from the model. Once a list of independent variables that were free of collinearity problems was identified, logistic regression was used to determine the link between the captivity-related factors and ovarian acyclicity. Logistic regression allows for the prediction of the dichotomous dependent variable (i.e. noncycling or cycling) from one or more independent variables [Demaris, 1992].

TABLE 1. Definitions of questions and response options on questionnaires that were used to assess the temperament of ex situ female African elephants in North American zoos

Variable	Question	Response options
Aggression	Does this female act more aggressively or submissively towards the other females in her herd?	0 = Neither aggressive nor submissive 1 = Always submissive 2 = Usually submissive 3 = Depends on herdmate involved 4 = Equally aggressive and submissive 5 = Usually aggressive 6 = Always aggressive
Discipline	Does this female tend to dole out more discipline to the herd (act as a peacekeeper) or receive more discipline?	0 = Neither gives nor receives discipline 1 = Only receives discipline 2 = Receives more discipline than gives 3 = Depends on herdmate involved 4 = Gives and receives equally 5 = Usually gives more than receives 6 = Primary peacekeeper/chief disciplinarian
Enrichment	When presented with a new or preferred enrichment activity (toy) while in the presence of herdmates, this female typically	0 = Shows no interest 1 = Actively avoids object out of deference 2 = Waits until others are done with it 3 = Freely shares 4 = Resists sharing it 5 = Blocks others from it
Food	When presented with a new or preferred food item while in the presence of herdmates, this female typically	0 = Shows no interest 1 = Actively avoids food out of deference 2 = Waits until others are done 3 = Freely shares 4 = Resists letting other have some 5 = Blocks others from the food
Keeper	How does this female behave towards you?	0 = You do not work with this female 1 = Always acts submissive and subordinate 2 = Well-behaved 3 = Sometime defiant and/or misbehaves 4 = Generally defiant 5 = Tries to exert dominance over you
Obedience	How well does this female obey/listen to your commands?	1 = You do not work with this female 2 = Always obeys the first time 3 = Typically obeys quickly 4 = Commands must be repeated before obeys 5 = Rarely obeys commands
People	How does this female behave towards people other than her normal keepers?	1 = Timid and/or fearful 2 = Uninterested 3 = Interested by "minds her manners" 4 = Makes dominance displays 5 = Acts overtly aggressive

TABLE 1. Continued

Variable	Question	Response options
Status	The majority of the time, what is the status of this female within the hierarchy of the herd?	1 = Most subordinate 2 = Subordinate 3 = Middle 4 = Subdominant 5 = Dominant

TABLE 2. Additional questionnaire, climate, and studbook data acquired to predict the ovarian status of ex situ captive African elephants in North American facilities

Variables	Description
Age	Age of female (yr)
Births	Calves born into the herd within the last 5 years (#)
BMI	Body mass index of elephant (kg/m^2)
Deaths	Herdmates that died within the last 5 years (#)
Elevation	Elevation of the facility (m)
Females	Female herdmates (#)
Latitude	Latitude of the facility (°N)
Longitude	Longitude of the facility (°W)
Males	Male herdmates (#)
Management[a]	Management system (free or protected contact)
Moves	Times elephant has been transferred between facilities (#)
Precipitation	Mean annual precipitation (cm)
Temperature	Mean annual temperature (°C)
Together	Longest relationship with at least one other elephant at the facility (yr)
Transfers In	Herdmates added to the facility within the last 5 years (#)
Transfers Out	Herdmates that left the facility within the last 5 years (#)
Years	Time at the facility (yr)

[a]Categorical variable converted to binary responses: 1 = free and 0 = protected contact.

Statistical analyses were computed using SigmaStat (2004, v. 3.01.0, Systat Software, Inc., San Jose, CA) and SigmaPlot (2001, v. 7.1, Systat Software, Inc., San Jose, CA). Kolmogorov–Smirnov test was used to test for normality of the underlying population and the Levene Median test was used to measure for equal variances. All values were reported as mean $\pm$ SEM and statistical significance was assumed at a $P < 0.05$.

