Noninvasive Stress and Reproductive Measures of Social and Ecological Pressures in Free-Ranging African Elephants

C. A. H. FOLEY,* S. PAPAGEORGE,† AND S. K. WASSER†‡

*Tarangire Elephant Project, P.O. Box 2703, Arusha, Tanzania
†Center for Conservation Biology, Department of Zoology, University of Washington
School of Medicine, Box 354693, Seattle, WA 98195, U.S.A.

Abstract: *The African elephant (*Loxodonta africana*) experienced a poaching-related 60% population decline between 1979 and 1988 that was inordinately concentrated on adults. This, coupled with political pressures to delist the elephant, has created a need for noninvasive physiological measures that can quantify the long-term effects of past mortality patterns of this long-lived species. We collected fresh fecal samples from 16 female elephants in three different groups over 23 months at Tarangire National Park, Tanzania, and analyzed them for fecal progesterone and cortisol metabolites. Social and ecological measures were collected concurrently. Fecal progesterone metabolite measures corresponded significantly with stage of gestation, and appear to be able to confirm pregnancy in female elephants from as early as 3 months of gestation. We found that progesterone metabolite concentrations were significantly lower during the dry season than during the wet season after controlling for stage of gestation. Fecal cortisol metabolite concentrations showed the opposite seasonal pattern, being significantly higher in the dry season and inversely correlated with rainfall across seasons. Fecal cortisol metabolite concentrations also increased with group size and were correlated positively with dominance rank in the largest group. Our results suggest that measures of progesterone and cortisol metabolites in feces provide indices of reproductive function and physiological stress that can quantify both natural and human disturbances in African elephants. These measures are ideally suited for monitoring the long-term effects of social disruption from poaching and a variety of other management concerns.*

Estrés No Invasivo y Medidas Reproductivas de Presiones Sociales y Ecológicas en Elefantes Africanos Libres

Resumen: *Debido a la cacería furtiva, la población de elefante africano (*Loxodonta africana*) declinó en un 60%, principalmente adultos, entre 1979 y 1988. Esto, aunado a presiones políticas para eliminar al elefante de las listas de especies en peligro, ha creado la necesidad de medidas fisiológicas no invasivas que puedan cuantificar efectos a largo plazo de patrones de mortalidad en el pasado de esta especie longeva. Recolectamos muestras fecales de 16 elefantes hembras en tres grupos diferentes en el Parque Nacional Tarangire, Tanzania a lo largo de 23 meses, y las analizamos para detectar metabolitos de progesterona fecal y de cortisol. Al mismo tiempo se recolectaron medidas sociales y ecológicas. Las medidas de metabolitos de progesterona fecal correspondieron significativamente con la etapa de gestación, y parecen permitir la confirmación de preñez en elefantes hembras tan temprano como a los tres meses de gestación. Las concentraciones de metabolitos de progesterona fueron significativamente menores durante la época de sequía que en la de lluvias después de controlar para la etapa de gestación. Las concentraciones de metabolitos de cortisol fecal mostraron un patrón estacional opuesto, siendo significativamente más altas en la época de sequía e inversamente correlacionados con la precipitación en todas las estaciones. Las concentraciones de metabolitos de cortisol fecal también incrementaron con el tamaño del grupo y se correlacionaron positivamente con el rango de dominancia en el grupo más grande. Nuestros resultados sugieren que las medidas de metabolitos de progesterona y cortisol en las heces proporcionan índices de la función reproductiva y del estrés fisiológico*

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‡*Address correspondence to S. K. Wasser, email wassers@u.washington.edu*

Paper submitted October 29, 1999; revised manuscript accepted November 22, 2000.

que puede cuantificar perturbaciones, tanto naturales como humanas, en elefantes africanos. Estas medidas son idealmente adecuadas para monitorear efectos a largo plazo de la disrupción social por la cacería furtiva y así como una variedad de aspectos del manejo.

Introduction

Environmental disturbance is a major cause of population decline in endangered species (Wilson 1988). But mitigation remains difficult because, to date, there has been a dearth of early warning measures that can definitively demonstrate such effects. Frequently, environmental disturbances are demonstrated when it is too late to contain the damage. Noninvasive physiologic measures of the effects of environmental disturbances could change this, enabling disturbance effects to be readily quantified early in the event and efficiently tracked over time. Few circumstances illustrate the need for such measures better than the biology and politics surrounding the trade ban on African elephant (*Loxodonta africana*) ivory. We examined previously validated fecal progesterone and cortisol metabolites (Wasser et al. 1996, 2000) as correlates of reproductive function and physiological stress associated with social and ecological disturbances in free-ranging African elephants. Our results suggest that these measures should prove highly useful as indices of environmental disturbance in this species.

