

Musth References
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Bates, L. A., R. Handford, P. C. Lee, N. Njiraini, J. H. Poole, K. Sayialel, S. Sayialel, C. J. Moss and R. W. Byrne (2010). "**Why do african elephants (*loxodonta africana*) simulate oestrus? an analysis of longitudinal data.**" PLoS ONE **5**(4).

Female African elephants signal oestrus via chemicals in their urine, but they also exhibit characteristic changes to their posture, gait and behaviour when sexually receptive. Free-ranging females visually signal receptivity by holding their heads and tails high, walking with an exaggerated gait, and displaying increased tactile behaviour towards males. Parous females occasionally exhibit these visual signals at times when they are thought not to be cycling and without attracting interest from musth males. Using demographic and behavioural records spanning a continuous 28-year period, we investigated the occurrence of this "simulated" oestrus behaviour. We show that parous females in the Amboseli elephant population do simulate receptive oestrus behaviours, and this false oestrus occurs disproportionately in the presence of naïve female kin who are observed coming into oestrus for the first time. We compare several alternative hypotheses for the occurrence of this simulation: 1) false oestrus has no functional purpose (e.g., it merely results from abnormal hormonal changes); 2) false oestrus increases the reproductive success of the simulating female, by inducing sexual receptivity; and 3) false oestrus increases the inclusive fitness of the simulating female, either by increasing the access of related females to suitable males, or by encouraging appropriate oestrus behaviours from female relatives who are not responding correctly to males. Although the observed data do not fully conform to the predictions of any of these hypotheses, we rule out the first two, and tentatively suggest that parous females most likely exhibit false oestrus behaviours in order to demonstrate to naïve relatives at whom to direct their behaviour. © 2010 Bates et al.

Bertschinger, H., A. Delsink, J. F. Kirkpatrick, A. Human, D. Grobler and J. J. van Altena (2006). "**Management of elephant populations in private South African game reserves with porcine zona pellucida vaccine.**" 2006 Proceedings American Association of Zoo Veterinarians.

Control of African elephant populations has become an absolute necessity in a number of game reserves in southern Africa. The two main methods used to control populations so far are culling and translocation. Culling, besides being regarded as inhumane and unacceptable in many quarters, is not suitable for smaller populations. It requires that whole family units are culled simultaneously which could mean that in reserves with 10 to 50 elephants a considerable

portion, if not the entire population, is killed. As far as translocation is concerned, limited new space is available for elephants. The only alternative to the two above options is to control the rate of reproduction. The porcine zona pellucida (pZP) vaccine has been used to successfully contracept wild horses and other wildlife species. Work on the contraception of African elephants was initiated in the Kruger National Park in 1995 when the potential for using the porcine zona pellucida (pZP) was investigated. Subsequently the first field trials on wild elephants were carried out in Kruger and the results clearly showed that elephants could be contracepted with the pZP vaccine, although the efficacy achieved was 80%. During these field trials safety and reversibility were demonstrated. In 2000 an elephant contraceptive program was initiated at Makalali Private Game Reserve, RSA, which has become the flagship model for immunocontrol in African elephants. The preliminary findings have been reported in three publications. During the first year, all 18 cows that were individually identified and older than 12 yr of age were treated. During the next 4 yr the number of cows contracepted increased to 23 as young animals were added to the program. The standard vaccination procedure during the first year consisted of a primary vaccination (600 µg or 400 µg pZP with 0.5 ml Freund's modified complete adjuvant) followed by boosters (200 µg pZP with 0.5 ml Freund's incomplete adjuvant) at 3 to 6-wk intervals. Annual boosters to maintain antibody titers and contraceptive effect followed. To date, the success rate on cows that have passed reserve-specific intercalving period of 56 mo has been 100%. The population stabilized within 3 yr by which time when all cows that had been pregnant at the time of first vaccination in 2000 had calved. Once again safety during pregnancy (14 cows pregnant at 2-21 mo gestation when first treated gave birth to normal healthy calves) as well as side effects that were limited to occasional lumps at the site of vaccination could be shown. Following ground darting, behavioral patterns returned to pre-darting status within 2 days. During 2003 and 2004 most boosters were administered from a helicopter; whereas, previously they had been done from a vehicle or on foot. In all cases, drop-out darts were used. Time taken for vaccination from helicopter take-off to landing was about 30 min (1.5 min per cow; 30 min for total time). This required prior knowledge of the locations of family units or that an individual in each unit is radio-collared. Herds settled down much more quickly (1-2 days) than if darted from the ground. Since then we have vaccinated another 107 elephant cows in eight game reserves. The cow populations have ranged from 4 to 43. In one of the reserves, Mabula, RSA, two of the four cows vaccinated have passed the mean intercalving intervals of the reserve with neither of them producing a calf. Treatment at the remaining reserves was initiated in 2004 or 2005 and it is too early to evaluate results. The most difficult reserve in terms of the vaccination process was Welgevonden, RSA, (35 000 ha) with 43 cows. The reserve is mountainous and heavily wooded. None of the elephants were collared and individuals could not be easily identified on the day of primary vaccination. The total flying time during which individuals were identified and vaccinated was 4.5 hr. Administration of the first booster took about 2 hr to locate and vaccinate each cow. Between the first and second booster the first rains occurred, followed by the spring flush of the vegetation. By the time the second booster was attempted late in November, the trees all had foliage. Only half the cows were located and darted because the elephants were very difficult to spot under the tree canopies. The valuable lessons we learned from this were: 1) that helicopter vaccinations should be performed when most trees are bare, and 2) when larger populations are vaccinated repeatedly during the first year, one cow in each family unit should be radio-collared. This makes rapid location of each unit possible and cuts down on the major cost factor that is flying time. Elephant behavior is being monitored in all eight reserves where contraception is being applied. Because most of them have been

contracepted recently, only the data from Makalali is available. The elephants at Makalali have been monitored intensively almost on a daily basis. To date, no anomalies in terms of aggressive or indifferent behavior with regards to nursing time, nursing behavior and calf proximity have been noted. No change in the cows' social hierarchy has been noted. Since January 2003, a total of 15 heats were observed in 10 cows (nine in 2003 and six in 2004) with four mating episodes. For the same period, 38 musth occasions were seen in five bulls (26 in 2003 and 12 in 2004). These occasions include musth displayed in the same bull during consecutive days or within the same musth cycle. The greatest occurrence of musth was recorded in the largest, dominant bull. Bulls were not observed harassing or separating cows off from their herds or calves as a result of increased estrous frequency. Thus, the Makalali program demonstrates that pZP does not cause herd fragmentation, harassment by bulls, change in rank and other negative behaviors normally associated with hormonal contraceptives. In conclusion we feel that it is important to emphasize the following points: The pZP vaccine can be used successfully to contracept African elephants. The vaccine is safe during pregnancy and has no negative effect on birth or calf raising. It has no side effects other than occasional swelling at the site of vaccination. It is reversible. Other than an increased incidence of heat no behavioral side effects were seen.

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Musth has not been well documented in captive African elephants. A 37-year-old African bull elephant in the Kansas City Zoological Park was observed during periods of behavioral musth and non-musth. Androstenedione and luteinizing hormone (LH) concentrations in urine were measured by radioimmunoassay. Urinary androstenedione and LH levels were significantly higher in musth urine than in non-musth samples. A positive correlation ($P > 0.001$) existed between urinary LH and androstenedione concentrations. These results indicate that musth can occur in a zoo-maintained African elephant and that urinary androgen levels are elevated during musth, possibly as a result of LH stimulation of testicular steroidogenesis.

Brown, J. L., M. Bush, D. E. Wildt, J. P. Raath, V. de Vos and J. G. Howard (1993). "**Effects of GnRH analogues on pituitary-testicular function in free-ranging African elephants (*Loxodonta africana*).**" *Journal of Reproduction and Fertility* **99**(2): 626-634.

In the first of 2 experiments, 6 free-living adult male elephants were given 4 or 12 mg GnRH antagonist (Detirelix) or saline intramuscularly on day 0. Animals were then recaptured about 48 h later and given 300 µg GnRH intravenously to assess the ability of the antagonist to block pituitary activity. Detirelix reduced ($P < 0.05$) basal concentrations of serum LH and testosterone on day 2 compared with day 0, with no effect of dose. Similarly, LH and testosterone release induced by GnRH were also reduced ($P < 0.05$) in the Detirelix-treated bulls (50-70% reduction in peak concentration). In the 2nd experiment, elephants were given 30 mg of a structurally similar GnRH antagonist (103-201-40; $n = 6$), 22.5 mg of a long-acting GnRH agonist (Lupron Depot; $n = 4$) or D-mannitol carrier ($n = 4$) intramuscularly on day 0. All bulls were recaptured and given GnRH on day 2 (103-201-40 treatment group) or on days 2 and 20 (Lupron Depot group) after the initial injection. In contrast to Detirelix, the antagonist 103-201-40 did not inhibit basal or GnRH-induced LH or testosterone secretion. Pituitary-testicular responses to Lupron Depot were initially stimulatory, as evidenced by increased ($P < 0.05$) LH and testosterone secretion on days 0 and 2. By day 20, basal LH concentrations had returned to baseline values and the response to

GnRH was markedly reduced ($P < 0.05$), indicating that the pituitary was at least partially desensitized. Basal testosterone concentrations had also returned to baseline values by day 20 after Lupron Depot treatment. However, despite the attenuated LH response to GnRH, subsequent testosterone secretion was increased ($P < 0.05$) compared with controls, suggesting that the testes of agonist-treated bulls had become hyper-responsive to small increases in LH secretion. It is suggested that GnRH analogues can suppress the pituitary-gonadal axis in African elephants. However, longer treatment periods, more frequent injection intervals or higher doses are probably needed to completely inhibit testosterone secretion and, thus, musth.

Brown, J. L. (2014). "**Comparative reproductive biology of elephants.**" *Adv Exp Med Biol* **753**: 135-169. The ability to serially collect blood samples and conduct ultrasound examinations in Asian and African elephants has provided unique opportunities to study the biology of these endangered species. As a result, many unique aspects of elephant reproduction have been identified. For females, there are interesting differences in luteal steroidogenic activity, follicular maturation, pituitary gonadotropin secretion, fetal development and reproductive tract anatomy, while males exhibit the unique phenomenon of musth and an unusual reproductive anatomy (internal testes, ampullary semen storage). However, problems associated with uterine and ovarian pathologies hamper captive propagation efforts. Older, nulliparous cows are particularly susceptible, leading to speculation that continuous ovarian cyclicity of non-bred females in zoos is having a negative and cumulative effect on reproductive health. There are notable species differences in reproductive mechanisms as well (e.g., ovarian acyclicity, prolactin secretion, sperm cryosensitivity), implying that species-specific approaches to management and application of assisted reproductive techniques are needed for maximal reproductive efficiency and enhancement of genetic management.

Brown, J. L. (2014). **Comparative reproductive biology of elephants.** *Advances in Experimental Medicine and Biology*, Springer New York LLC. **753**: 135-169.

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Brown, J. L., M. Somerville, H. S. Riddle, M. Keele, C. K. Duer and E. W. Freeman (2007). "**Comparative endocrinology of testicular, adrenal and thyroid function in captive Asian and African elephant bulls.**" *General and Comparative Endocrinology* **151**(2): 153-162.

Concentrations of serum testosterone, cortisol, thyroxine (free and total T4), triiodothyronine (free and total T3) and thyroid stimulating hormone (TSH) were measured to assess adrenal and

thyroid function as they relate to testicular activity and musth in captive elephants. Blood samples were collected approximately weekly from Asian ($n = 8$) and African ($n = 12$) bulls at seven facilities for periods of 4 months to 9.5 years. Age ranges at study onset were 8-50 years for Asian and 10-21 years for African elephants. Based on keeper logs, seven Asian and three African bulls exhibited behavioral and/or physical (temporal gland secretion, TGS, or urine dribbling, UD) signs of musth, which lasted 2.8 ± 2.5 months in duration. Serum testosterone was elevated during musth, with concentrations often exceeding 100 ng/ml. Patterns of testosterone secretion and musth varied among bulls with no evidence of seasonality ($P > 0.05$). Only three bulls at one facility exhibited classic, well-defined yearly musth cycles. Others exhibited more irregular cycles, with musth symptoms often occurring more than once a year. A number of bulls (1 Asian, 9 African) had consistently low testosterone (<10 ng/ml) and never exhibited significant TGS or UD. At facilities with multiple bulls ($n = 3$), testosterone concentrations were highest in the oldest, most dominant male. There were positive correlations between testosterone and cortisol for six of seven Asian and all three African males that exhibited musth (range, $r = 0.23-0.52$; $P < 0.05$), but no significant correlations for bulls that did not ($P > 0.05$). For the three bulls that exhibited yearly musth cycles, TSH was positively correlated (range, $r = 0.22-0.28$; $P < 0.05$) and thyroid hormones (T3, T4) were negatively correlated (range, $r = -0.25$ to -0.47 ; $P < 0.05$) to testosterone secretion. In the remaining bulls, there were no clear relationships between thyroid activity and musth status. Overall mean testosterone and cortisol concentrations increased with age for all bulls combined, whereas thyroid activity declined. In summary, a number of bulls did not exhibit musth despite being of adequate physical maturity. Cortisol and testosterone were correlated in most bulls exhibiting musth, indicating a possible role for the adrenal gland in modulating or facilitating downstream responses. Data were generally inconclusive as to a role for thyroid hormones in male reproduction, but the finding of discrete patterns in bulls showing clear testosterone cycles suggests they may facilitate expression or control of musth in some individuals. © 2007 Elsevier Inc. All rights reserved.

Buss, I. O., J. A. Estes, L. E. Rasmussen and G. L. Smuts (1976). "**The role of stress and individual recognition in the function of the African elephant's temporal gland.**" *Mammalia* 40(3): 437-451.

Biochemical measurements were made from a sample of temporal gland secretion from each of five wild African elephant bulls (23 to 38 years of age) collected in Kruger National Park, South Africa between November 1974 and April 1975. Total protein content was high (26-57 mg/ml), acid phosphatase ranged between 1.9 and 6.3 mM/h/mgm protein, and lactic dehydrogenase levels were undetectable. Total lipid content in the secretion averaged 80 mg% and ranged from 75 to 87 mg%. Triglycerides were just detectable, varying from 2 to 8 mg%, and phospholipids ranged from 9 to 11 mg% (ave. 10 mg%). Cholesterol content was surprisingly high, measuring 12, 19, 26, 36, and 70 mg% for five samples of secretion. Field observations indicated that stress triggers liberation of temporal gland secretion. Among 116 elephants collected in Uganda, secretory activity of their temporal glands was more frequent during dry (probably more stressful) than during wet seasons. Among 62 elephants driven by helicopter to roadways for collection in Kruger National Park, 23 driven relatively far and fast were in prominent musth; most of those driven slower and shorter distances showed no evidence of musth. The matriarchal leader of an elephant family near Lake Albert, Uganda developed very prominent temporal gland activity after an hour and 45 minutes of vigorously defending three of her family members. Chemical individuality of cholesterol levels in temporal glands of five adult bulls suggests a pheromone-producing function which serves for individual recognition by

the African elephant. Direct observations of wild elephants also suggest that the temporal gland functions as a scent gland helping to recognize other members of the group or to find them.