RESULTS

Fifty-four facilities completed at least one of the three surveys. More temperament than health or socio-environmental surveys were completed on each female (Table 3). Three hundred and seventy-six temperament surveys were received for 123 elephants, with an average of 3.1 ± 0.2 surveys per female. Health surveys were completed on 107 elephants at 45 facilities, whereas 49 socio-environmental surveys were returned describing the captive environment of 113 females (Table 3). All three surveys were returned from 46 facilities describing 106 females (64 cycling,

TABLE 3. Surveys received on North American female African elephants

	Surveys received			
Ovarian status	Temperament	Health	Socio-environmental	All three
Cycling	70	64	64	64
Noncycling	31	27	30	27
Undetermined	22	16	19	15
Total	123	107	113	106

Numbers indicate females surveyed that exhibit normal estrous cycles (cycling) and no ovarian activity based on serum progestagen analyses (noncycling), or whose ovarian status was not currently being evaluated (undetermined).

TABLE 4. Major components of individual behavioral variation (temperament variables) and studbook data (social history) of 123 captive African elephants at 54 North American facilities obtained through principal components analysis

	Temperament variables			Social history
	I "Herd"	II "Human"		I "History"
Aggression	0.80	0.15	Moves	−0.67
Discipline	0.82	−0.09	Together	0.84
Enrichment	0.90	−0.04	Years	0.86
Food	0.89	−0.02		
Keeper	−0.04	0.86	Eigenvalue	1.89
Obedience	−0.12	0.67	Variance (%)	63.08
People	0.17	0.65		
Eigenvalue	2.94	1.63		
Variance (%)	42.05	23.32		

27 noncycling and 15 undetermined). Because ovarian status was not known for the undetermined elephants, they were excluded from subsequent data analyses.

Tables 1 and 2 present the independent variables extracted from the surveys and the studbook that were used in our analyses. PCA of the temperament survey variables (Table 1) resulted in two components with eigenvalues >1 and accounted for 65.37% of variance in the data (Table 4). Temperament component I showed high loadings for interactions with herdmates and was named "herd." Temperament component II showed high loadings for interactions with people and was named "human." To determine the social history of each elephant at their current facility and with their current herdmates, PCA was conducted on the variable moves, together and years (Table 4), which resulted in one component with an eigenvalue >1 and accounted for 63.08% of variance in the data.

Many of the model variables on the social dynamics, population demographics and life history of elephants were significantly correlated ($P \leq 0.05$; Table 5). For example, age had a positive correlation to history and social status. History had a negative correlation to the number of males and changes to the herd structure. Females had a positive correlation to males and changes, but a negative correlation

TABLE 5. Spearman rank order correlation coefficients of the model variables

	BMI	Changes	Elev.	Females	Herd	History	Human	Lat.	Long.	Males	Manage.	Precip.	Status	Temp.
Age	0.21	−0.11	0.04	−0.03	0.17	0.55[b]	−0.16	0.17	−0.12	−0.13	−0.07	0.05	0.29[b]	0.01
BMI		0.00	0.07	−0.01	0.04	0.08	0.15	−0.14	−0.01	0.05	0.10	0.20	0.11	0.07
Changes			0.12	0.31[b]	0.05	−0.32[b]	−0.21[a]	−0.17	−0.17	0.46[b]	0.30[b]	0.28[b]	−0.00	0.00
Elev.				−0.02	−0.02	0.00	−0.11	0.39[b]	0.30[b]	−0.07	0.20	−0.27[b]	−0.04	−0.24[a]
Females					0.03	−0.08	−0.18	−0.35[b]	0.01	0.44[b]	−0.26[b]	0.20[a]	−0.12	0.30[b]
Herd						−0.02	−0.00	−0.00	−0.13	−0.05	0.06	0.09	0.78[b]	−0.03
History							0.03	0.15	−0.05	−0.26[b]	0.00	−0.05	0.04	−0.20[a]
Human								0.15	0.06	−0.09	−0.12	−0.17	−0.06	0.08
Lat.									0.12	−0.46[b]	0.32[b]	−0.40[b]	0.04	−0.13
Long.										−0.03	−0.11	−0.69[b]	−0.05	−0.17
Males											−0.22[b]	0.19	−0.04	0.17
Manage.												0.11	0.04	−0.32[b]
Precip.													−0.00	0.36[b]
Status														−0.14

Significant relationships are denoted by a letter.
[a] $P \leq 0.05$.
[b] $P \leq 0.01$.