The African elephant was subjected to heavy poaching during the late 1970s and 1980s. During this period, population numbers showed an alarming decrease from 1.3 million to approximately 500,000 individuals (Douglas-Hamilton 1987). This prompted the Convention on International Trade in Endangered Species (CITES) to list the African elephant as an Appendix 1 species, banning all international ivory sales. At the same time, several southern African nations continued to have problems associated with overcrowding of elephants and argued for the need to reduce population densities by culling (Pienaar 1983). The expense of these culling operations has put pressure on CITES to allow the latter countries to sell their ivory to offset the cost of culling. This has led to concerns that relaxing the ivory-trade ban would once again promote large-scale poaching in other countries, at a time when elephants have yet to recover from the social disruption of a 60% poaching-related population decline that was heavily concentrated on adults (Poole 1989).

These concerns make it increasingly important to assess the degree to which different populations are experiencing the long-term effects of poaching and other disturbances. Such information directly bears on the effects of relaxing the ivory ban. The ability to determine the effect of human and natural disturbances on elephant populations has thus far been restricted to the observation of behavioral indicators (Whyte 1993) and long-term demographic changes (Moss 1988; Abe 1994). More rapid quantitative measures are needed to address these critical management concerns. Here we describe the potential for using fecal progesterone and cortisol metabolite measures (Wasser et al. 1996, 2000) to these ends. We also provide the first complete profiles of progesterone and cortisol metabolites over the entire gestation period of free-ranging African elephants.

Methods

Study Area and Population

The 2600-km^2 Tarangire National Park (lat. 3° 40′E–5° 35′S long. 35° 45′–37′E) has an annual rainfall of 600 mm distributed almost entirely during the wet season (early wet, December–February; late wet, March–May; early dry, June–August; late dry, September–November). The Tarangire elephants increased from 440 in 1960 (Lamprey 1962) to 2000 in 1996 (Tarangire Conservation Project 1997). This increase was caused by immigration of elephants from peripheral populations into the relative safety of the park, a refuge from poaching during the 1970s and 1980s. Most of these elephants have become permanent or semipermanent residents, forming three separate subpopulations that use different areas of the park. We focused on the northern subpopulation in which over 300 individual elephants, representing 32 family groups, were individually identified from ear patterns (C.A.H.F., unpublished data). This represents all the animals in the northern subpopulation. We collected fecal samples over 2 years from all females in three family groups. The largest group (A) had an intact age structure, and two smaller groups had altered age structures characteristic of poaching (Poole 1989). The large group had eight adult females (group total of 16), including two females over 35 years of age. The two smaller groups had five (Si group) and three (I group) adult females, respectively (group totals, 16 in Si and 9 I), with no females over 30 years of age. We considered females over 10 years of age to be adults.

Female Reproductive Status

We determined the reproductive status of all pregnant and preconceptive females at the time of sample collection retrospectively by back dating 660 days (Laws et al. 1975; Moss 1988) from the observed time of parturition to determine stage of gestation, conception date, or preconceptive status. The dates of all births for the study animals were accurately recorded. Not all pregnancies were monitored completely, however, because some females had conceived prior to the onset of the study and others gave birth after the end of the hormone study period.

The minimum interval between calving and the next conception is approximately 1 year (Laws et al. 1975). Because females lactate until their next conceptive cycle (Spinage 1994), we classified samples as preconceptive during the 16 weeks prior to conception (equivalent to one estrous cycle; Wasser et al. 1996). Of the 28 females that had previously given birth, whose time of parturition had been accurately noted between 1993 and 1996, only one did not conceive on her first postpartum estrus cycle. In a small number of cases, samples were collected at the time of observed estrus.

All females except one gave birth during the period of the extended study. No nonconceptive cycles were recorded, and only one female, who was deemed infertile, failed to conceive during the study period.