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Full text: A total of 140 captive rogue tuskers were successfully tranquilized and translocated during the period for April 1979 to December 1988. Most of the animals were those used in festivals or in lumbering operations. The requests handled by the tranquilization team were of urgent nature and no kunkies were available to assist the operation. Hence the animals were tranquilized retaining certain amount of ambulatory property and not allowing the animals to assume recumbency. After ascertaining complete sedation which took nearly 45 minutes after darting the limbs were noosed with polypropylene ropes and pulled by volunteers numbering from 15 to 20 on each rope on the forelimb. The animals were also given oral and percussion commands and coaxed to move. Animals could be moved on an average of 100 meters to be tied in a safe tethering area. The chemical used at first was nicotine and was subsequently replaced by xylazine alone or its combinations for better margin of safety. The combination of xylazine with acepromazine and ketamine was discarded due to photosensitization of elephants and subsequent skin lesions on the back of the elephants. The dose of xylazine varied from 100 to 120 mg/ton body weight. The data show that 85% of the cases were attended while the bulls were in pre-musth or post-musth period indicating lack of sufficient precaution taken by the mahouts.

Chelliah, K. and R. Sukumar (2015). "**Interplay of male traits, male mating strategies and female mate choice in the Asian elephant, *Elephas maximus*.**" Behaviour **152**(7-8): 1113-1144.

Elaborate male traits with no apparent adaptive value may have evolved through female mate

discrimination. Tusks are an elaborate male-only trait in the Asian elephant that could potentially influence female mate choice. We examined the effect of male body size, tusk possession and musth status on female mate choice in an Asian elephant population. Large/musth males received positive responses from oestrous females towards courtship significantly more often than did small/nonmusth males. Young, tusked non-musth males attempted courtship significantly more often than their tuskless peers, and received more positive responses (though statistically insignificant) than did tuskless males. A positive response did not necessarily translate into mating because of mateguarding by a dominant male. Female elephants appear to choose mates based primarily on traits such as musth that signal direct fertility benefits through increased sperm received than for traits such as tusks that may signal only indirect fitness benefits. © 2015 Koninklijke Brill NV, Leiden.

Chelliah, K. and R. Sukumar (2013). "**The role of tusks, musth and body size in male-male competition among Asian elephants, *Elephas maximus*.**" *Animal Behaviour* **86**(6): 1207-1214.

The evolution of sexually dimorphic, elaborate male traits that are seemingly maladaptive may be driven by sexual selection (male-male competition and or female mate choice). Tusk possession in the Asian elephant is sexually dimorphic and exaggerated but its role in male-male competition has not yet been determined. We examined the role of the tusks in establishing dominance along with two other known male-male signals, namely, body size and musth (a temporary physiologically heightened sexual state) in an Asian elephant population in northeastern India with equal proportions of tusked and tuskless males. We observed 116 agonistic interactions with clear dominance outcomes between adult (>15 years) males during 458 field days in the dry season months of 2008-2011. A generalized linear mixed-effects model was used to predict the probability of winning as a function of body size, tusk possession and musth status relative to the opponent. A hierarchy of the three male-male signals emerged from this analysis, with musth overriding body size and body size overriding tusk possession. In this elephant population tusk possession thus plays a relatively minor role in male-male competition. An important implication of musth and body size being stronger determinants of dominance than tusk possession is that it could facilitate rapid evolution of tuskless males in the population under artificial selection against tusked individuals, which are poached for ivory. © 2013 The Association for the Study of Animal Behaviour.

Cooper, K. A., J. D. Harder, D. H. Clawson, D. L. Fredrick, G. A. Lodge, H. C. Peachey, T. J. Spellmire and D. P. Winstel (1990). "**Serum testosterone and musth in captive male African and Asian elephants.**" *Zoo Biol* **9**: 297-306.

Testosterone concentrations in serum samples collected weekly over a 5-year period from a young adult male Asian elephant (*Elephas maximus*) and a young adult male African forest elephant (*Loxodonta africana cyclotis*) were measured by radioimmunoassay. Testosterone profiles during this maturational period were compared between the two species and related to the occurrence of *musth*, a recurring physiological and behavioral condition exhibited by most mature Asian, and some African, bull elephants. Musth is characterized by secretion from the bull's temporal glands, dribbling urine, and increased aggression. Serum testosterone concentrations in the Asian bull were elevated substantially between April and September each year, coincident with the presence of temporal gland secretion, urine dribbling, and aggressive behavior. Testosterone levels from April through September averaged (\pm SEM) 41.2 ± 2.8 ng/ml, compared to 7.6 ± 1.0 ng/ml during the rest of the year. In contrast, the testosterone profile of the African bull showed greater variability and lower levels overall, the only pattern being a

tendency for levels to be lowest from November to February (avg. 6.8 ± 1.5 vs. 10.3 ± 0.8 ng/ml during the rest of the year). Temporal gland secretion and other signs of musth were first observed in this bull in 1988, at age 17. While his testosterone values did not show a pattern comparable to that in the Asian bull, average testosterone values were significantly greater in 1988 compared to previous years. The Asian bull showed sexual attention to preovulatory (estrous) cows whether in musth or not, and exposure to estrous cows did not appear to alter the highly consistent, annual pattern of musth as evidenced by temporal gland flow.

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Addresses: Hendrix Coll, Dept Chem, Conway, AR 72032 USA ;Duke Univ, Dept Biol Sci, Durham, NC 27706 USA

de Oliveira, C. A., G. D. West, R. Houck and M. Leblanc (2004). "Control of musth in an Asian elephant bull (*Elephas maximus*) using leuprolide acetate **716**." J. Zoo. Wildl. Med **35**(1): 70-76.

The results of long-term administration of leuprolide acetate (LA) depot in a 52-yr-old Asian elephant bull (*Elephas maximus*) for control of musth are presented. Twelve injections were administered for 6 yr during our interpretation of early musth or "premusth." Intervals between musth periods during the study varied from 2 to 34 mo. Blood samples, drawn weekly, were assayed for serum testosterone concentrations; mean levels were 11.78 ± 1.97 nmol/L throughout the first 26 mo of the study, 7.28 ± 1.28 nmol/L during the following 21 mo, and 0.45 ± 0.035 nmol/L in the last 34 mo of this study. Early musth signs ceased within 3 days of drug administration after 10 of 12 injections. The mean serum testosterone concentrations were significantly decreased by the last 34 mo of the study. The results suggest leuprolide is a suitable alternative for controlling or preventing (or both) musth in captive Asian elephants, although permanent reproductive effects may occur. Zoos and wildlife conservation institutions could benefit from the use of LA in Asian elephants to increase the male availability in captivity, consequently ensuring genetic diversity and the perpetuation of the species

De Oliveira, C. A., G. D. West, R. Houck and M. Leblanc (2004). "Control of musth in an Asian elephant bull (*Elephas maximus*) using leuprolide acetate." Journal of Zoo and Wildlife Medicine **35**(1): 70-76.

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Dickerman, R. D., N. Y. Zachariah, M. Fouraker and W. J. McConathy (1997).

"**Neuroendocrine-associated behavioral patterns in the male Asian elephant (*Elephas maximus*).**" *Physiology and Behavior* **61**(5): 771-773.

Steroid-responsive behaviors have been reported in various species; however, the reports thus far on the male Asian elephant (bull) during musth are few in number and most have been conducted on single captive animals for short time periods. The purpose of this investigation was to perform a longitudinal study on steroid-responsive behavior in 3 male Asian elephants from a captive herd of 11 male Asian elephants in Nepal. Male Asian elephants were 18, 25, and 43 years old. The animals had serum collected for 11 months and were observed on a daily basis for aggressive behavior according to the Species Survival Plan (SSP) collection protocol on SSP data sheets. Testosterone (T) and dihydrotestosterone (DHT) were measured in each animal by radioimmunoassay. Testosterone levels rose during musth 26-fold compared to nonmusth, and DHT was elevated 12-fold in musth. Maximal aggressive behavior episodes occurred during peak elevations of T and DHT, with correlation coefficients of 0.82 and 0.89, respectively. Therefore, we suggest that the aggressive episodes are dependent on elevated circulating androgens acting on androgen-responsive neural tissues.

Diephuis, E. P. (1993). "**Oestrus and pregnancy detection by flehmen-like responses of Asian bull elephants to urine samples of Asian female elephants.**" *Zoologische Garten* **63**(4): 235-245.

Urine samples were taken twice a week over a period of 130 days from 12 female Asian elephants of various reproductive status at 4 Dutch zoos. Pools, each of 12 urine samples from 6 cows, were offered to 4 male Asian elephants at 3 Dutch zoos. Flehmen responses by the bulls to the individual urine samples were recorded to detect oestrus and pregnancy in the cows. Serum progesterone data were used as a reference. During the tests, one of the 4 bulls showed

hardly any flehmen responses; the others showed flehmen responses, with considerable variation between the 3 bulls in number of responses per sample (0.68 ± 0.90 , 0.93 ± 1.24 and 1.14 ± 1.52 per sample resp.). Correlations of flehmen responses between bulls were very low or moderate and negative. The repeatability of the response to urine samples averaged 64%. In the present study oestrus could not be detected by recording flehmen responses, and the information obtained about pregnancy was not conclusive. Several peaks of flehmen responses scattered over the 130-day period per cow were found, not exclusively during periods of low serum progesterone level (i.e. oestrous periods). Peaks for individual bulls did not usually match those of the other bulls. Urine samples from 2 cows evoked relatively few flehmen responses, which might indicate pregnancy. One of these 2 cows gave birth to a full-term calf on 1 June 1992. Pregnancy of the 2nd cow could not be confirmed. The present study showed that bulls display flehmen responses to urine samples from cows regardless of whether the cow is present or is familiar to the bull. Probably musth did not affect the interest of bulls in urine samples during flehmen tests. However, the maturity of the bull and the degree of sexual activity the bull displays may influence the interest of bulls in urine samples.

Dow, T. L., W. Roudebush, F. N. Parker and J. L. Brown (2011). "**Influence of age and gender on secretion of anti-Müllerian hormone in Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants.**" Theriogenology **75**(4): 620-627.

Anti-Müllerian hormone (AMH) secretion was studied in Asian and African elephants varying in age and reproductive status. Overall mean concentrations did not differ ($P > 0.05$) between species, but were markedly higher in male than female Asian elephants (31.01 ± 4.22 ng/mL and 0.19 ± 0.02 ng/mL, mean \pm SEM) and African elephants (40.27 ± 3.18 ng/mL, 0.17 ± 0.04 ng/mL), respectively. Anti-Müllerian hormone secretion was not significantly affected by ovarian cyclicity status (cycling vs noncycling), but was higher ($P < 0.05$) in prepubertal (0.40 ± 0.10 ng/mL) than reproductive age (8-35 y; 0.18 ± 0.04 ng/mL) and aged (≥ 36 y; 0.16 ± 0.03 ng/mL) females. In males, AMH secretion was not significantly affected by musth status, but was age-related, with higher concentrations ($P > 0.05$) in prepubertal (49.08 ± 6.11 ng/mL) as compared to aged (≥ 36 y; 22.27 ± 5.82 ng/mL) bulls; concentrations in mature bulls (8-35 y; 37.01 ± 3.17 ng/mL) were similar to prepubertal and older bulls. We concluded that circulating AMH concentrations in elephants were similar between species and not affected by reproductive status; however, concentrations were significantly higher in males than females, and in younger animals. The diagnostic value of AMH to assess fertility status of individual elephants remains to be determined. © 2011 Elsevier Inc.

Druce, H., K. Pretorius, D. Druce and R. Slotow (2006). "**The effect of mature elephant bull introductions on resident bull's group size and musth periods: Phinda Private Game Reserve, South Africa.**" South African Journal of Wildlife Research **36**(2): 133-137.

African elephants have been reintroduced into small, enclosed reserves in South Africa, many populations being established with orphans <10 years old. This has resulted in abnormal behaviour in some elephant populations, which was corrected in Pilanesberg National Park by introducing older bulls and culling certain problem elephants. In July 2003, three older bulls (29-41 years old) were introduced into Phinda Private Game Reserve, KwaZulu-Natal, South Africa, in order to normalize the bull age structure and in an attempt to reduce the abnormally long musth period of one particular resident bull. These introduced bulls were monitored intensively after release, as was the resident bull population, both before and after introduction of the older bulls. The introduced bulls all came into musth within eleven months.

postrelease. The older bulls do not appear to have had any influence on the musth periods of the oldest resident bull (36 years old at introduction). Detailed behavioural studies of the effects of management actions on elephant populations, within small, enclosed reserves provide information and resources for future management decisions. This study demonstrates that old bulls can be successfully introduced to very small areas provided that electrification of the entire perimeter is secure. Further, the introduction has no detectable medium-term (one year) effect on the behaviour of a relatively dense population of resident elephants, and the welfare of the elephants was not greatly affected.

Duer, C., T. Tomasi and C. I. Abramson (2016). "**Reproductive Endocrinology and Musth Indicators in a Captive Asian Elephant (*Elephas maximus*)**." Psychological Reports **119**(3): 839-860.

Even in the best situations, the artificial social constructs of captivity alter natural elephant behavior and unfortunately create distress. Asian elephants are powerful and intelligent animals that require consideration for their well-being and prudent management. The males present particular difficulties due to a temporary state of heightened aggressive behavior unique to male elephants called musth. When he is in this state, the danger the elephant poses to other animals and the people around him is considerable. In addition to antagonistic behavior, musth is also characterized by temporal gland secretion and urine dribbling. In previous studies, musth has been attributed to elevated testosterone levels. This study attempted to enhance the knowledge base concerning these phenomena by examining hormone concentrations (n=357) in Onyx, a male Asian elephant housed at Dickerson Park Zoo, with intermittent access to females (n=1-5) over a 12-year period. Behavior and signs of musth also were recorded daily by elephant department staff. Musth indicators (temporal gland secretion, aggression, urine dribbling) increased with musth but not prior to it. We confirmed that temporal gland secretion was a better indicator of behavioral musth than urine dribbling. Hormones concentrations increased as musth approached, and presumably initiated musth indicators, but variability was high. Therefore, these hormones cannot be used to predict the onset of musth in this individual. Rather, the free/total testosterone ratio was a good indication of the 60-day pre-musth period. In addition, testosterone production and musth indicators increased in intensity when a young bull at the zoo started entering musth.