TABLE 6. Multiple logistic regression coefficients (+SE) for survey and studbook variables that were related to ovarian acyclicity in captive African elephants

Variables	Estimate	SE	*t*-Ratio
Constant	2.50	6.495	0.39
Age	−0.06	0.10	−0.66
BMI	0.02	0.01	2.31*
Changes	−0.35	0.48	−0.73
Elevation	0.01	0.01	−1.05
Females	0.15	0.49	0.31
Herd interactions	0.05	0.16	0.34
History	1.35	0.68	1.98*
Human interactions	−0.46	0.50	−0.93
Latitude	−0.11	0.12	−0.90
Longitude	−0.07	0.04	−1.60
Management	0.56	1.36	0.41
Status	−0.04	0.45	−0.09
Temperature	−0.10	0.14	−0.61

*$P \leq 0.05$.

with management. Similarly, males had a negative correlation with management, but a positive correlation with changes. Lastly, herd interactions had a positive correlation with social status.

Many of the location and climate variables were significantly related to each other ($P \leq 0.05$), as well as to the demographic and social variables (Table 5). Latitude was negatively correlated to precipitation, females and males, and positively correlated to elevation and management. Longitude had a negative correlation with precipitation and a positive correlation with elevation. Elevation was negatively correlated to temperature and precipitation. Lastly, temperature had a positive correlation with precipitation and females, but a negative correlation with history and management.

Given the number of correlated variables within our model, we ran multiple linear regressions of each variable against all of the other independent variables to test for multicollinearity. Regression of the variable males had an $r^2 = 0.82$. Males also had a VIF > 4.00 when regressed as an independent variable against the dependent variables of age, body mass index (BMI), herd, people, social rank, latitude, longitude, elevation, temperature, precipitation, management and history (everything except females and changes). Regression of precipitation had an $r^2 = 0.82$. Similar to males, precipitation had a VIF > 4.0 when it was regressed as an independent variable against the dependent variables of age, BMI, females, herd, people, social rank, latitude, elevation, temperature, precipitation, management, changes and history (everything except longitude). Linear regression of all of the other model variables had $r^2 < 0.80$. We removed males and precipitation from the model and reran the multiple linear regressions. All of the remaining variables had $r^2 < 0.80$ and VIF < 4.0.

To determine what contributed the most to the occurrence of ovarian acyclicity a multiple logistic regression was run on the remaining model variables (Table 6). The model was significant ($\chi^2 = 25.75$, d.f. = 13, $P < 0.05$) and had a relatively strong fit ($r^2 = 0.47$). History and BMI were the only significant variables in the multiple logistic model ($P < 0.05$) and they were both positively related to a female being acyclic.

DISCUSSION

Surveys of the captive African elephant population identified several variables that were related to the occurrence of ovarian acyclicity. Results demonstrate that physical size and social history of captive African elephants have a relationship with ovarian acyclicity. Our model suggests that females with a higher BMI and those that have moved less frequently between facilities and have longer relationships with cohorts are more likely to be acyclic.

BMI was the only health variable related to acyclicity, suggesting that some noncycling elephants may be overweight. Obesity has been related to reproductive dysfunction in humans [Pasquali et al., 2003], horses [Vick et al., 2006], bats [Chanda et al., 2003], sheep [Christman et al., 2000] and rats [Marin-Bevins and Olster, 1999]. In humans, obese women are more likely to have irregular cycles or chronic anovulation and have increased risks of miscarriage, pre-term delivery and maternal death [Pasquali et al., 2003]. The exact mechanism by which excess weight negatively affects reproduction is not well understood [Grodstein et al., 1994; Pasquali et al., 2003] and likely is species-specific. Obesity acquired through overeating can have a direct effect on reproduction, or obesity may be related to a more complex metabolic disorder that results in energy being stored in adipose tissue rather than being available for other bodily functions, such as reproduction [Wade et al., 1996]. One reason to suspect that obesity may not be because of simple overeating is that weight loss has varied effects on reinitiating normal estrous cycle activity. In women, losing excess weight can improve fertility and facilitate conception [Bray, 1997; Clark et al., 1995; Norman et al., 2004; Pasquali et al., 2003]. However, in other species, feed restriction does not alter estrous cycle activity [horses, Vick et al., 2006; Zucker rats, Marin-Bevins and Olster, 1999]. These latter studies suggest that excess body weight may not cause reproductive dysfunction per se, but rather may only be a contributing factor [Wade et al., 1996; Marin-Bevins and Olster, 1999; Vick et al., 2006]. Because of species differences in the relationship between weight and reproduction, interpretation of the finding of higher BMI associated with ovarian acyclicity in elephants should be done cautiously. Regardless of whether acyclicity in elephants is because of a direct or indirect effect of increased BMI, however, it makes sense to control the weight of zoo elephants. It also will be necessary to determine whether captive elephants become overweight because of an improperly balanced diet [Hatt and Clauss, 2006], overeating or metabolic disorders that impact energy storage of adipose tissue [Wade et al., 1996].