Sample Collections and Analyses

Fresh fecal samples were collected from each individual approximately once every 3–4 weeks. The sampling interval was deemed sufficient given the 16-week estrous cycle (Wasser et al. 1996) and 22-month gestation (Laws et al. 1975; Moss 1988) of the African elephant; it generated 22 ± 2.24 SE samples per female. The entire fecal dropping was thoroughly mixed to assure an even distribution of hormones (Wasser et al. 1996). Approximately 100 g of the mixed sample was then stored in a 2.5:1 ratio of 90% ethanol (as a preservative) per gram of feces and subsequently analyzed for progestins and glucocorticoid metabolites as described by Wasser et al. (1996, 2000). For each sample, parasites visible to the naked eye were recorded as present or absent.

All hormone measures were expressed per gram of dry weight, because this has been shown to control for diet-related changes in hormone-excretion rates (Wasser et al. 1993). Sample processing and extraction procedures were initially optimized in two ways. Radiolabel infusion of C14-progesterone and H3-estradiol demonstrated a 30-hour lag between secretion of steroid hormones in blood and their excretion in feces. These studies also demonstrated the need to thoroughly mix the large fecal mass prior to subsampling for freeze drying (lyophilization) and to mix the sifted lyophilized feces prior to subsampling for extraction to assure that hormones are distributed evenly in all subsamples. Comparison of matched fecal and serum samples demonstrated that processing samples in this manner produced profiles of fecal progesterone metabolites that corresponded nicely with profiles of serum progesterone and hence satisfactorily characterized reproductive function in the African elephant (Wasser et al. 1996).

We used the ICN I125 corticosterone assay (Costa Mesa, California) to measure glucocorticoid metabolites, following validation through an adrenocorticotropin hormone (ACTH) challenge (Wasser et al. 2000). The ACTH induces the adrenal gland to rapidly release cortisol into the bloodstream; the resultant peak in cortisol metabolites should be measured in feces 30 hours later, given their excretion lag time (Wasser et al. 1996, 2000). In both individuals, ACTH injection produced a four- to five-fold rise in serum cortisol; a comparable rise was also found in fecal cortisol metabolites measured by the ICN I125 corticosterone assay, delayed, as predicted, by the 30-hour steroid excretion lag time (Wasser et al. 1996, 2000). Thus, the ACTH challenge study demonstrated that our fecal corticosterone measures provide a reliable measure of the glucocroticoid stress response in the African elephant.

Population and Ecological Measures

Data were systematically collected on rainfall, group composition, body condition, demographic changes, and aggressive interactions within and between groups of African elephants. Body condition was established by assessing the degree of concavity around the elephant's lumbar depression and scapular area. Based on studies of culled animals, the lumbar depression has been shown to be a potentially useful indicator of body condition in elephants, corresponding well with the kidney fat index and increasing in depth during the dry season across all sex and age classes (Albl 1971). We used the following index, from the worst to the best condition: (1) animal emaciated, as exhibited by clearly protruding bone structures around face, ribs, ilium and pelvis; (2) ribs no longer visible, but depression around wing of ilium and lumbar region clearly apparent, highly concave skin on pelvis area; (3) depression around wing of ilium and lumbar depression clearly visible, with skin on pelvic area shallowly concave; (4) lumbar depression flat or broadly convex and wing of ilium barely visible; and (5) scapular and pelvic bones not visible. The dominance status of females within and between family groups was determined through a combination of individual focal, group focal, and opportunistically collected behavior samples. We conducted 20-minute focal samples on each adult female in the three groups, recording all feeding behavior and aggressive interactions initiated and received on a monthly basis over a period of 3 years. In addition to individual focal sampling, we made focal samples of the entire family group for at least 1 hour each month, and we collected observations of all other aggressive interactions between females on an opportunistic basis.

Aggression data collected during feeding were supplemented by data collected at waterholes. At the beginning and middle of the dry season, elephant groups congregate in large herds at subterranean river sites to drink from carefully excavated water holes, which provide a source of much competition among females. Three areas in the park were used regularly by elephants for drinking and offered good vantage points from which all elephants entering the river could be watched. At times when elephant herds were congregating in these areas, all-day focal samples were conducted from various vantage points. We recorded the identity and time of elephants entering and leaving the river, as well as observed aggressive interactions.