Durrheim, D. N. and D. N. Durrheim (1999). "**Risk to tourists posed by wild mammals in South Africa.**" J Travel Med **6**(3): 172-179.

BACKGROUND: One of South Africa's principal tourist attractions is the opportunity to encounter Africa's large mammals in the wild. Attacks by these mammals can be exceptionally newsworthy with potentially deleterious effects on tourism. Little is known about the risk of injury and death caused by wild mammals to visitors to South Africa's nature reserves. The aim of this study was to determine the incidence of fatal and nonfatal attacks on tourists by wild mammals in South Africa and to ascertain avoidable factors, if any. **METHODS:** Commercial press records covering all South African Newspapers archived at the Independent Newspapers' central library were systematically reviewed for a 10-year period, January 1988 to December 1997 inclusive, to identify all deaths and injuries to domestic and international tourists resulting from encounters with wild mammals in South Africa. All of these incidents were analyzed to ascertain avoidable factors. **RESULTS:** During the review period seven tourists, including two students from Thailand and a German traveler, were killed by wild mammals in South Africa. Three of the four deaths ascribed to lions resulted from tourists carelessly approaching prides on foot in lion reserves. A judicial inquiry found that the management of a KwaZulu-Natal Reserve was culpable

for the remaining death. Tourist ignorance of animal behavior and flagrant disregard of rules contributed to the two fatalities involving hippopotami. The unusual behavior manifested by the bull elephant responsible for the final death, resulted from discomfort caused by a dental problem to this pachyderm. During the same period there were 14 nonfatal attacks on tourists, including five by hippo, three by buffalo, two by rhino, and one each by a lion, leopard, zebra and musth elephant. Only the latter occurred while the visitor was in a motor vehicle. Tourist ethological naivete and failure to determine the experience of trail guides prior to travel, resulted in inadvertent agonistic behavior, unnecessary risk-taking and avoidable injury.

CONCLUSIONS: This retrospective study has shown that attacks on tourists by wild mammals in South Africa are an uncommon cause of injury and death. Sensible precautions to minimize this risk include remaining in a secure motor vehicle or adequately fenced precincts while in the vicinity of large mammals, rigidly observing nature reserve instructions, never approaching animals that appear ill, malnourished, displaying aggressive behavior traits or female wild mammals with young, and demanding adequately trained and experienced game rangers when embarking on walking trails. Any behavior that might be construed as antagonistic and which could provoke an attack by large mammals should be avoided (e.g., driving directly at a lion). Visitors need to be informed of classic signs of aggression, in particular in elephants, which will allow timely avoidance measures to be taken. The risk-enhancing effect of excessive alcohol intake is undesirable in the game reserve setting, as is driving at high speed after dusk in areas where hippos graze. Local advice on personal safety in wildlife reserves and the credentials of trail guides should be obtained from lodge or reserve management, tourism authorities or the travel industry prior to travel to game reserves.

Fernando, P., E. D. Wikramanayake, H. K. Janaka, L. K. A. Jayasinghe, M. Gunawardena, S. W. Kotagama, D. Weerakoon and J. Pastorini (2008). "**Ranging behavior of the Asian elephant in Sri Lanka.**" Mammalian Biology **73**(1): 2-13.

We studied the ranging patterns of 10 elephants in and around the Yala protected area complex, southern Sri Lanka, using VHF radio telemetry. All tracked elephants displayed similar ranging patterns. The observed home ranges were small (mean=115.2±64.0 km²) relative to reported home ranges in India, possibly in response to high habitat productivity and abundant perennial water sources. Elephants showed high fidelity to their ranges. Home ranges had relatively large core areas, suggesting intensive use of habitat. No geographically distinct seasonal ranges or migratory behavior was observed. Home range overlap was high, and territoriality was absent. Male musth ranges were considerably larger than non-musth ranges and may signify mate searching. Most elephants ranged both in and outside protected areas, suggesting that resources outside protected areas were important for their survival. Thus, translocating and restricting elephants to protected areas will be detrimental to their survival, as it limits resource access. The ranging patterns of Asian elephants suggest that conservation of the species requires their management both in and outside protected areas. © 2007 Deutsche Gesellschaft für Säugetierkunde.

Ferrier, A. J. (1947). **The care and management of elephants in Burma.** London, Steel Brothers.

Flanagan, H. O. and F. O. Flanagan (1983). "**Castration of African elephant *Loxodonta africana africana.***" Zimbabwe Vet. J **13**(3-4): 50-51.

The successful castration of an African bull elephant, *Loxodonta africana africana*, is described, with a resultant increase in docility. It is possible that, with castration, more use could be made

of baby bulls captured during culling operations.

Fowler, M. E. (1972). "Castration of an elephant." Proc Am Assoc Zoo Vet: 25-27.

Fowler, M. E. (1973). "Castration of an elephant." Journal of Zoo and Wildlife Medicine **4**: 25-27.

Gale, U. T. (1974). Burmese timber elephant. Rangoon, Burma, Trade Corporation.

Ganswindt, A., M. Heistermann and J. K. Hodges (2001). **Faecal Glucocorticoid and Androgen Metabolite Excretion in Male African Elephants (*Loxodonta africana*)**. A Research Update on Elephants and Rhinos; Proceedings of the International Elephant and Rhino Research Symposium, Vienna, June 7-11, 2001, Schuling Verlag.

Ganswindt, A., R. Palme, M. Heistermann, S. Borragan and J. K. Hodges (2003). "Non-invasive assessment of adrenocortical function in the male African elephant (*Loxodonta africana*) and its relation to musth." Gen Comp Endocrinol **134**(2): 156-166.

German Primate Centre, Department of Reproductive Biology, Kellnerweg 4, 37077 Gottingen, Germany. ganswindt@www.dpz.gdwg.de

Adult male elephants periodically show the phenomenon of musth, a condition associated with increased aggressiveness, restlessness, significant weight reduction and markedly elevated androgen levels. It has been suggested that musth-related behaviours are costly and that therefore musth may represent a form of physiological stress. In order to provide data on this largely unanswered question, the first aim of this study was to evaluate different assays for non-invasive assessment of adrenocortical function in the male African elephant by (i) characterizing the metabolism and excretion of [3H]cortisol (3H-C) and [14C]testosterone (14C-T) and (ii) using this information to evaluate the specificity of four antibodies for determination of excreted cortisol metabolites, particularly with respect to possible cross-reactions with androgen metabolites, and to assess their biological validity using an ACTH challenge test. Based on the methodology established, the second objective was to provide data on fecal cortisol metabolite concentrations in bulls during the musth and non-musth condition. 3H-C (1 mCi) and 14C-T (100 microCi) were injected simultaneously into a 16 year old male and all urine and feces collected for 30 and 86 h, respectively. The majority (82%) of cortisol metabolites was excreted into the urine, whereas testosterone metabolites were mainly (57%) excreted into the feces. Almost all radioactive metabolites recovered from urine were conjugated (86% 3H-C and 97% 14C-T). In contrast, 86% and >99% of the 3H-C and 14C-T metabolites recovered from feces consisted of unconjugated forms. HPLC separations indicated the presence of various metabolites of cortisol in both urine and feces, with cortisol being abundant in hydrolysed urine, but virtually absent in feces. Although all antibodies measured substantial amounts of immunoreactivity after HPLC separation of peak radioactive samples and detected an increase in glucocorticoid output following the ACTH challenge, only two (in feces against 3alpha,11-oxo-cortisol metabolites, measured by an 11-oxo-etiocholanolone-EIA and in urine against cortisol, measured by a cortisol-EIA) did not show substantial cross-reactivity with excreted 14C-T metabolites and could provide an acceptable degree of specificity for reliable assessment of glucocorticoid output from urine and feces. Based on these findings, concentrations of immunoreactive 3alpha,11-oxo-cortisol metabolites were determined in weekly fecal samples collected from four adult bulls over periods of 11-20 months to examine

whether musth is associated with increased adrenal activity. Results showed that in each male levels of these cortisol metabolites were not elevated during periods of musth, suggesting that in the African elephant musth is generally not associated with marked elevations in glucocorticoid output. Given the complex nature of musth and the variety of factors that are likely to influence its manifestation, it is clear, however, that further studies, particularly on free-ranging animals, are needed before a possible relationship between musth and adrenal function can be resolved. This study also clearly illustrates the potential problems associated with cross-reacting metabolites of gonadal steroids in EIAs measuring glucocorticoid metabolites. This has to be taken into account when selecting assays and interpreting results of glucocorticoid metabolite analysis, not only for studies in the elephant but also in other species.

Ganswindt, A., H. B. Rasmussen, M. Heistermann and J. K. Hodges (2005). "**The sexually active states of free-ranging male African elephants (*Loxodonta africana*): defining musth and non-musth using endocrinology, physical signals, and behavior.**" *Horm Behav* **47**(1): 83-91.

Musth in male African elephants, *Loxodonta africana*, is associated with increased aggressive behavior, continuous discharge of urine, copious secretions from the swollen temporal glands, and elevated androgen levels. During musth, bulls actively seek out and are preferred by estrous females although sexual activity is not restricted to the musth condition. The present study combines recently established methods of fecal hormone analysis with long-term observations on male-female associations as well as the presence and intensity of physical signals to provide a more detailed picture about the physical, physiological, and behavioral characteristics of different states of sexual activity in free-ranging African elephants. Based on quantitative shifts in individual bull association patterns, the presence of different physical signals, and significant differences in androgen levels, a total of three potential sub-categories for sexually active bulls could be established. The results demonstrate that elevations in androgen levels are only observed in sexually active animals showing temporal gland secretion and/or urine dribbling, but are not related to the age of the individual. Further, none of the sexually active states showed elevated glucocorticoid output indicating that musth does not represent an HPA-mediated stress condition. On the basis of these results, we suggest that the term "musth" should be exclusively used for the competitive state in sexually active male elephants and that the presence of urine dribbling should be the physical signal used for defining this state.

Ganswindt, A., M. Heistermann and K. Hodges (2005). "**Physical, physiological, and behavioral correlates of musth in captive African elephants (*Loxodonta africana*)** 594." *Physiol Biochem. Zool* **78**(4): 505-514.

Although musth in male African elephants (*Loxodonta africana*) is known to be associated with increased aggressiveness, urine dribbling (UD), temporal gland secretion (TGS), and elevated androgens, the temporal relationship between these changes has not been examined. Here, we describe the pattern of musth-related characteristics in 14 captive elephant bulls by combining long-term observations of physical and behavioral changes with physiological data on testicular and adrenal function. The length of musth periods was highly variable but according to our data set not related to age. Our data also confirm that musth is associated with elevated androgens and, in this respect, show that TGS and UD are downstream effects of this elevation, with TGS responding earlier and to lower androgen levels than UD. Because the majority of musth periods were associated with a decrease in glucocorticoid levels, our data also indicate that musth does not represent a physiological stress mediated by the hypothalamic-pituitary-adrenal axis. Furthermore, we demonstrate that the occurrence of musth is associated with increased

aggression and that this is presumably androgen mediated because aggressive males had higher androgen levels. Collectively, the information generated contributes to a better understanding of what characterizes and initiates musth in captive African elephants and provides a basis for further studies designed to examine in more detail the factors regulating the intensity and duration of musth

Ganswindt, A., S. Muenscher, M. Henley, S. Henley, M. Heistermann, R. Palme, P. Thompson and H. Bertschinger (2010). "**Endocrine correlates of musth and the impact of ecological and social factors in free-ranging African elephants (*Loxodonta africana*)**." *Horm Behav* **57**(4-5): 506-514.

Sexual activity in mature male African elephants is predominantly associated with the occurrence of musth, a state or condition which refers to a set of physical, physiological and behavioral characteristics, including an elevation in androgen levels. Although musth appears to be energetically costly, the degree to which it is associated with changes in adrenal endocrine function (e.g., glucocorticoid output) is still unclear. To investigate the possible effect of musth on adrenocortical function, and the impact of socioecological changes on androgen and glucocorticoid levels, six adult African elephant bulls were followed for 13 months in the Kruger National Park, South Africa, and observations and fecal sample collection for endocrine monitoring was carried out about twice weekly. Our data showed that the occurrence of musth was associated with reduced glucocorticoid output, suggesting that musth does not represent a physiological stress mediated by the hypothalamic-pituitary-adrenal axis. This confirms previous findings in captive-housed animals, providing evidence for a suppressive effect of the musth condition on adrenocortical activity. Furthermore, a seasonal effect on androgen and glucocorticoid levels was found, which appears to vary depending on the reproductive status of the animal. The results also indicate a relationship between the presence or absence of social partners and changes in testicular and adrenal endocrine activity. Finally, the data confirm previous findings in captive-housed elephants, that an elevation in androgen concentrations usually occurs before the onset of physical musth signs, and therefore support the idea that the change in androgen levels represents the initial stimulus for the musth condition.

Gehring, H. and H. D. Schroder (1982). **Castration of an elephant *Elephas maximus***. *Zool. Gart Teilkastration eines elefantenbullen (*Elephas maximus*)*. **52**: 365-368.

Ghosal, R., A. Ganswindt, P. B. Seshagiri and R. Sukumar (2013). "**Endocrine correlates of musth in free-ranging Asian elephants (*Elephas maximus*) determined by non-invasive faecal steroid hormone metabolite measurements**." *PLoS ONE* **8**(12).

The occurrence of musth, a period of elevated levels of androgens and heightened sexual activity, has been well documented for the male Asian elephant (*Elephas maximus*). However, the relationship between androgendependent musth and adrenocortical function in this species is unclear. The current study is the first assessment of testicular and adrenocortical function in free-ranging male Asian elephants by measuring levels of testosterone (androgen) and cortisol (glucocorticoid - a physiological indicator of stress) metabolites in faeces. During musth, males expectedly showed significant elevation in faecal testosterone metabolite levels. Interestingly, glucocorticoid metabolite concentrations remained unchanged between musth and non-musth periods. This observation is contrary to that observed with wild and captive African elephant bulls and captive Asian bull elephants. Our results show that musth may not necessarily represent a stressful condition in free-ranging male Asian elephants. © 2013 Ghosal et al.