The significant, positive relationship between social history and ovarian acyclicity suggests that females maintained for long-term at a facility with the same herdmates are more likely to be acyclic. Sociality is an important factor for wild female African elephants that live in strongly bonded family groups of related cows. Each individual holds a social status based on her age, size and individual disposition [Dublin, 1983; Thouless, 1996; Archie et al., 2006] and the largest, eldest female in the group is the matriarch and she is crucial to family survival [Douglas-Hamilton, 1972; Poole and Moss, 1989; Archie et al., 2006]. Bull elephants leave their family group in their teens (12–15 yr of age) and then live either alone or in small bachelor groups [Poole, 1987]. Because of the fission–fusion society, social groups are dynamic and change daily and seasonally, even though the family unit remains stable [Poole and Moss, 1989; Wittemyer et al., 2005]. Matriarchs are crucial to herd survival because of their knowledge of natural resources and coordination of herd defense [Douglas-Hamilton, 1972; Dublin, 1983; McComb et al., 2001; Poole and Moss, 1989].

In some aspects, captive elephant social groups resemble those in the wild. Females are traditionally housed together and most males are removed from the herd at a relatively young age [Schulte, 2000]. Many behaviors of captive elephants also resemble those of their wild counterparts [Adams and Berg, 1980; Garai, 1992; Schulte, 2000]. There are some major differences, however. Captive herds are traditionally composed of unrelated females often of similar age; thus, there is no age-ordered hierarchy of related individuals. Additionally, most captive individuals have limited contact with new females, calves or males [Schulte, 2000], and most females are nulliparous. Thus, the majority of elephants within captive herds have not had the opportunity to acquire social knowledge based on the range of behavioral interactions normally found in the wild, which may explain why creating long-term social bonds by maintaining females together within small, captive groups throughout their lifetime seems to increase the tendency for some females to become acyclic. Although this finding suggests that keeping captive elephants together for a long time may be detrimental to fecundity, we believe that social stability is vital to captive elephant welfare. The challenge then is to design a management strategy that will maximize breeding success among reproductive-aged cows without compromising herd stability.

Analyses of previous temperament surveys demonstrated that dominant females tend to be acyclic [Freeman et al., 2004]. In this study, at all but two of the 21 facilities that housed both cycling and noncycling elephants, the dominant female was acyclic. Without long-term studies on captive elephants exposed to different socio-environmental changes, it may be impossible to establish a cause and effect relationship among these trends. Still, these data are the first to link social history with a specific reproductive problem in elephants.