We used the following aggression scale, ranging from mild to severe: (1) aggressor walks toward recipient; (2) aggressor walks with ears spread out or flaps ear outward toward the recipient or gives a headshake toward the recipient; (3) aggressor raises its head and spreads its ears out toward the recipient; (4) aggressor raises its head to the recipient, spreads its ears out, and folds them horizontally across the center; (5) aggressor walks fast with head up and ears spread out and folded; lunges at or hits recipient; (6) aggressor runs toward and chases recipient; (7) aggressor chases and tusks recipient, or fights recipient. In all cases, the individual that retreated in response to an act of aggression was termed the subordinate. Between-group hierarchies were determined by dominance interactions in which the matriarch of the subordinate group was displaced.

Statistical Analyses

We analyzed progesterone and cortisol metabolite concentrations by stage of gestation using linear and quadratic regression analyses. Linear regression was also used to examine the relation between progesterone and cortisol metabolites over time. We used hierarchical multiple-regression analyses to examine hormone concentrations in relation to group size, dominance status, season, and body condition among study subjects, after we controlled for stage of gestation. Analysis of variance was used to further examine differences within family groups.

Results

Demography, Body Condition, and Dominance

Demographic data on time of parturition for the entire subpopulation were collected from recorded births ($n = 82$) and combined with projected birth dates from recorded estrus events ($n = 67$), based on a standard gestation period of 22 months (Laws et al. 1975). A strong positive correlation was found between parturition and mean monthly rainfall ($F = 28.1$ $r^2 = 0.738, p < 0.0003$), with 72% of all births occurring during the wet season ($G = 15.99, p < 0.0001$; Fig. 1). Mean body-condition indices were significantly lower during the dry season (3.3 ± 0.032) than the wet season (4.01 ± 0.019; $t = -19.1, p < 0.0001$). Early dry season mean body-condition scores (3.8 ± 0.034) were significantly lower than wet-season scores (Fisher's PLSD, $p < 0.0001$), whereas mean body scores from the late dry season (2.8 ± 0.04) were lower than those in all other seasons (Fisher's PLSD, $p < 0.0001$).

Combining data from all sampling methods, we recorded 82 within-group dominance interactions in A group, 51 in Si group and 34 in I group. Within-group dominance hierarchies were exclusively size-based, with the largest animal always winning. No reversals were noted, demonstrating a highly linear dominance hierarchy within elephant groups. Between-group hierarchies were also predominantly dictated by the size of the matriarch. Group A had the largest female in the population and consequently enjoyed the highest status. This group suffered no intergroup displacements during 28 interactions with other matriarchs. Group Si was ranked sixteenth of 31 family groups based on 23 intergroup displacements, whereas group I ranked twenty seventh from 13 intergroup displacements.

Endocrine Concentrations

Progesterone metabolite concentrations showed significant linear ($r = 0.61$; $p < 0.0001$) and quadratic ($r = 0.78$; $p < 0.0001$) patterns as a function of day of gestation (Fig. 2). Mean progesterone metabolite concentrations increased gradually from 562 ± 60 ng/g prior to pregnancy to 1662 ± 309 ng/g during the first 50–100 days of gestation; they peaked at 2817 ± 242 ng/g dur-

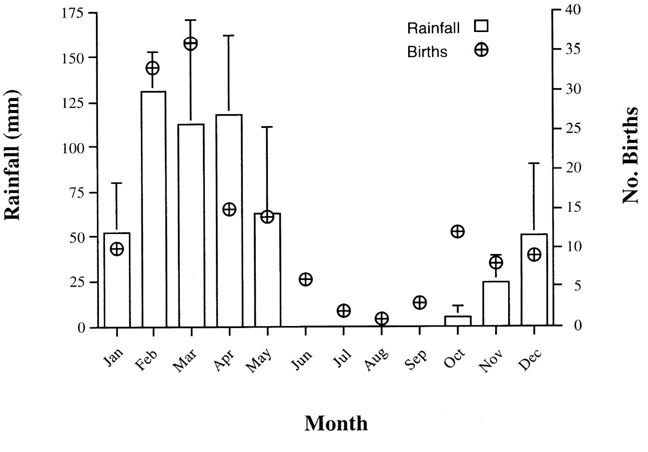

*Figure 1. Number of African elephant (*Loxodonta africana*) births by mean monthly rainfall.*