Glickman, S. E., R. V. Short and M. B. Renfree (2005). "**Sexual differentiation in three unconventional mammals: spotted hyenas, elephants and tammar wallabies** 566." Horm. Behav **48**(4): 403-417.

The present review explores sexual differentiation in three non-conventional species: the spotted hyena, the elephant and the tammar wallaby, selected because of the natural challenges they present for contemporary understanding of sexual differentiation. According to the prevailing view of mammalian sexual differentiation, originally proposed by Alfred Jost, secretion of androgen and anti-Mullerian hormone (AMH) by the fetal testes during critical stages of development accounts for the full range of sexually dimorphic urogenital traits observed at birth. Jost's concept was subsequently expanded to encompass sexual differentiation of the brain and behavior. Although the central focus of this review involves urogenital development, we assume that the novel mechanisms described in this article have potentially significant implications for sexual differentiation of brain and behavior, a transposition with precedent in the history of this field. Contrary to the "specific" requirements of Jost's formulation, female spotted hyenas and elephants initially develop male-type external genitalia prior to gonadal differentiation. In addition, the administration of anti-androgens to pregnant female spotted hyenas does not prevent the formation of a scrotum, pseudoscrotum, penis or penile clitoris in the offspring of treated females, although it is not yet clear whether the creation of masculine genitalia involves other steroids or whether there is a genetic mechanism bypassing a hormonal mediator. Wallabies, where sexual differentiation occurs in the pouch after birth, provide the most conclusive evidence for direct genetic control of sexual dimorphism, with the scrotum developing only in males and the pouch and mammary glands only in females, before differentiation of the gonads. The development of the pouch and mammary gland in females and the scrotum in males is controlled by genes on the X chromosome. In keeping with the "expanded" version of Jost's formulation, secretion of androgens by the fetal testes provides the best current account of a broad array of sex differences in reproductive morphology and endocrinology of the spotted hyena, and androgens are essential for development of the prostate and penis of the wallaby. But the essential circulating androgen in the male wallaby is 5alpha androstane-3beta,20-dione, locally converted in target tissues to DHT, while in the pregnant female hyena, androstenedione, secreted by the maternal ovary, is converted by the placenta to testosterone (and estradiol) and transferred to the developing fetus. Testicular testosterone certainly seems to be responsible for the behavioral phenomenon of musth in male elephants. Both spotted hyenas and elephants display matrilineal social organization, and, in both species, female genital morphology requires feminine cooperation for successful copulation. We conclude that not all aspects of sexual differentiation have been delegated to testicular hormones in these mammals. In addition, we suggest that research on urogenital development in these non-traditional species directs attention to processes that may well be operating during the sexual differentiation of morphology and behavior in more common laboratory mammals, albeit in less dramatic fashion

Goldenberg, S. Z., I. Douglas-Hamilton, D. Daballen and G. Wittemyer (2017). "**Challenges of using behavior to monitor anthropogenic impacts on wildlife: a case study on illegal killing of African elephants.**" Animal Conservation **20**(3): 215-224.

Monitoring anthropogenic impacts on wildlife can be challenging, particularly when human activities affecting wildlife are cryptic. Using anti-predator behaviors as proxies for perceived pressure is appealing because of the relative ease with which they can be recorded and the presumed relationship between the threat of interest and a predator stimulus. However,

behaviors are plastic and affected by factors unrelated to human activity. Consequently, it is critical to assess the relationship between behavioral indicators and their context before interpretation. In this study we used a combination of behavior, movement and demography from a threatened population of African elephants in northern Kenya to determine whether reaction to research vehicles was indicative of poaching pressure. We used mixed-effects models predicting reaction of elephants to observer vehicle approaches in which we treated individuals as random effects and included ecological, anthropogenic, spatial, social and demographic predictor variables. Contrary to our hypothesis, recorded levels of reactive behavior did not increase with poaching levels in either a population-level dataset or a data subset of individuals whose spatial behavior was precisely known via radio-tracking. Rather, primary productivity positively predicted reactive behavior in both datasets. This relationship was heightened by the presence of musth males in the radio-collar dataset. Reactivity was not related to the time since entering the protected areas, but increased among groups that spent less time in the protected areas. Inter-individual differences were apparent, suggesting the importance of inherent differences (e.g. personality) across groups. In our study, elephants plagued by a severe human threat did not react defensively to humans in another context, suggesting nuanced discrimination of threats. Our study demonstrates the caution that should be taken in designing studies that use behavioral indices to represent threat and contributes to a growing body of literature employing behavioral indicators to monitor wildlife populations of conservation concern. © 2016 The Zoological Society of London

Goldenberg, S. Z., S. de Silva, H. B. Rasmussen, I. Douglas-Hamilton and G. Wittemyer (2014).

"Controlling for behavioural state reveals social dynamics among male African elephants, *Loxodonta africana*." *Animal Behaviour* **95**: 111-119.

The drivers of social affiliation may vary over time as individuals change their goals with respect to changing environments or physical condition. Studies of companion preference rarely consider shifts in motivational state, despite the potential importance of such shifts in structuring association and population processes. Ignoring state dependence in social behaviour may weaken the ability to recognize social properties and identify their underlying drivers. Modifying established approaches, we apply a state-specific analysis to investigate social properties in male African elephants, which are thought to be weakly social. Specifically, we delineate associations during distinct sexually active and inactive periods and quantify common social metrics (network size, density, betweenness and the number and age of preferred companions) to examine how sexual states may relate to male elephant social relationships. We found that state-dependent association index values were higher and quantitative definitions of preferred companions were more conservative than those derived when sexual state was not taken into account. Preferred companions tended to be closer in age among sexually inactive dyads relative to sexually active dyads, indicating that bulls seek out age-mates when sexually inactive. Networks were larger and denser when sexually inactive. By accounting for dynamic behaviour in social systems, this study demonstrates that male African elephants show more social preference than had been previously thought. © 2014 The Association for the Study of Animal Behaviour.

Goodwin, T. E., L. J. Broederdorf, B. A. Burkert, I. H. Hirwa, D. B. Mark, Z. J. Waldrip, R. A. Kopper, M. V. Sutherland, E. W. Freeman, J. A. Hollister-Smith and B. A. Schulte (2012). **"Chemical signals of elephant musth: temporal aspects of microbially-mediated modifications."** *J Chem Ecol* **38**(1): 81-87.

Mature male African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants exhibit

periodic episodes of musth, a state in which serum androgens are elevated, food intake typically decreases, aggressiveness often increases, and breeding success is enhanced. Urine is a common source of chemical signals in a variety of mammals. Elephants in musth dribble urine almost continuously for lengthy periods, suggesting that the chemicals in their urine may reveal their physiological condition to conspecifics. We investigated the volatile urinary chemicals in captive male elephants using automated solid phase dynamic extraction (SPDE) and gas chromatography-mass spectrometry (GC-MS). We found higher levels of alkan-2-ones, alkan-2-ols, and some aromatic compounds in urine from males in musth than in urine from non-musth males or from females. Levels of ketones and alcohols increased as the urine aged, likely due to microbial metabolism of fatty acids. Protein-derived aromatic metabolites also increased in abundance after urination, likely due to microbial hydrolysis of hydrophilic conjugates. We suggest that microbes may play an important role in timed release of urinary semiochemicals during elephant musth.

Gravett, N., A. Bhagwandin, R. Sutcliffe, K. Landen, M. J. Chase, O. I. Lyamin, J. M. Siegel and P. R. Manger (2017). "**Inactivity/sleep in two wild free-roaming African elephant matriarchs - Does large body size make elephants the shortest mammalian sleepers?**" *PLoS ONE* **12**(3): e0171903.

The current study provides details of sleep (or inactivity) in two wild, free-roaming African elephant matriarchs studied in their natural habitat with remote monitoring using an activwatch subcutaneously implanted in the trunk, a standard elephant collar equipped with a GPS system and gyroscope, and a portable weather station. We found that these two elephants were polyphasic sleepers, had an average daily total sleep time of 2 h, mostly between 02:00 and 06:00, and displayed the shortest daily sleep time of any mammal recorded to date. Moreover, these two elephants exhibited both standing and recumbent sleep, but only exhibited recumbent sleep every third or fourth day, potentially limiting their ability to enter REM sleep on a daily basis. In addition, we observed on five occasions that the elephants went without sleep for up to 46 h and traversed around 30 km in 10 h, possibly due to disturbances such as potential predation or poaching events, or a bull elephant in musth. They exhibited no form of sleep rebound following a night without sleep. Environmental conditions, especially ambient air temperature and relative humidity, analysed as wet-bulb globe temperature, reliably predict sleep onset and offset times. The elephants selected novel sleep sites each night and the amount of activity between sleep periods did not affect the amount of sleep. A number of similarities and differences to studies of elephant sleep in captivity are noted, and specific factors shaping sleep architecture in elephants, on various temporal scales, are discussed.

Greenwood, D. R., D. Comeskey, M. B. Hunt and L. E. Rasmussen (2005). "**Chemical communication: chirality in elephant pheromones** **528.**" *Nature* **438**(7071): 1097-1098.

Musth in male elephants is an annual period of heightened sexual activity and aggression that is linked to physical, sexual and social maturation. It is mediated by the release of chemical signals such as the pheromone frontalin, which exists in two chiral forms (molecular mirror images, or enantiomers). Here we show that enantiomers of frontalin are released by Asian elephants in a specific ratio that depends on the animal's age and stage of musth, and that different responses are elicited in male and female conspecifics when the ratio alters. This precise control of communication by molecular chirality offers insight into societal interactions in elephants, and may be useful in implementing new conservation protocols

Hall-Martin, A. J. (1987). "**The role of musth in the reproductive strategy of the African elephant (*Loxodonta africana*)**." *S. Afr. J. Sci* **83**: 616-620.

Behavioral and endocrinological data on African elephants (*Loxodonta africana*) are integrated to provide a hypothesis of the adaptations reflected in the phenomenon of musth in bulls. Occupation of home ranges, movements, male dominance hierarchies and intra-specific agonistic behavior are reviewed. Bulls in musth leave their home range, travel far and fast, imitate more contacts with distant breeding herds, show aggression which overrides normal social male hierarchies, probably mate more frequently than non-musth bulls and then return to their home range. This behaviour is associated with elevated levels of serum testosterone and dihydrotestosterone. Elephants normally show a high degree of fidelity to sexually segregated adjoining home ranges, which results in regular contact between the same bulls and cows. This breeding strategy is applicable to older, dominant bulls within the locally resident hierarchy. The musth adaptation is a second strategy, whereby younger, lower ranking bulls (25-35 years) can ensure more contacts with cows and maximize their chances of breeding. Because musth bulls mate far from their normal ranges the strategy promotes gene flow and ensures outbreeding. In English with Afrikaans summary.

Hall-Martin, A. J. and L. A. van der Walt (1984). "**Plasma testosterone levels in relation to musth in the male African elephant**." *Koedoe* **27**: 147-149.

Hollister-Smith, J. A., S. C. Alberts and L. E. L. Rasmussen (2008). "**Do male African elephants, *Loxodonta africana*, signal musth via urine dribbling?**" *Animal Behavior* **76**: 1829-1841.

The phenomenon of musth in male elephants involves increased sexual activity, heightened aggression and nearly continuous dribbling of pungent smelling urine. Urine chemistry during musth is altered, suggesting that urine may signal the musth status of the individual. Signalling musth remotely may benefit individuals if it reduces the likelihood of physical confrontation between males, which can lead to injury and even death. Few studies, however, have asked whether and how male elephants respond to urine of other males. We tested two predictions of the hypothesis that urine signals musth status to male conspecifics: (1) that male African elephants differentiate musth and nonmusth urine, and (2) that males differentiate between urine dribbled during early and late musth. The second prediction stems from the observation that males lose weight and presumably body condition during musth. We conducted two related bioassays with 26 captive nonmusth males ranging from 13 to 52 years of age. In each assay, subjects were simultaneously presented with three urine samples (nonmusth, early musth, late musth), each from a different donor male, and a control. We found that subjects differentiated between musth and nonmusth samples using their vomeronasal organ system, but did not discriminate between the samples using their main olfactory system. Males did not differentiate early from late musth. In addition, we found that subject contextual factors, specifically age, dominance status and social grouping, significantly predicted response. We discuss these results within the framework of male elephant longevity and social relationships and their importance to reproductive success.

Hollister-Smith, J. A., J. H. Poole, E. A. Archie, E. A. Vance, N. J. Georgiadis, C. J. Moss and S. C. Alberts (2007). "**Age, musth and paternity success in wild male African elephants, *Loxodonta africana***." *Animal Behaviour* **74**(2): 287-296.

Male African elephants experience intense intrasexual selection in gaining access to oestrous females, who represent a very scarce and highly mobile resource. An unusual combination of

behavioural and physiological traits in males probably reflects this intense selection pressure. Males show prolonged growth, growing throughout much or perhaps all of their long life span (ca. 60-65 years), and they show musth, a physiological and behavioural condition exclusive to elephants, which is manifested by bouts of elevated testosterone and aggression and heightened sexual activity. Most observed matings are by males over 35 years of age and in musth, suggesting that age and musth are both important factors contributing to male reproductive success. Here we report the results of a genetic paternity analysis of a well-studied population of wild African elephants. Patterns of paternity for 119 calves born over a 22-year period showed significant effects of both age and musth on paternity success. Among males in musth, paternity success increased significantly with age until the very oldest age classes, when it modestly declined. When not in musth, males experienced relatively constant, low levels of paternity success at all ages. Thus, despite the importance of both musth and age in determining male paternity success, adult males both in and out of musth, and of all ages, produced calves. In general, however, older males had markedly elevated paternity success compared with younger males, suggesting the possibility of sexual selection for longevity in this species. © 2007 The Association for the Study of Animal Behaviour.

Howard, J., M. Bush, V. De Vos and D. E. Wildt (1984). "**Electroejaculation, semen characteristics and serum testosterone concentrations of free-ranging African elephants (*Loxodonta africana*)**." Journal of Reproduction and Fertility **72**(1): 187-195.