In many mammalian species, dominant females often use social interactions to suppress reproduction in subordinates [e.g. Packard et al., 1985; Faulkes et al., 1990; Creel et al., 1992]. Whether reproductive suppression is important in free-ranging African elephants is not clear. It has been suggested that dominant females use aggressive behaviors to suppress subordinates when resources are limited [Sikes, 1971; Dublin, 1983], but this has yet to be systematically tested. Physiological and demographic analyses show that reproductive rates of African elephants decline with age [Laws et al., 1970; Smuts, 1975; Moss, 2001; Freeman et al., 2008] and as they reach matriarchal status (B. Archie, Amboseli, data unpublished). Density and behavioral mechanisms can cause older females to reach reproductive senescence at an earlier age in the wild [Laws, 1969; Laws et al., 1970]. It is not known whether the decline in fertility in older wild elephants is because of social pressures or reproductive senescence. If it is socially mediated, such an adaptation may explain why so many older, dominant females are not cycling in captivity. Necropsies of an elephant culled in Kruger National Park, South Africa, revealed that many females over 50 years of age have inactive ovaries; i.e. no follicle, corpus luteum or corpus albicantia [Freeman et al., 2008]. Although it seems likely that these older females were no longer cycling, systematic studies of endocrine activity have not been monitored in free-ranging matriarchs. If some older females do stop cycling once they reach matriarchal status, it could be functionally similar to what occurs in the North America population, albeit at a younger age.

An examination of environmental conditions found no significant effect of facility location or climate on ovarian cyclicity status. In the wild, seasonal and annual fluctuations in rainfall and the availability of quality browse affect African elephant social behaviors, coordinate herd movements [Wittemyer, 2001; Wittemyer et al., 2005] and influence birth rates [Laws et al., 1970; Foley et al., 2001; Moss, 2001; Wittemyer, 2001; Wittemyer et al., 2007b]. Additionally, decreased seasonal precipitation causes a decrease in the availability of browse and causes reductions in progestagen concentrations in pregnant cows [Foley et al., 2001; Wittemyer et al., 2007a]. It is not expected that seasonal fluctuations in precipitation similarly affect captive elephants because they are provided regular allocations of food and water year round [Schulte, 2000].

In recent years, questions have been raised about whether elephants should be kept in zoos in northern latitudes because of harsh climates. To date, there is little scientific evidence to support this belief. In fact, wild African elephants are known to be highly adaptable to a wide range of temperatures, altitudes, latitudes and terrains, and can withstand extreme conditions such as drought or heat waves for considerable lengths of time [Sikes, 1971]. One study of African elephants at a zoo in Rhode Island found a higher incidence of temporary ovarian inactivity during some winter months [Schulte et al., 2000]. The authors speculated that it was because of increased time spent indoors and exposure to indoor contaminants and/or pheromones. However, results of our multi-institutional study found no relationship between ovarian acyclicity and facility latitude or mean annual temperature, both of which are correlated with time spent indoors in the winter [Freeman, 2005].

Multivariate, multi-institutional studies of other exotic species have demonstrated that social and management factors contribute to breeding success [Carlstead et al., 1999a,b; Mellen, 1994; Wielebnowski, 1999; Wielebnowski et al., 2002]. In addition, knowledge acquired from these types of studies has been used to change management practices [Wielebnowski et al., 2002]. One encouraging finding from this study is that acyclicity does not appear to be a permanent condition in captive African elephants [Hermes et al., 2004; Schulte et al., 2000]. There now are several examples of noncycling females that resumed cycling, either after a transfer or alteration in the herd dynamics (Brown, unpublished). Unfortunately, there also are cases of cycling females that shut down reproductive cyclicity after similar changes.

Results of this study suggest that there are a few changes captive managers can make to return acyclic females to the breeding pool. Reducing the weight of young, acyclic cows may be an important first step to reinitiating normal ovarian cycle activity. Although there has been some reluctance to moving individuals in the past because it might disrupt the captive unit, survey data suggest that transferring elephants should not affect long-term cyclicity status. One possibility might be to create herds that contain an older, nonreproductive-aged female that acts as the noncycling matriarch, allowing younger females to cycle normally. That could potentially maximize reproductive potential within the herd without compromising social stability. For those facilities reluctant to move animals, it might be efficacious to use hormone treatments to stimulate normal ovarian activity, although none have been proven to be effective as yet [Brown et al., 2004a].

CONCLUSIONS

1. Multiple logistic analyses suggest that social history is related to ovarian acyclicity in captive African elephants. Acyclic elephants are more likely to have long-term social relationships with their captive herdmates and facilities. These results suggest that transferring elephants between facilities should not negatively affect cyclicity status.
2. The majority of acyclic females hold a dominant social status within the herd.
3. BMI was the only health-related factor associated with ovarian acyclicity. Controlling weight of acyclic elephants may help reinitiate normal cyclicity.

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