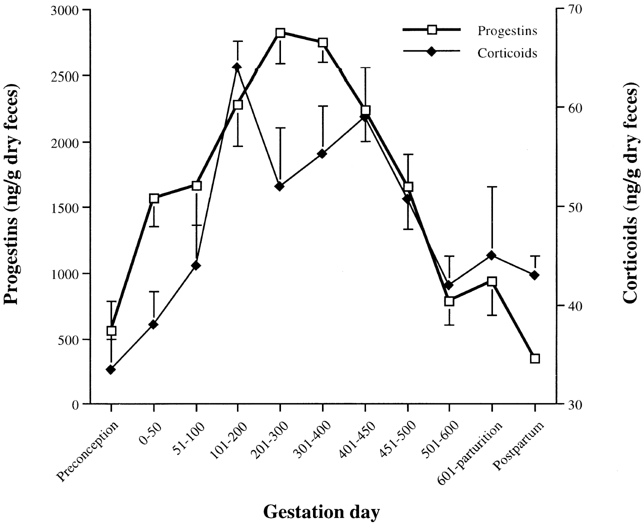

*Figure 2. Mean (±SE) fecal progesterone (progestins) and cortisol (corticoids) metabolite concentrations throughout gestation for 16 wild female African elephants (*Loxodonta africana*).*

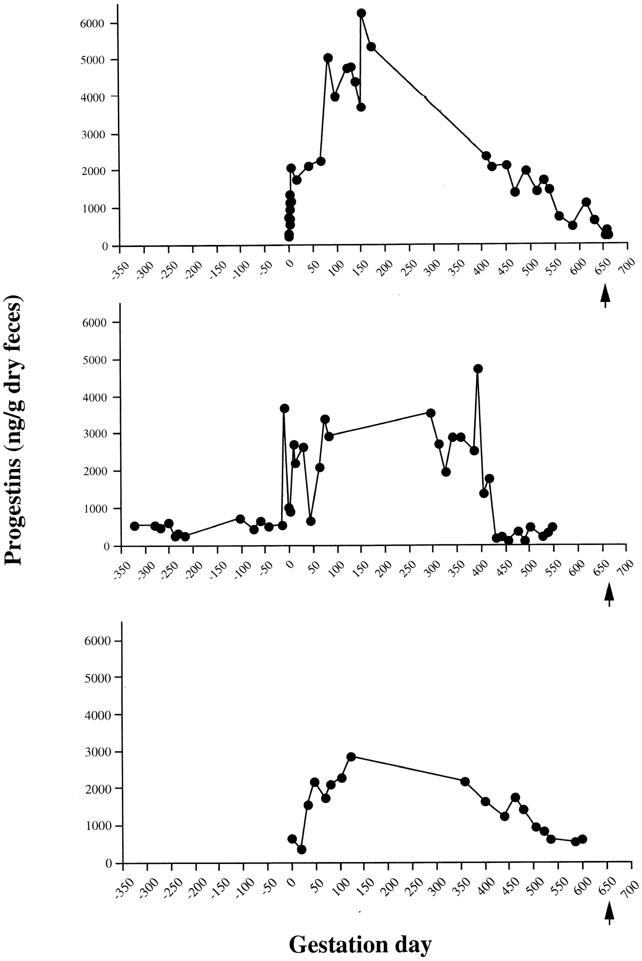

*Figure 3. Progestin concentrations throughout gestation for three female African elephants (*Loxodonta africana*). Arrow indicates day of parturition.*

ing days 200–300 of gestation, declined slightly to 2462 ± 121 ng/g during gestation days 300–450, and then dropped sharply to 789 ± 183 ng/g from around month 17 of gestation (500–660) until parturition. The characteristic drop in progesterone metabolite concentrations below 1000 ng/g in the last trimester of pregnancy ranged from day 400 to day 550 of gestation across females. These temporal patterns were remarkably similar between individuals but differed in absolute concentrations (Fig. 3). Progesterone metabolite concentrations were significantly lower in the dry season than in the wet season after we controlled for day of gestation ($t = 2.94$, $p < 0.003$). Further subdividing the wet and dry seasons into early and late portions revealed significantly lower progesterone metabolite concentrations in the late dry season than during any other season ($t = 2.58$, $p = 0.01$ for late dry versus early wet season; $t = 4.06$, $p < 0.0001$ for late dry versus late wet season; $t = 3.55$, $p < 0.0005$ for late dry versus early dry season). Progesterone and cortisol metabolite concentrations were positively correlated with each other during gestation ($t = 4.22$, $p < 0.0001$; Fig. 2). For the entire regression model predicting progesterone metabolite concentrations, $r^2 = 0.48$ ($p < 0.0001$).