A regimented electroejaculation protocol (120 electrical stimulations; 10-30 V) was used to collect semen and characterize ejaculate quality from 9 adult, free-ranging African elephants under anaesthesia. Eight of the 9 ejaculates contained high concentrations of progressively motile spermatozoa. The overall mean ejaculate volume, sperm concentration/ml ejaculate, sperm motility, sperm status and ejaculate pH were 93.3 ml, 2408.6 x 10⁶ spermatozoa/ml, 70%, 3.9 and 7.4, respectively. A high percentage (mean 77.5%) of spermatozoa within each ejaculate was morphologically normal. Of the aberrant spermatozoa, 72% had a cytoplasmic droplet defect. When sperm viability was tested in vitro at 37°C, sperm motility rating declined by at least half of the initial assessment within 3.5 h of semen collection. Generally, spermatozoa maintained motility in vitro for <6 h. Serum testosterone ranged from 1.4 to 8.2 ng/ml in 4 males evaluated in the morning (07:30-08:00 h). In 4 of the 5 bulls assessed in the afternoon (15:00-18:00 h), testosterone levels were <0.9 ng/ml. The remaining bull evaluated at 16:00 h, had exceptionally high testosterone concentrations (peak 25.6 ng/ml) and a preputial discharge potentially indicative of 'musth'. The present study demonstrates that high quality semen can be collected consistently from the African elephant and that striking differences exist in serum testosterone amongst free-ranging males which may be due, in part, to a diurnal rhythm.

Jacob, V., K. Cheeran, K. Chandrasekharan and K. Radhakrishnan (1983). "**Immobilization of elephant in musth using xylazine hydrochloride**." 7th Annual Symposium of the Indian Society of Veterinary Surgeons.

Jainudeen, M. R., G. McKay and J. F. Eisenberg (1972). "**Observations on musth in the domesticated Asiatic elephant (*Elephas maximus*)**." Mammalia **36**: 247-261.

Jainudeen, M. R., C. B. Katongole and R. V. Short (1972). "**Plasma testosterone levels in relation to musth and sexual activity in the male Asiatic elephant, *Elephas maximus***." J. Reprod. Fertil **29**(1):

99-103.

Testosterone was measured in the peripheral blood plasma of eleven male Asiatic elephants, using a competitive protein-binding assay. When the animals showed no signs of musth, the testosterone levels were low (<0.2 to 1.4 ng/ml); as they began to come into musth and the temporal glands started to enlarge, the testosterone levels rose (4.3 to 13.7 ng/ml), and when the animals were in full musth, with discharging temporal glands and an aggressive temperament, the levels were extremely high (29.6 to 65.4 ng/ml). Musth may therefore be comparable to the rutting behavior of some seasonally breeding mammals, although, in the elephant, there is some indication that it may be induced by sexual activity.

Jainudeen, M. R. (1970). "**The use of etorphine hydrochloride for restraint of a domesticated elephant (*Elephas maximus*)**." *J. Am. Vet. Med. Assoc* **157**(5): 624-626.

A domestic male Asian elephant (*Elephas maximus*) in "musth" (aggressive state) was successfully immobilized with 8 mg. of etorphine hydrochloride (M.99). The clinical signs of immobilization were comparable to those reported in the African elephant (*Loxodonta africana*). Cyprenorphine hydrochloride (M.285) reversed the immobilizing effects almost immediately and completely. Recovery was uncomplicated.

Jainudeen, M. R., T. A. Bongso and B. M. O. A. Perera (1971). "**Immobilisation of aggressive working elephants (*Elephas maximus*)**." *Vet. Rec* **89**(26): 686-688.

The capture of aggressive working elephants, *Elephas maximus*, by the drug immobilisation technique is described. Doses of 5 mg to 8 mg etorphine hydrochloride alone, satisfactorily immobilised four adult elephants. Cyprenorphine hydrochloride reversed the immobilising effects almost immediately and completely. Recovery was uncomplicated. The value of this method of capture is discussed in relation to aggressive working elephant.

Jayewardene, J. (1994). **The Elephant in Sri Lanka**. Colombo, Sri Lanka, WHT Publications Ltd.

John, M. C. and R. Suramanian (1991). "**The elephant**." *Zoos' Print Journal*: 1-4.

Joshua, J. and A. J. T. Johnsingh (1995). Ranging Patterns of Elephants in Rajaji National Park: Implications for Reserve Design. **A Week with Elephants; Proceedings of the International Seminar on Asian Elephants**. J. C. Daniel. Bombay, India, Bombay Natural History Society; Oxford University Press: 256-260.

Kaewmanee, S., G. Watanabe, M. Keio, Y. Yamamoto, T. Yamamoto, M. Kishimoto, K. Nagaoka, E. Narushima, M. Katayanagi, R. Nakao, Y. Sakurai, S. Morikubo, M. Kaneko, M. Yoshihara, T. Yabe and K. Taya (2011). "**A surge-like increase in luteinizing hormone preceding musth in a captive bull African elephant (*Loxodonta africana*)**." *J Vet Med Sci* **73**(3): 379-383.

This study was conducted to determine the correlation between reproductive hormones and musth in a male African elephant. Changes in circulating luteinizing hormone (LH), follicle stimulating hormone (FSH), testosterone and immunoreactive (ir-) inhibin and the degree of musth were evaluated for 4 years. LH increased 4 weeks before musth began. The highest concentrations of testosterone and ir-inhibin were observed from April to October. There were positive correlations among testosterone, ir-inhibin and musth behavior. These findings suggested that the surge-like LH in the pre-musth period might stimulate secretion of testosterone and ir-inhibin and thus initiate the musth behavior. This study also suggested that

the high LH level before musth might be a useful biomarker for the beginning of the musth season.

Kahl, M. P. and B. D. Armstrong (2000). **Visual displays in wild musth males of the African Elephant.** Proceedings of the Fifth International Elephant Research Symposium.

Kaimal, R. (1996). "**Musth: observations based on studies on 140 elephants in Kerala over 10 years.**" Zoos' Print Journal **XI**(6): 26-27.

Kock, N., M. Kock, A. Arif and M. N. S. A. Wahid (1984). **Immobilization techniques and complications associated with a bull Indian elephant (*Elephas maximus indicus*) during musth.** Proc.Am.Assoc.Zoo Vet.

Kock, N. and M. Kock (1984). **Management of two Indian elephants (*Elephas maximus indicus*) in a middle eastern zoo.** Proc. Amer. Assoc. Zoo Vet.

Kumar, G. A., K. N. A. Ghosh, T. Sreekumaran and K. Chandrasekharan (2002). "**Reproduction in elephants.**" Journal of Indian Veterinary Association Kerala **7**(3): 38-40, 48-48.

Kumar, V., V. Palugulla Reddy, A. Kokkiligadda, S. Shivaji and G. Umopathy (2014). "**Non-invasive assessment of reproductive status and stress in captive Asian elephants in three south Indian zoos.**" Gen Comp Endocrinol **201**: 37-44.

Asian elephants in captivity need immediate attention to be bred so as to meet the increasing demand for captive elephants and to overcome the dependence on supplementing the captive stock with wild animals. Unfortunately, captive breeding programs across the globe have met with limited success and therefore more effort is needed to improve breeding in captivity. Endocrine profiling of reproductive hormones (progestagens and androgens) and the stress hormone (glucocorticoids) could facilitate better management and breeding strategies. In the present study, we investigated reproductive and stress physiology of 12 captive Asian elephants for 10-27 months using a non-invasive method based on steroid analysis of 1700 elephant dung samples. Most of the elephants were cycling regularly. Males during musth showed increased fecal androgen metabolite concentrations and exhibited a slight increase in fecal glucocorticoid metabolite levels. Elephants used in public festivals and processions showed significantly increased in faecal glucocorticoid metabolite levels. The results indicate that captive elephants require periodic health care, better husbandry practices and scientific management for sustainable captive population.

Kundu, S., R. Singh, D. Mandal and A. K. Singh (2014). "**First documentation of musth like secretion from the temporal glands of a dead wild female Asian Elephant from Corbett Landscape, Uttarakhand, India.**" Ecology Environment and Conservation **20**(2): 577-579.

The present observation from the wild is first of its kind in the Corbett landscape and adds to the records of Musth like secretion from temporal glands in female Asian elephants from India. This is also the first observation in the whole North Indian elephant range. No such observation is been reported from Corbett Land scape prior to this article. It also indicates that though the phenomenon of temporal gland secretion is rare in female Asian elephants but could be seen in some individual female elephants during the instances of pregnancy.

Kurt, F. and C. Touma (2001). **Musth in Wild - Living and Captive Asian Elephants in Sri Lanka**. A Research Update on Elephants and Rhinos; Proceedings of the International Elephant and Rhino Research Symposium, Vienna, June 7-11, 2001, Schuling Verlag.

Lincoln, G. A. and W. D. Ratnasooriya (1996). "**Testosterone secretion, musth behaviour and social dominance in captive male Asian elephants living near the equator.**" Journal of Reproduction and Fertility **108**(1): 107-113.

Blood samples collected weekly over a 5-year period from 6 adult (19- to 40-year old) male Asian elephants (*Elephas maximus maximus*) living in captivity in Sri Lanka (7°N). Testosterone profiles were very variable within and between animals. Long-term phasic changes in blood concentrations of testosterone, associated with periods of musth (temporal gland secretion, drip urination and aggressive behaviour), occurred in 3 of the 6 elephants, the most pronounced cyclicity occurring in the oldest animal. Musth occurred annually after periods of high androgen secretion and the duration of musth was positively correlated with the mean concentration of testosterone during the previous 2 months. The time of musth, while consistent for an individual, varied between animals. In 4 bulls living in 1 social group, social rank was positively correlated with the mean concentration of testosterone over the 5-year period, and only the dominant animal showed periodic musth. Short-term changes in testosterone concentration occurred in blood samples collected every 15 min for 7 h, and after the injection of 20 µg GnRH, consistent with regulation through the pulsatile secretion of LH. The results support the view that fully mature male Asian elephants living near the equator express an asynchronous, cyclical, circannual pattern of gonadal activity. The periodic increase in testosterone secretion during the gonadal cycle induces the development of musth; however, androgen withdrawal following a period of hypersecretion may be the cause of some aspects of musth behaviour (aggression, unpredictability, disobedience) which make bull elephants very difficult to manage in captivity.

Lueders, I., D. Young, L. Maree, G. van der Horst, I. Luther, S. Botha, B. Tindall, G. Fosgate, A. Ganswindt and H. J. Bertschinger (2017). "**Effects of GnRH vaccination in wild and captive African Elephant bulls (*Loxodonta africana*) on reproductive organs and semen quality.**" PLoS ONE **12**(9): e0178270.

OBJECTIVES: Although the African elephant (*Loxodonta africana*) is classified as endangered by the International Union for Conservation of Nature (IUCN), in some isolated habitats in southern Africa, contraception is of major interest due to local overpopulation. GnRH vaccination has been promoted as a non-invasive contraceptive measure for population management of overabundant wildlife. We tested the efficacy of this treatment for fertility control in elephant bulls. **METHODS:** In total, 17 male African elephants that were treated with a GnRH vaccine were examined in two groups. In the prospective study group 1 (n = 11 bulls, ages: 8-36 years), semen quality, the testes, seminal vesicles, ampullae and prostate, which were all measured by means of transrectal ultrasound, and faecal androgen metabolite concentrations were monitored over a three-year period. Each bull in the prospective study received 5 ml of Improvac(R) (1000 mug GnRH conjugate) intramuscularly after the first examination, followed by a booster six weeks later and thereafter every 5-7 months. In a retrospective study group (group 2, n = 6, ages: 19-33 years), one examination was performed on bulls which had been treated with GnRH vaccine for 5-11 years. **RESULTS:** In all bulls of group 1, testicular and accessory sex gland sizes decreased significantly after the third vaccination. In six males examined prior to vaccination and again after more than five vaccinations, the testis size was reduced by 57.5%. Mean testicular height and length decreased from 13.3 +/- 2.6 cm x 15.2 +/- 2.8 cm at the beginning to 7.6 +/- 2.1 cm x 10.2 +/- 1.8 cm at the end of the study. Post pubertal

bulls (>9 years, n = 6) examined prior to vaccination produced ejaculates with viable spermatozoa (volume: 8-175 ml, sperm concentration: 410-4000x10⁶/ml, total motility: 0-90%), while after 5-8 injections, only 50% of these bulls produced ejaculates with a small number of immotile spermatozoa. The ejaculates of group 2 bulls (vaccinated >8 times) were devoid of spermatozoa. Faecal androgen metabolite concentrations measured in captive males decreased significantly after the fourth vaccination. None of the males entered musth during the treatment period. **CONCLUSIONS:** Our results showed a marked decrease in semen quality, testicle and secondary sex gland sizes following repeated GnRH vaccinations. After 2-4 years of continuous treatment every 5-7 months, the effects were similar to surgical castration.

Lueders, I., T. B. Hildebrandt, C. Gray, S. Botha, P. Rich and C. Niemuller (2014). "**Suppression of testicular function in a male asian elephant (*Elephas maximus*) treated with gonadotropin-releasing hormone vaccines.**" Journal of Zoo and Wildlife Medicine **45**(3): 611-619.

The ability to control testosterone concentrations and sperm production is of great interest in both Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. GnRH vaccination may pose an alternative to surgical castration. This is a case report of a male Asian elephant treated with two commercial GnRH vaccines (Equity® and Improvac®). Beginning at the age of 7 yr, the male was vaccinated monthly for 6 consecutive months, then every 6 mo and, finally, every 12 to 24 mo over a period of 6 yr. In order to evaluate the GnRH vaccine as a potential method of immunologic castration, behavioral observations, testosterone level analysis, body weights, ultrasound examinations, and semen collection were part of the routine monitoring of this bull (no. 1) and a half-brother (bull 2) who remained untreated and served as control. The results showed a decrease in serum testosterone concentrations after the second booster. Levels stayed continuously below 5.0 ng/ml within the study period. The combined testicle diameter of 9.03 ± 0.3 cm prior to treatment had decreased to a size of 6.93 ± 0.19 cm (P < 0.001) when measured 2 yr later. Accessory sex gland fluid content disappeared and penile atrophy was observed. Semen collections yielded no spermatozoa 1 yr after the initial treatment. Bull 1 showed slowed weight gain as compared to bull 2 and, due to its friendly temperament and the absence of musth, remained in free contact. This report documents the GnRH vaccine as a possible noninvasive and inexpensive method for immunocastration. © 2014 American Association of Zoo Veterinarians.

Malhotra, A. K. and M. Kumar (2003). "**Management of musth Indian elephant at National Zoological Park, New Delhi.**" Zoos' Print Journal **18**: 10.

McGaughey, C. A. (1963). "**Musth.**" Ceylon Vet. J **11**: 105-107.

Molamure, A. H. E. (1969). "**Elephants -- Marginal notes on musth and mating.**" Loris **11**: 345-346.

Murwira, A. and A. K. Skidmore (2005). "**The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape.**" Landscape Ecology **20**(2): 217-234.