Cortisol metabolite concentrations were significantly associated with socioecological pressures (season and group size) after we controlled for the significant association between cortisol metabolites and day of gestation ($t = 2.68$, $p < 0.007$) and cortisol and progesterone metabolites ($t = 5.45$, $p < 0.0001$) in a hierarchical multiple-regression analysis. Cortisol metabolite concentrations were significantly correlated with season ($t = 6.85$, $p < 0.0001$), with the highest concentrations in the dry season (Fig. 4). Subdividing season into early and late periods did not increase the amount of explained variance in cortisol metabolite concentrations. The cortisol metabolite concentrations during the dry season that followed the low-rainfall wet season of 1995 were significantly higher than those during the dry season that followed the high-rainfall wet season of 1996 ($t = 3.42$, $p < 0.0008$). Similarly, cortisol metabolite concentrations were significantly higher during the low-rainfall wet season of 1995 than were those during the high-rainfall wet season of 1996 (unpaired t test, $t = 3.26$, $p < 0.001$; Fig. 4). Cortisol metabolite concentrations were also positively correlated with group size, with the largest group having higher concentrations than the two smaller groups ($t = 2.7$, $p < 0.006$). This difference was apparent only during the dry season, when overall cortisol metabolite concentrations were highest. For the entire regression model predicting cortisol metabolite concentrations, $r^2 = 0.24$ ($p < 0.0001$). Cortisol metabolite concentrations were significantly correlated with behav-

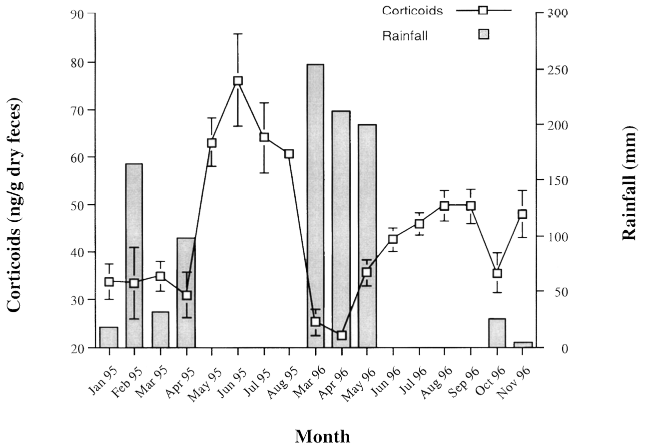

*Figure 4. Mean (± mean SE) corticoid concentrations for 16 wild female African elephants (*Loxodonta africana*) matched to monthly rainfall data.*

ioral measures of dominance in the largest group ($t = 3.6$, $p < 0.0005$), where cortisol metabolite concentrations were highest among the lowest-ranking females. This relationship failed to reach significance in the two smaller groups.

Large numbers of 1-cm-long white nematodes were found in the feces of five animals. The corresponding samples of these individuals also exhibited the highest peaks in cortisol metabolites recorded over the entire study period.

Discussion

Effects of environmental disturbances are difficult to quantify in long-lived, slowly reproducing species such as elephants because many events may transpire before the survival and reproductive consequences of the disturbances actually appear. Noninvasive physiological measures can help resolve these problems by providing tools to temporally link the disturbances to their physiological effects (Wasser et al. 1996). The results of our study demonstrate the potential utility of such tools for elephant conservation and management.

Both progesterone and cortisol metabolite concentrations were positively correlated with stage of gestation and with each other, as also occurs among other mammals (Carr et al. 1991; Kriesten & Murawski 1988; Lockwood et al. 1996; Mulay et al. 1973). After we controlled for these relations, however, progesterone and cortisol metabolites showed opposite correspondences with rainfall. Progesterone metabolite concentrations (which correspond to reproductive function) decreased, whereas cortisol metabolite concentrations (which correspond to physiological stress) increased during the dry season as food, water availability, and body condition declined. Moreover, the seasonal decline of progesterone metabolite concentrations was particularly pronounced during the harshest portion of the dry season, when food, water availability, and body condition were again at their lowest. These season-related results cannot be explained by dietary effects on fecal hormone excretion because (1) expressing hormone concentrations per gram of dry weight controls for most diet-related effects on hormone excretion (Wasser et al. 1993), and (2) progesterone and cortisol metabolite concentrations changed in opposite directions in response to season. Therefore, the seasonal progesterone and cortisol metabolite patterns suggest that both reproductive function and physiological stress are being affected negatively by limited access to food and water.

These conclusions are also consistent with the associated decline in body condition during the dry season. Elephant diet changes seasonally from high-quality grass in the wet season to less nutritious and more sparsely distributed leaves and bark in the dry season (Western & Lindsay 1984; Spinage 1994). Inter-individual feeding distances within elephant groups also increase during the dry season (Foley, personal observation). That cortisol metabolite concentrations were correlated positively with group size, but only during the dry season, suggests that intragroup competition may play a precipitating role. This possibility was further supported by the correlation between dominance and cortisol metabolites in our largest study group, with the most subordinate individuals having cortisol metabolite concentrations almost double those of the highest ranking individuals.

Other studies have shown that reproduction among female elephants is influenced strongly by environmental variables (Moss 1988). During a severe drought in Tarangire in 1993, only 9% of the potentially available females conceived; this figure rose to 70% the following year after heavy rains. These observations, combined with results from our study, suggest that female progesterone metabolite levels are highly responsive to environmental conditions, compromising implantation or early pregnancy during severe drought. Studies among other mammalian species have also linked poor body condition to reduced progesterone metabolites levels, both of which can be detrimental to gestation (O'Leary et al. 1996). Increases in cortisol with declining nutritional intake and body condition have been noted in a number of other mammalian species as well (Saltz & White 1991; Delguidice et al. 1992; Tsuma et al. 1996).

Several conservation and management implications can be drawn from our study. First, fecal progesterone metabolite concentrations can be used to confirm pregnancy noninvasively and to estimate the onset of parturition in free-ranging elephants. Two consecutive fecal progesterone metabolite samples of >1000 ng/g dry feces, collected at 60-day intervals, should be sufficient to distinguish pregnant from nonpregnant females through the first 15 months of gestation. Only 2 of our 93 samples of nonpregnant female elephants in Tarangire had fecal progesterone metabolite concentrations over 1000 ng/g dry weight. There is individual variation in the time and degree that progesterone metabolite levels rise following conception, and pregnancy may thus be confirmed at a much earlier stage in some individuals. Although progesterone metabolite concentrations fall below 1000 ng/g beyond month 15 of gestation, visible cues—enlargement of the breasts and visible signs of swelling around the lumbar region as parturition approaches (Moss 1988)—should be sufficient to distinguish pregnant from nonpregnant females during the third trimester. When coupled with progesterone metabolite concentrations below 1000 ng/g, these visible pregnancy cues should also predict the occurrence of parturition within a 100- to 200-day period. Such indices could allow rapid, noninvasive assessment of reproductive condition among free-ranging elephant herds during surveys (e.g., Berger et al. 1999). In the past, these data have been extremely difficult to collect. Investigators have simply tallied the number of newborn infants and projected the reproductive condition of elephants 2 years prior to the survey (given the 22-month gestation period). Such data are distorted easily by miscarriages, early infant mortality, and changing environmental conditions. In contrast, noninvasive measures of fecal progesterone metabolite concentrations provide a snapshot of the current reproductive status of the population, which may be used to accurately ascertain the percentage of pregnant females.

Serial sample collections should also be useful for assessing both fetal and perinatal mortality in individually recognized animals. Two consecutively collected progesterone metabolite samples of >1000 ng/g in a female that were not followed by visible pregnancy signs and birth would constitute a fetal loss, whereas those followed by visible pregnancy signs and no apparent birth would constitute a perinatal mortality. Progesterone metabolite concentrations at a known stage of gestation may also help identify individuals whose progesterone concentrations are insufficient to sustain a healthy pregnancy.

Such estimates become even more reliable when coupled with cortisol metabolite concentrations at the same gestational stage. These combined measures could provide more comprehensive measures of whether past or present human disturbances are causing suppressed reproductive potential or physiological stress in an elephant population and, consequently, whether such populations are in need of greater levels of protection. Anecdotal observations of a correspondence between cortisol metabolite concentrations and parasite loads in our study suggest that measures of fecal cortisol metabolites may also provide useful indices of immunosuppression in elephants under physiological stress (e.g., Nelson & Demas 1996).