Based on the agricultural landscape of the Sebungwe in Zimbabwe, we investigated whether and how the spatial distribution of the African elephant (*Loxodonta africana*) responded to spatial heterogeneity of vegetation cover based on data of the early 1980s and early 1990s. We also investigated whether and how elephant distribution responded to changes in spatial heterogeneity between the early 1980s and early 1990s. Vegetation cover was estimated from a normalised difference vegetation index (NDVI). Spatial heterogeneity was estimated from a

new approach based on the intensity (i.e., the maximum variance exhibited when a spatially distributed landscape property such as vegetation cover is measured with a successively increasing window size or scale) and dominant scale (i.e., the scale or window size at which the intensity is displayed). We used a variogram to quantify the dominant scale (i.e., range) and intensity (i.e., sill) of NDVI based congruent windows (i.e., 3.84 km x 3.84 km in a 61 km x 61 km landscape). The results indicated that elephants consistently responded to the dominant scale of spatial heterogeneity in a unimodal fashion with the peak elephant presence occurring in environments with dominant scales of spatial heterogeneity of around 457-734 m. Both the intensity and dominant scale of spatial heterogeneity predicted 65 and 68% of the variance in elephant presence in the early 1980s and in the early 1990s respectively. Also, changes in the intensity and dominant scale of spatial heterogeneity predicted 61% of the variance in the change in elephant distribution. The results imply that management decisions must take into consideration the influence of the levels of spatial heterogeneity on elephants in order to ensure elephant persistence in agricultural landscapes.

Niemuller, C., P. A. Gentry and R. M. Liptrap (1990). "**Longitudinal study of haematological and biochemical constituents in blood of the Asian elephant (*Elephas maximus*).**" Comp. Biochem. Physiol. [A] **96**(1): 131-134.

1. Haematological parameters and biochemical analyses were determined in four elephants over a period of one year.
2. The haematological profile remained constant over time and was similar between animals.
3. Values for biochemical analyses were stable except for alkaline phosphatase, gamma glutamyl transferase and creatinine which rose during musth in male elephants.
4. The association of elevated enzyme levels and increased testosterone concentration is discussed.

Niemuller, C. and R. M. Liptrap (1991). "**Altered androstenedione to testosterone ratios and LH concentrations during musth in the captive male Asian elephant (*Elephas maximus*).**" J. Reprod. Fertil **91**(1): 139-146.

Greater concentrations of androstenedione than testosterone were usually present during periods of non-musth in plasma collected weekly for periods up to 2 years in 8 male Asian elephants (4-35 years of age). For the 6 males that exhibited musth the androstenedione/testosterone ratio shifted greatly in favour of testosterone. The severity of musth was assessed weekly using a scale of 1 to 5 for each of 8 behavioural traits including urine dribbling, temporal gland secretion and aggression. Brief shifts in the ratio of the two androgens when testosterone predominated (n=106) were seen during the non-musth period in 3 of the males studied continuously for 2 years. In 82% of these instances, stimuli of a sexual or aggressive nature had occurred in the preceding 48 h (χ^2 , $p < 0.01$). A heterologous bovine assay was used to measure LH values in plasma collected every 15 minutes for 12h. Increases in testosterone concentrations followed pulsatile increases in plasma LH concentrations during 7 non-musth periods in 4 animals. Apart from pulse frequency, increases in the variables describing pulsatile LH secretion were seen in 2 strong musth and 2 mild musth episodes compared to non-musth values. A strong musth, however, was characterized by a much greater increase in pulsatile testosterone secretion than was a mild musth and which may be a function of the duration of musth.

Niemuller, C. A. and R. M. Liptrap (1991). "**Altered androstenedione to testosterone ratios and LH concentrations during musth in the captive male Asian elephant (*Elephas maximus*).**" Journal of

Reproduction and Fertility **91**(1): 139-146.

Greater concentrations of androstenedione than testosterone were usually present during periods of non-musth in plasma collected weekly for various periods up to 2 years in 8 male Asian elephants (4-35 years of age). For the 6 males that exhibited musth the androstenedione/testosterone ratio shifted greatly in favour of testosterone. The severity of musth was assessed weekly using a scale of 1 to 5 for each of 8 behavioural traits including urine dribbling, temporal gland secretion and aggression. A significant correlation ($P < 0.05$) was noted between plasma testosterone concentrations and the musth score value in 5 of 6 musth episodes. Brief shifts in the ratio of the two androgens when testosterone predominated ($n = 106$) were seen during the non-musth period in 3 of the males studied continuously for 2 years. In 82% of these instances, stimuli of a sexual or aggressive nature had occurred in the preceding 48 h (χ^2 , $P < 0.01$). A heterologous bovine assay was used to measure LH values in plasma collected every 15 min for 12 h. Increases in testosterone concentrations followed pulsatile increases in plasma LH concentrations during 7 non-musth periods in 4 animals. Apart from pulse frequency, increases in the variables ribing pulsatile LH secretion were seen in 2 strong musth and 2 mild musth episodes compared to non-musth values. A strong musth, however, was characterized by a much greater increase in pulsatile testosterone secretion than was a mild musth and which may be a function of the duration of musth.

Niemuller-Hare, C., C. Gray and R. Liptrap (1988). **A preliminary report on musth in male Asian elephants.** Proc. Ann. Elephant Workshop 9.

Perrin, T. E., L. E. L. Rasmussen, R. Gunawardena and R. A. Rasmussen (1996). **"A method for collection, long-term storage, and bioassay of labile volatile chemosignals."** J. Chemical Ecology **21**: 207-221.

A procedure for headspace sampling and long-term storage of organic volatiles coupled with gas chromatographic-mass spectrometric (GC-MS) analysis was used to study the volatile chemosignals in a biological secretion prior to bioassay. The approach involved collecting the volatiles in evacuated canisters from an apparatus in which 1 ml of secretion was dispersed for headspace sampling. These canisters, stainless steel, 850 ml, and 100% internally electropolished, have been demonstrated to store volatile compounds, in chemically stable form, for several weeks. The GC-MS analyses provided the quantitation and identification of compounds from C_3 through C_{14} at concentrations as low as 0.10 parts per billion volume. The approach was used to study chemosignals of musth temporal gland secretions (TGS) from a male Asian elephant (*Elephas maximus*). Fresh TGS material loses its biological activity within 1 hr. TGS material stored at -20°C usually loses its activity within 30 days. The usefulness of this method for long-term storage of the volatile chemosignals was demonstrated by the retention of biologically active TGS headspace compounds, as determined through bioassays, stored in these canisters for one year.

Perrin, T. E. and L. E. L. Rasmussen (1994). **"Chemosensory responses of female Asian elephants (*Elephas maximus*) to cyclohexanone."** J. Chem. Ecol **20**: 2577-2586.

Cyclohexanone, a naturally occurring component of male Asian elephant temporal gland secretion, was tested as a candidate elicitor of bioresponses from female Asian elephants (*Elephas maximus*). Four female Asian elephants were presented with synthetic cyclohexanone samples during a standardized bioassay. Four types of bioresponses, some or all of which may be important in intersexual communication, were monitored: flehmen, palatal pit area contact, scrub, and check responses. Cyclohexanone evoked persistent responses of all bioresponse

types by two females, moderate response by a third female, and very few responses by a relatively unresponsive female. The results suggest that cyclohexanone may provide chemical information to females about male elephants, particularly regarding their state of musth.

Poole, J. H., L. H. Kasman, E. C. Ramsay and B. L. Lasley (1984). "**Musth and urinary testosterone concentrations in the African elephant (*Loxodonta africana*)**." *J. Reprod. Fertil* **70**(1): 255-260.

Urine samples were obtained from free-ranging African elephants that were considered to be in and out of musth. Testosterone concentrations, measured by radioimmunoassay were significantly greater in males that were in or around the time of behavioral musth. This study supports a correlation between the observed behavioral characteristics of musth and urinary testosterone levels.

Poole, J. H. (1987). "**Rutting behavior in African elephants: the phenomenon of musth**." *Behavior* **102**: 283-316.

Poole, J. H. (1989). "**Announcing intent: the aggressive state of musth in African elephants**." *Anim. Behav* **37**: 140-152.

Predictions derived from game theory suggest that animals should not signal their intentions during conflict situations. However, during the period of musth, male elephants, *Loxodonta africana*, announce a state of heightened aggression with signals that are unbluffable. Since smaller musth males in poor condition are able to dominate larger, normally higher-ranking, non-musth males in good condition, musth provides a useful system with which to examine the possibility of honest signaling of motivation, rather than of fighting ability. Despite the highly aggressive state of males in musth, escalated contests are extremely rare. The behaviour of musth and non-musth males suggests that opponents are able to estimate their often rapidly changing roles in the asymmetries with relative accuracy. Since, unlike most other rutting animals, elephants have asynchronous sexually active periods, resource value varies both with age and the fluctuating sexual state of a particular individual. It is suggested that musth may be a case where information about resource value is conveyed.

Poole, J. (1987). "**Elephants in musth, lust**." *Nat. Hist* **96**(11): 46-55.

Poole, J. (1987). "**Raging bulls**." *Animal Kingdom* **90**(6): 18-25.

Poole, J. (1989). "**Mate guarding, reproductive success and female choice in African elephants**." *Anim. Behav* **37**(5): 842-849.

Male guarding of females, male mating success and female choice were studied for 8 years among a population of African elephants, *Loxodonta africana*. Males were not able to compete successfully for access to oestrous females until approximately 25 years of age. Males between 25 and 35 years of age obtained mating during early and late oestrous, but rarely in mid-oestrus. Larger, older males ranked above the younger, smaller males and the number of females guarded by males increased rapidly late in life. Body size and longevity are considered important factors in determining the lifetime reproductive success of male elephants. Oestrous females exercised choice by soliciting guarding behavior from musth, but not non-musth males. Females in mid-oestrus gave loud, very low frequency calls that may attract distant males and incite male-male competition. The behavior of oestrous females resulted in their mating with males who were old, vigorous and healthy.

Poole, T. B., V. J. Taylor, S. B. U. Fernando, W. D. Ratnasooriya, A. Ratnayeke, G. A. Lincoln, A. M. V. R. Manatunga and A. S. Mcneilly (1997). "**Social behaviour and breeding physiology of a group of captive Asian elephants.**" *Int. Zoo Ybk* **35**: 297-310.

In 1986 at the Pinnawala Elephant Orphanage, Sri Lanka, a study of 4.4 Asian elephants *Elephas maximus* was carried out to establish the physical and behavioural changes associated with the female oestrous cycle and the male musth cycle. At Pinnawala the elephants are maintained in mixed-sex groups which has resulted in successful breeding. This paper describes the management of elephants at the orphanage and details their social and reproductive behaviour. It is suggested that successive matings throughout the oestrous cycle and on multiple cycles may be required to ensure successful breeding.

Poole, J. H. (1999). "**Signals and assessment in African elephants: evidence from playback experiments.**" *Animal Behaviour* **58**(1): 185-193.

A series of playback experiments using two elephant vocalizations, the 'musth rumble' and the 'oestrous call', was carried out in Amboseli National Park to examine signaling and assessment in African elephants, *Loxodonta africana*. In response to the musth rumble of a high-ranking male other musth males approached the speaker aggressively, whereas nonmusth males walked away from the stimulus. The call of an oestrous female, too, attracted musth males who approached the speaker rapidly, while nonmusth males listened and then walked away. Females listened and often showed considerable interest in the musth rumbles of males, approaching the speaker and sometimes responding by vocalizing and or secreting from the temporal glands. The experiments bear out earlier observational data and game theory predictions which suggest that by being in or out of musth a male may be conveying information about the relative value he places on contesting his dominance rank and his access to oestrous females. When not visibly in musth, a male may be indicating his intention not to contest access to oestrous females.

Poole, J. H. and C. J. Moss (1981). "**Musth in the African elephant, *Loxodonta africana*.**" *Nature* **292**(5826): 830-831.

The phenomenon of musth in male Asian elephants, *Elephas maximus*, has long been recognized¹. Musth, which has been likened to rutting behaviour in ungulates², refers to a set of physical and behavioural characteristics displayed periodically by adult male elephants. The most obvious manifestations are a sharp rise in aggressive behaviour, copious secretions from and enlargement of the temporal glands, and the continuous discharge of urine³. It has been speculated that a similar phenomenon occurs in males of the African genus, *Loxodonta africana*, but most workers have concluded that it does not exist⁴⁻⁷. Here we show that musth does occur in the African elephant and that its manifestations are similar to those in the Asian elephant. © 1981 Nature Publishing Group.

Prasad, A., M. T. Dinesh, P. S. Hareesh, S. Biju, S. Harikumar and P. C. Saseendran (2000). "**Analysis of musth episodes in captive Asian elephants (*Elephas maximus*).**" *Zoos' Print Journal* **15**(9): 322-327.

Analysis of data on musth episodes of 29 Asian elephants (*Elephas maximus*) collected from Punnathoor Kotta of Guruvayoor (1990-2000) revealed that the duration of musth was 99±36 days, increasing as age advances. Hours of bright sunshine had pronounced influence on the duration of musth. The number of elephants coming to musth showed peaks during January and August, which are the post monsoon periods in Kerala. Musth first occurred at 23 years of age (range 16 to 35).

Rajaram, A. and V. Krishnamurthy (2003). "**Elephant temporal gland ultrastructure and androgen secretion during musth.**" *Current Science* **85**(10): 1467-1471.

We have investigated the ultrastructure of the temporal gland of the Asian elephant (*Elephas maximus*) in the musth condition. We find that the organelles are highly evolved for the production of the androgen, testosterone which is reported to be very high in the Asian male elephant in full musth. The mitochondria bear cristae which are profuse and tubular, and occur along with many Golgi bodies. There is hypertrophy of smooth endoplasmic reticulum. All the structures involved in the production of androgen, as in the Leydig cell or the cells of the adrenal cortex, are thus found in abundance. Cellular structures also seem singularly evolved for the secretion of androgen and its degradation products.

Rasmussen, L. E. L., D. L. Hess and A. Hall-Martin (1990). "**Chemical profiles of temporal gland secretions from captive Asian bull elephants during musth and from African bull elephants living in wild but crowded conditions.**" *Chemical Senses* **15**: 628.

Full-text: This study compares the volatile components of the temporal gland secretions of captive Asian bull elephants in musth and a distinctive group of wild African bull elephants, confined to a national park. The captive Asian population has been well studied (Rasmussen *et al.*, 1984; Rasmussen, 1988). Serum testosterone was elevated at specific times; aggressive behaviors occurred concomitantly with temporal gland secretions, although aggression and elevated serum testosterone were not always related. Selected volatiles among the 23 compounds identified demonstrated concentration changes during the progression of musth, at times simultaneously with alterations in testosterone levels (Rasmussen *et al.*, in press). The African bull elephants have been monitored, behaviorally and physiologically, by radiocontrolled tracking and monthly sampling during the past 5 years. Aggressive behaviors similar to those of Asian bull elephants have been documented; serum and temporal gland testosterone were elevated concomitantly in a cyclical fashion similar to musth in Asian elephants. Chemical characterization of the volatiles of the temporal gland secretions from these bulls revealed several similarities to the compounds described in Asian bulls, including several compounds not previously described in African temporal gland secretions. It is suggested that these chemicals, or other, more ephemeral compounds, may chemically inform other bulls and cows of the musth-like state of these bulls.