A primary focus of our study was to validate fecal-hormone monitoring tools to assess the long-term effects of poaching on African elephant populations owing to the likely consequences of lifting the trade ban on ivory. Of greatest concern is the social disruption from the slaughter of older matriarchs for their large tusks, leaving family groups led by relatively young females (Poole 1989). In Mikumi National Park, Tanzania, for example, it is still common to find highly fragmented family groups, often comprised of a single adult female or two females and their direct offspring. Many individuals are tailless, presumably from high rates of aggression; tusklessness also is common in that population (S. K. W. Wasser, personal observation). These breakdowns in traditional family group structure are likely to increase the susceptibility of infants to predation and reduce other social benefits such as allomothering (Dublin 1983). Two surveys of the population in 1987 and 1989 found the rate of recruitment to be low, with few elephants under 5 years of age (Poole 1989). In Queen Elizabeth National Park, Uganda, many dispersed family groups merged into a single large group following an 85% population decline over 20 years (Poole 1989; Abe 1994). A similar grouping phenomenon has also been found in the southern subpopulation of elephants in Tarangire National Park, which also experienced a lower infant-to-mother ratio than the northern subpopulation in Tarangire (Foley, unpublished data). The persistence of these patterns suggests that some populations may not have recovered from the effects of poaching during the previous decade. It is essential that these effects be quantified given the persistent pressures on CITES to relax the trade ban in ivory and the potential risk this poses for elephant recovery over the long-term.

Recognizing the importance of monitoring the effects of ongoing poaching on key elephant populations throughout Africa, CITES implemented in 1998 a program called MIKE, (monitor illegal killing of elephants). Our methods nicely complement the stated objectives of MIKE, and the ease of elephant fecal sampling by patrolling antipoaching rangers makes such methods particularly feasible. For example, our fecal steroid measures make it possible to monitor stress across a large number of populations in different habitat types. Within-season comparisons of fecal cortisol metabolite measures from random dung samples across populations known to vary in past poaching pressures can help quantify the long-term effects of the resultant social disruption. Measures of progesterone metabolite concentrations in those same samples, when coupled with infant counts, might also provide a broad picture of the reproductive health of the population and its rate of recovery in the post-poaching era. Such data could aid CITES in assessing whether recovery time has been sufficient to warrant further relaxing of the trade ban on ivory. Our methods may prove particularly valuable in forest populations, where dense vegetation and difficult terrain greatly hamper monitoring by observation alone (Walsh & White 1999), particularly when coupled with DNA analyses of race, gender, and individuality from the same fecal samples (Wasser et al. 1997*a*; Nyakaana & Arctander 1999; Comstock et al. 2000).

Finally, fecal stress and reproductive measures could be used to help assess the effects of some of the more controversial management tools currently employed on elephant herds. For example, if culling is to occur, fecal hormone measures could be used to assess the stress of these management actions on nontargeted individuals in proximity to a cull. Whyte (1993) reported significant stress-related animal movements among individuals as far away as 7 km from a cull; he suggests that these occur in response to infrasonic signals emitted by dying elephants during the cull. Responses to culling are variable, however, making it difficult to evaluate stress effects based on movement patterns alone (Whyte 1993). Fecal cortisol and progesterone metabolite measures could be used to quantify such stress, as well as to determine whether culling is more stressful for nonculled individuals during particular times of year. Culling in Kruger National Park typically occurs in the middle to late dry season, when carcasses can be readily removed before rotting (de Vos et al. 1983). If physiological stress is lowest overall in the wet season, however, managers may be able to reduce stress on nonculled animals by culling as early as possible in the dry season. Comparison of fecal cortisol and progesterone metabolite concentrations among nontargeted individuals exposed to culls at different time periods could be used to test such management-related hypotheses.

Acknowledgments

We thank the Serengeti Wildlife Research Institute and the Commission for Science and Technology for permission to conduct research in Tanzania, and the Tanzania National Park for permission to work in Tarangire National Park. Our fieldwork was supported largely by Princeton University and Friends of Serengeti. All laboratory and a portion of the fieldwork was supported by a grant to S.K.W. from the U.S. Fish and Wildlife Service Elephant Conservation Act. We thank K. Cooper for assistance with laboratory analyses.

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