Rasmussen, L. E. L. (1988). "**Chemosensory responses in two species of elephants to constituents of temporal gland secretion and musth urine.**" *J. Chem. Ecol* **14**(8): 1687-1711.

This report discusses three areas of investigation: (1) The chemical components in the temporal gland secretion (TGS) of Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants were characterized by radioimmunoassay (RIA) for testosterone (T) and dihydrotestosterone (DHT) levels and by on-column capillary column gas chromatographic analysis of volatiles. An inverse relationship between TGS testosterone levels and (E)-farnesol levels was observed. (2) African elephants responded preferentially toward a particular constituent of African elephant (TGS). (3) Urine from Asian bull elephants in musth was partially fractionated by high-performance liquid chromatography. Specific chromatographic regions elicited dramatic avoidance responses from female African elephants. These results support the suggestion that the TGS plays multiple chemocommunicative roles.

Rasmussen, L. E. L. and T. E. Perrin (1999). "**Physiological correlates of musth: lipid metabolites and**

chemical composition of exudates. " *Physiology and Behavior* **67**(4): 539-549.

Physiological changes related to lipid metabolism, behaviour and chemicals released in body exudates were studied during musth in the Asian elephant (*Elephas maximus*) as a case study. During musth, changes in serum testosterone and triglyceride concentrations followed similar patterns, with the former increasing sooner than the latter. Deviant behaviour increased during changing androgen levels. The observed high concentrations of testosterone were positively and significantly correlated with increased triglycerides. Lipase activity elevated significantly immediately before and after musth. Blood pH increased significantly in alkalinity. Urine and temporal gland secretions released variable amounts of compounds, some of which may be chemical signals. During musth, temporal gland and urinary exudates demonstrated increased acetone and other ketones indicative of lipid metabolic alterations. Large quantities of nonmethane hydrocarbons, especially 2-butanone, were released from the seemingly dry orifice of the temporal gland before the start of over musth and before maximum blood elevations were observed; isoprene release was similar. However, maximal acetone levels occurred simultaneously in blood, temporal gland secretions, and urine. Metabolically, musth is a series of interwoven, changing stages of increasing and decreasing hormones and lipid-related constituents. Released chemicals can be quantitatively related to these internal physiological events; some observed behaviours appear to result from altered chemical signals.

Rasmussen, L. E. L. (1999). "**Evolution of chemical signals in the Asian elephant, *Elephas maximus*: behavioural and ecological influences.**" *Journal of Biosciences* **24**(2): 241-251.

In antiquity, the Asian elephant, *Elephas maximus*, gradually spread southward and eastward to become a successfully surviving, ecologically dominant megaherbivore in the tropical environment of south-east Asia. The changing physical environment forced dynamic fluxes in its social structure and altered its metabolism. Such events shaped the production and ultimately the stability of certain chemicals released by body effluvia. Some of these chemicals took on significance as chemical signals and/or pheromones. This article demonstrates by experimental and observational evidence, and hypothesizes based on speculative reasoning, how and why specific chemical signals evolved in the modern Asian elephant. Evidence, including the functional criteria required by elephant social structure and ecology, is presented for the hypothesis that the recently identified female-emitted, male-received sex pheromone, (Z)-7-dodecenyl acetate evolved first as a chemical signal. Subsequently, the cohesiveness and harmony of small, matriarchally-led female groups were strengthened by a female-to-female chemical signal, recently defined behaviourally. The looser societal structure of freer, roaming males also became bounded by chemical signals; for the males, breath and temporal gland emissions, as well as urinary ones function in chemical signaling. Basic knowledge about elephant chemical signals is now linking chemical information to behaviour and beginning to demonstrate how these signals affect elephant social structure and enable the species to cope with environmental changes.

Rasmussen, L. E. L. and B. A. Schulte (1998). "**Chemical signals in the reproduction of Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants.**" *Animal Reproduction Science* **53**(1-4): 19-34.

Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants exhibit polygynous mating that involves female choice of mates and male-male competition for access to females. Chemical signals mediate intersexual and intrasexual interactions associated with reproduction. The need for reliable and honest signals is accentuated by the markedly different social structure of adult males and females. Adult female elephants live in matriarchal herds consisting

of a dominant female and several generations of offspring. Adult males are solitary or travel with other males except during breeding periods. Because females have a long 16-week oestrous cycle with a brief 1-week receptive period and a 4-5 year interval between births, a sexually active female is a limited resource. Asian elephant females advertise a forthcoming ovulation by releasing (Z)-7-dodecen-1-yl acetate in their urine during the preovulatory period. African elephants probably produce a sex pheromone as well. Females regularly contact the ano-genital region of other females and show heightened chemosensory responsiveness to urine during the follicular phase. The physiological impacts of this ability to detect reproductive condition (e.g. possible synchronizing or suppressing of oestrus) are uncertain. Males experience an annual period of heightened aggressiveness and highly elevated testosterone concentrations known as musth. Males secrete fluid copiously from their temporal gland and dribble strongly odoriferous urine during musth. Females appear to prefer musth males as mates, and captive Asian females exhibit greater chemosensory responses to urine from males in musth than not. Males in musth are competitively dominant to all other males, even those larger than themselves. Nonmusth males avoid males in musth, and captive Asian bulls show greater interest in musth than nonmusth urine. In captivity subordinate Asian females back away from musth secretions, and females with calves sometimes display protective behaviour. Clearly, chemical signals play an important role in communication by elephants between and within the sexes. Further work is needed to identify more of these chemical messengers and to understand their complete function in mediating reproductive interactions in the elephant social system.

Rasmussen, L. E. L. and V. Krishnamurthy (2000). "**How chemical signals integrate Asian elephant society: the known and the unknown.**" *Zoo Biology* **19**(5): 405-423.

The importance of chemical senses to elephants was recognized in anecdotal observations by ancient humans. Modern scientific tools, such as molecular biological techniques, highly sensitive gas chromatographic/mass spectrometric instrumentation, and statistically valid ethological methods, have allowed the study of real events of chemical communication between elephants. Such communication encompasses long- and short-range navigation, relationship recognition, and inter- and intra-sexual exchange of reproductive condition, metabolic state, and social status. Asian elephants emit large amounts of complex chemical mixtures in breath and urine, and in secretions from the temporal gland, inter-digital glands, and ears. Some emitted chemicals originate in blood and may be metabolic products; others are secretory products, at times apparently under hormonal control. The wide variety of emitted compounds includes hormones, proteins, and volatile compounds; selected volatile ketones and an acetate ((Z)-7-dodecanyl acetate) function as chemical signals and a pheromone, respectively. Some of these specific chemicals identified in emissions from Asian elephants dwelling in the United States have been found to be present in the exudates from elephants in India. This similarity is demonstrable for three metabolic conditions: pregnancy in females and pre- and post-musth males. Future chemical communication studies on male elephants should focus on musth and its relevance to reproduction and male social structures. Such investigations should include hormones, metabolites, brain chemistry, and possible primer pheromones. For females, the factors influencing possible estrous synchrony, what role primer pheromones play in female reproduction, how chemical signals influence social behavior, and whether luteinizing hormone influences pheromone production are among remaining fundamental questions.

Rasmussen, L. E. and G. Wittemyer (2002). "**Chemosignalling of musth by individual wild African elephants (*Loxodonta africana*): implications for conservation and management.**" *Proc R Soc Lond B*

Biol Sci **269**(1493): 853-860.

Elephants have extraordinary olfactory receptive equipment, yet this sensory system has been only minimally investigated in wild elephants. We present an in-depth study of urinary chemical signals emitted by individual, behaviourally characterized, wild male African elephants, investigating whether these compounds were the same, accentuated, or diminished in comparison with captive individuals. Remarkably, most emitted chemicals were similar in captive and wild elephants with an exception traced to drought-induced dietary cyanates among wild males. We observed developmental changes predominated by the transition from acids and esters emitted by young males to alcohols and ketones released by older males. We determined that the ketones (2-butanone, acetone and 2-pentanone, and 2-nonanone) were considerably elevated during early musth, musth and late musth, respectively, suggesting that males communicate their condition via these compounds. The similarity to compounds released during musth by Asian male elephants that evoke conspecific bioresponses suggests the existence of species-free 'musth' signals. Our innovative techniques, which allow the recognition of precise sexual and musth states of individual elephants, can be helpful to managers of both wild and captive elephants. Such sampling may allow the more accurate categorization of the social and reproductive status of individual male elephants.

Rasmussen, L. E., H. S. Riddle and V. Krishnamurthy (2002). "**Mellifluous matures to malodorous in musth.**" Nature **415**(6875): 975-976.

Male Asian elephants in musth--an annual period of heightened sexual activity and intensified aggression--broadcast odoriferous, behaviourally influential messages from secretions of the temporal gland. From our observations in the wild, together with instantaneous chemical sampling and captive-elephant playback experiments, we have discovered that young, socially immature males in musth signal their naivety by releasing honey-like odors to avoid conflict with adult males, whereas older musth males broadcast malodorous combinations to deter young males, facilitating the smooth functioning of male society. As elephant--human conflicts can upset this equilibrium, chemically modulating male behaviour may be one way to help the conservation of wild elephants.

Rasmussen, L. E. L., A. J. Hall-Martin and D. L. Hess (1996). "**Chemical profiles of African bull elephants, *Loxodonta africana*: physiological and ecological implications.**" Journal of Mammalogy **77**(2): 422-439.

This study reports concentrations of testosterone and dihydrotestosterone in both serum and temporal-gland secretion of male African elephant (*Loxodonta africana*), including radiocollared elephants, and identifies a spectrum of volatile components in the temporal-gland secretions. Androgens in the serum (testosterone and dihydrotestosterone) were measured in 111 adult male African elephants, ages 21-40 years, from two national parks in South Africa during several years and seasons. About one-fifth (18.6%) of these mature, male, African elephants exhibited dramatically increased concentrations of testosterone in serum characteristic of male Asian elephants during musth. In Krueger National Park, six radiocollared male African elephants, ages 25-35 years, were tracked and serially samples for both serum and temporal-gland secretions during a 5-year period. Concentrations of testosterone in serum and temporal gland secretions were elevated cyclically at times when typical musth behaviors, including aggression, were observed. This study reports the first chemical characterization of the volatile compounds of the temporal gland secretions from male African elephants in musth. It reveals many similarities between the chemical constituents of the temporal-gland secretions of these male African elephants and the compounds identified in male Asian elephants. In addition,

several compounds, not previously identified in temporal-gland secretions of African elephants, are described. Such chemical data support the behavioral observations by ourselves and other researchers that male African elephants experience musth. Especially convincing are the concurrent hormonal and chemical data from the radiocollared males during episodic periods of behavioral musth. Implications of the incidence of musth in the past and present ecology of African elephants are discussed in view of the increasing compression within national parks.

Rasmussen, L. E. L. and B. A. Schulte (1999). Ecological and biochemical constraints on pheromonal signaling systems in Asian elephants and their evolutionary implications. **Advances in Chemical Communication in Vertebrates 8**. R. E. Johnston, D. Muller-Schwarze and P. W. Sorenson, Kluwer/Academic/ Plenum Press: 49-62.

The Asian elephant is an unusual example of how intraspecies chemical communication helps maintain societal cohesiveness within familial and herd units. The amount of multi-directional chemical communication is surprising, because long-lived elephants have a highly organized society, are capable of trans-generational passage of information, possess a sophisticated vocalization system, and are capable of complex learning and tool use. This paper discusses the ecological, behavioral, and biochemical aspects of chemical signals in elephants from an evolutionary perspective. Diverse bodily emissions are utilized as intraspecies chemical signals (including pheromones), often with imposed biochemical constraints. In this chapter, chemosignals released from the temporal gland secretions and breath of male Asian elephants in musth and a urinary female-to-male preovulatory pheromone are utilized as examples of these concepts. Furthermore, specific behavioral and biochemical studies with (Z)-7-dodecenyl acetate (a female-to-male urinary sex pheromone) demonstrate that social context significantly influences responsivity (demonstrated by field studies in Myanmar) and that additional biochemical requirements, perhaps lipocalin-like proteins, may be required for full bioactivity. The remarkable convergent evolution of (Z)-7-dodecenyl acetate, both structurally and functionally, in elephants and Lepidoptera, allows the use in elephant studies of effective biochemical tools developed for insect investigations. This convergence of chemical signaling systems of elephants and insects has several interesting implications.

Rasmussen, L. E. L., R. A. Gunawardena and R. A. Rasmussen (1997). "**Do Asian elephants, especially males in musth, chemically signal via volatiles in breath?**" Chemical Senses 22: 775.

Rasmussen, L. E. L., T. E. Perrin, R. A. Rasmussen and R. Gunawardena (1994). "**Isolation of potential musth-alerting signals from temporal gland secretions of male Asian elephants (*Elephas maximus*).**" Chemical Senses 19: 540.

Rasmussen, L. E. L. (1998). "**Chemical communication: An integral part of functional Asian elephant (*Elephas maximus*) society.**" Ecoscience 5(3): 410-426.

The matriarchally organized Asian elephant society is characterized by long-term stability and continuity. Flux within this society results from changing ecological conditions and the dynamics of its population. Its structure is influenced by age composition and physiological states within the female herd and by impinging influences of the peripheral males, especially during reproductive times. Recent behavioral studies of captive populations have substantiated older field studies and have demonstrated that chemical signals play a significant role in elephant society. Chemical investigations, based on previously substantiated behavioral interactions, have identified specific compounds or combinations of compounds in elephant emissions

(especially urine, temporal gland secretions and breath) that retain bioactivity throughout chemical extractions and playback experiments, based on behavioral and/or chemosensory responses. Chemosensory neuroreceptive systems in Asian elephants are reviewed, as well as behavioral and chemosensory effects of whole exudate chemical signals on lifestyles, especially related to mating. Several discrete and composite chemical signals have been deciphered in elephants, one of which is a preovulatory female-to-male pheromone, (Z)-7-dodecen-1-yl acetate. This pheromone and other recently described or potential chemical signals are compared to compounds in insect pheromone blends. Such knowledge of the chemical ecology of the Asian elephant has potentially important implications for conservation.

Rasmussen, L. E. L. and H. S. Riddle (2001). **Musth in Teenage Male Asian Elephants (*Elephas maximus*): The What & the Why of their Chemical Signals**. A Research Update on Elephants and Rhinos; Proceedings of the International Elephant and Rhino Research Symposium, Vienna, June 7-11, 2001, Schuling Verlag.

Rasmussen, L. E. L., H. S. Riddle and V. Krishnamurthy (2002). "**Mellifluous matures to malodorous in musth; Mood-altering secretions by excited male elephants smooth out social interactions.**" *Nature* **415**: 975-976.

Rasmussen, L. E. and D. R. Greenwood (2003). "**Frontalin: a chemical message of musth in Asian elephants (*Elephas maximus*).**" *Chemical Senses* **28**(5): 433-446.

Musth is an important male phenomenon affecting many aspects of elephant society including reproduction. During musth, the temporal gland secretions (as well as the urine and breath) of adult male Asian elephants (*Elephas maximus*) discharge a variety of malodorous compounds together with the bicyclic ketal, frontalin. In contrast, teenage male elephants in musth release a sweet-smelling exudate from their facial temporal gland. We recently demonstrated that the concentration of frontalin becomes increasingly evident as male elephants mature. In the present study, we demonstrate that behaviors exhibited towards frontalin are consistent and dependent on the sex, developmental stage and physiological status of the responding conspecific individual. To examine whether frontalin functions as a chemical signal, perhaps even a pheromone, we bioassayed older and younger adult males, and luteal- and follicular-phase and pregnant females for their chemosensory and behavioral responses to frontalin. Adult males were mostly indifferent to frontalin, whereas subadult males were highly reactive, often exhibiting repulsion or avoidance. Female chemosensory responses to frontalin varied with hormonal state. Females in the luteal phase demonstrated low frequencies of responses, whereas pregnant females responded significantly more frequently, with varied types of responses including those to the palatal pits. Females in the follicular phase were the most responsive and often demonstrated mating-related behaviors subsequent to high chemosensory responses to frontalin. Our evidence strongly suggests that frontalin, a well-studied pheromone in insects, also functions as a pheromone in the Asian elephant: it exhibits all of the determinants that define a pheromone and evidently conveys some of the messages underlying the phenomenon of musth. Department of Biochemistry and Molecular Biology, OGI School of Science and Engineering, Oregon Health & Science University, Beaverton, OR 97006-8921, USA. betsr@bmb.ogi.edu

Rasmussen, B. (2003). "**Why musth elephants use pheromones?**" *Biologist* **50**(4): 195-196.

Rasmussen, L. E. L., V. Krishnamurthy and R. Sakumar (2005). "**Behavioural and chemical confirmation of the preovulatory pheromone, (Z)-7-dodecenyl acetate, in wild Asian elephants: its relationship to musth.**" *Behaviour* **142**(3): 351-396.

Mammalian breeding strategies vary depending on particular social contexts and sensory systems emphasized in various species. Among sexually dimorphic non-territorial Asian elephants, *Elephas maximus*, a multiplex olfactory chemical signaling system has been implicated in ensuring effective reproduction. This study explores how, using chemosensory mechanisms, widely roaming, wild male elephants locate periovulatory females in matriarchal-led female family units and precisely assess their ovulatory status. In this species, the dual obstacles of separately living sexes and infrequent oestrus are overcome by lengthy female cycles. During an extended preovulatory period captive females release increasing concentrations of the urinary pheromone (Z)-7-dodecenyl acetate, timed to reach a maximum just before ovulation. The current field studies combined chemical identification and quantification of female urinary (Z)-7-dodecenyl acetate with behavioural observations, monitoring the frequencies of chemosensory responses and pre-mating behaviours by various categories of males. The results suggest the temporal extension of the preovulatory period effectively provides a synchrony between sexes for successful reproduction. Male elephants undergo a two-decade-long maturation process that involves physical, sexual, social, and physiological maturation. Males older than 30 years are generally large, sexually active, socially adept and capable of sustaining long periods of musth, during which they release secretions distinctive of adult musth. These older adult males in musth demonstrated significantly more chemosensory responses and pre-mating behaviours than their younger or non-musth counterparts; they apparently are more skilled at detecting the precise ovulatory status of females. Male-male interactions are affected by size, age, and musth; the winners gain greater access to females, as indicated by the high incidence of mate guarding. The Asian elephant shares some breeding tactics common to other mammals including some primates (e.g. orangutans) and whales, while the musth parameter adds a unique feature. Fusion-fission events are influenced by elephant reproductive strategies, as roving males join female groups while tracking preovulatory pheromone concentrations.

Rasmussen, H. B., A. Ganswindt, I. Douglas-Hamilton and F. Vollrath (2008). "**Endocrine and behavioral changes in male African elephants: linking hormone changes to sexual state and reproductive tactics.**" *Horm. Behav.* **54**(4): 539-548.

Hormones play a crucial role in mediating genetic and environmental effects into morphological and behavioral phenotypes. In systems with alternative reproductive tactics (ART) shifts between tactics are hypothesized to be under proximate hormonal control. Most studies of the underlying endocrine changes behind ART have focused on fish and amphibians rather than mammals and few have investigated the potential interaction between different endocrine axes in regulating shifts between conditional dependent tactics. Using a combination of endocrine and behavioral data from male African elephants we expand on our previously published analysis and show that the initial increase in androgens predates the behavioral shifts associated with reproductively active periods, supporting the role of androgens in activating sexually active periods in males. A strong interactive effect between androgens and glucocorticoids was found to determine the presence or absence of temporal gland secretion and urine dribbling, signals associated with the competitive reproductive tactic of musth, with elevated glucocorticoids levels suppressing the occurrence of musth signals. In addition external environmental conditions affected hormone levels. The presence of receptive females resulted in elevated

androgens in dominant musth males but increased glucocorticoids in subordinate non-musth males. The presented data on hormones, behavior and reproductive tactics strongly support an underlying endocrine mechanism for mediating the translation of intrinsic as well as extrinsic local conditions into the conditional dependent reproductive tactics in male elephants via interactions between the hypothalamic-pituitary-gonadal and -adrenal axes

Rasmussen, L. E., D. L. Hess and J. D. Haight (1990). "**Chemical analysis of temporal gland secretions collected from an Asian bull elephant during a four-month musth episode.**" J Chem Ecol **16**(7): 2167-2181.

The temporal glands, modified facial apocrine sweat glands unique to elephants, release collectable secretions during an unusual physiological state termed "musth" in the Asian bull elephant (*Elephas maximus*). Recently we began the characterization of the chemical components of musth, especially in the temporal gland secretions (TGS), and the examination of the role of such secretions as agents for chemical communication between elephants. The present study focuses on possible correlations between testosterone levels in the serum and temporal gland secretions. We were especially interested in possible qualitative and/or quantitative changes in volatile compounds as the testosterone levels varied during a discrete musth period. Quantitative changes in TGS and serum testosterone were determined by radioimmunoassay. Qualitative and semiquantitative changes occurring in volatile composition were studied by high-resolution gas chromatography (fused silica capillary column, on column injection). Compound identification was by nuclear magnetic resonance, gas chromatography-mass spectrometry, and gas chromatography internal standards. Twenty-three major compounds and a number of minor components were identified. Androgen concentrations were correlated with TGS-specific volatiles including benzoic acid, 2-nonanone, 5-nonanol, tetradecanoic acid, and decanoic acid. The latter two compounds and (E)-farnesol, a major component of African TGS, demonstrated an inverse relationship to T levels.

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Rasmussen, H. B., J. B. A. Okello, G. Wittemyer, H. R. Siegismund, P. Arctander, F. Vollrath and I. Douglas-Hamilton (2008). "**Age- and tactic-related paternity success in male African elephants.**" Behavioral Ecology **19**(1): 9-15.

Information on age- and tactic-related paternity success is essential for understanding the lifetime reproductive strategy of males and constitutes an important component of the fitness trade-offs that shape the life-history traits of a species. The degree of reproductive skew impacts the genetic structure of a population and should be considered when developing conservation strategies for threatened species. The behavior and genetic structure of species with large reproductive skew may be disproportionately impacted by anthropogenic actions affecting reproductively dominant individuals. Our results on age- and tactic-specific paternity success in male African elephants are the first from a free-ranging population and demonstrate that paternity success increases dramatically with age, with the small number of older bulls in the competitive state of musth being the most successful sires. However, nonmusth males sired 20% of genotyped calves, and 60% of mature bulls (>20 years old) were estimated to have sired offspring during the 5-year study period. The 3 most successful males sired less than 20% of the genotyped offspring. Hence, contrary to prediction from behavior and life-history traits, reproduction was not heavily skewed compared with many other mammalian systems with a similar breeding system. Nevertheless, these results indicate that trophy hunting and ivory poaching, both of which target older bulls, may have substantial behavioral and genetic effects on elephant populations. In addition, these results are critical to the current debate on methods for managing and controlling increasing populations of this species. © The Author 2007. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved.

Rasmussen, L. E. L. and G. Wittemyer (2002). "**Chemosignalling of musth by individual wild African elephants (*Loxodonta africana*): Implications for conservation and management.**" Proceedings of the Royal Society B: Biological Sciences **269**(1493): 853-860.

Elephants have extraordinary olfactory receptive equipment, yet this sensory system has been only minimally investigated in wild elephants. We present an in-depth study of urinary chemical signals emitted by individual, behaviourally characterized, wild male African elephants, investigating whether these compounds were the same, accentuated, or diminished in comparison with captive individuals. Remarkably, most emitted chemicals were similar in

captive and wild elephants with an exception traced to drought-induced dietary cyanates among wild males. We observed developmental changes predominated by the transition from acids and esters emitted by young males to alcohols and ketones released by older males. We determined that the ketones (2-butanone, acetone and 2-pentanone, and 2-nonanone) were considerably elevated during early musth, musth and late musth, respectively, suggesting that males communicate their condition via these compounds. The similarity to compounds released during musth by Asian male elephants that evoke conspecific bioresponses suggests the existence of species-free 'musth' signals. Our innovative techniques, which allow the recognition of precise sexual and musth states of individual elephants, can be helpful to managers of both wild and captive elephants. Such sampling may allow the more accurate categorization of the social and reproductive status of individual male elephants.

Rasmussen, L. E., I. O. Buss, D. L. Hess and M. J. Schmidt (1984). "**Testosterone and dihydrotestosterone concentrations in elephant serum and temporal gland secretions.**" *Biology of Reproduction* **30**(2): 352-362.

Serum and temporal gland secretions (TGS) were obtained from mature wild African (*Loxodonta africana*) and captive Asian elephants (*Elephas maximus*). Samples were obtained from five cows and eight bulls culled for management purposes in Kruger National Park, South Africa, and from four females and two males residing at the Washington Park Zoo, Portland, Oregon. Our purpose was to describe the levels of the androgens, testosterone (T), and dihydrotestosterone (DHT), and to correlate these observations with sex, species and behavioral status. Male-female differences in serum T were pronounced in the Asian species, whereas male and female concentrations overlapped in the African elephant serum. Serum T concentrations in African females were greater than in Asian females. Serum DHT reflected T levels, except that the striking elevation of testosterone in Asian bulls during musth was not paralleled by equal increases in DHT levels. A species difference observed among males was higher serum T levels in nonmusth Asian bulls (1.84-5.35 ng/ml) compared to the levels in African bulls (0.38-0.68 ng/ml), except for one dominant African bull (6.64 ng/ml). This single African value was still considerably lower than the serum T values of the Asian males during musth. These musth values were the highest serum androgen concentrations: T was between 19 and 40 ng/ml (average 26.10 ng/ml). The TGS values of T and DHT were much higher than serum levels except in the Asian female. T/DHT ratios in TGS were more similar than in serum. One dominant African bull had a T TGS value of 78 ng/ml, which was much higher than the rest of the African males or females, but considerably lower than as Asian bull in musth (547 ng/ml). It seems apparent that a change in androgen status as reflected in serum and TGS levels of T and DHT precedes or is concomitant with overt alteration in behavior in the Asian male. The temporal gland appears to actively concentrate androgens in both African males and females, but in the Asian male the gland secretes only during musth when the greatest concentration of both T and DHT were observed. The apparent difference in the degree of temporal gland secretory activity between the two species suggests a more specific communicative function within the Asian male.

Rasmussen, L. E. L., V. Krishnamurthy and R. Sukumar (2005). "**Behavioural and chemical confirmation of the preovulatory pheromone, (Z)-7-dodecenyl acetate, in wild Asian elephants: Its relationship to musth.**" *Behaviour* **142**(3): 351-396.

Mammalian breeding strategies vary depending on particular social contexts and sensory systems emphasized in various species. Among sexually dimorphic non-territorial Asian elephants, *Elephas maximus*, a multiplex olfactory chemical signaling system has been

implicated in ensuring effective reproduction. This study explores how, using chemosensory mechanisms, widely roaming, wild male elephants locate periovulatory females in matriarchal-led female family units and precisely assess their ovulatory status. In this species, the dual obstacles of separately living sexes and infrequent oestrus are overcome by lengthy female cycles. During an extended preovulatory period captive females release increasing concentrations of the urinary pheromone (Z)-7-dodecenyl acetate, timed to reach a maximum just before ovulation. The current field studies combined chemical identification and quantification of female urinary (Z)-7-dodecenyl acetate with behavioural observations, monitoring the frequencies of chemosensory responses and pre-mating behaviours by various categories of males. The results suggest the temporal extension of the preovulatory period effectively provides a synchrony between sexes for successful reproduction. Male elephants undergo a two-decade-long maturation process that involves physical, sexual, social, and physiological maturation. Males older than 30 years are generally large, sexually active, socially adept and capable of sustaining long periods of musth, during which they release secretions distinctive of adult musth. These older adult males in musth demonstrated significantly more chemosensory responses and pre-mating behaviours than their younger or non-musth counterparts; they apparently are more skilled at detecting the precise ovulatory status of females. Male-male interactions are affected by size, age, and musth; the winners gain greater access to females, as indicated by the high incidence of mate guarding. The Asian elephant shares some breeding tactics common to other mammals including some primates (e.g. orangutans) and whales, while the musth parameter adds a unique feature. Fusion-fission events are influenced by elephant reproductive strategies, as roving males join female groups while tracking preovulatory pheromone concentrations. © Koninklijke Brill NV, 2005.

Santiapillai, C., B. Read, G. Jacobson, S. Wijeyamohan and S. Rambukpotha (2011). "**A PARADIGM SHIFT IN THE MANAGEMENT OF MUSTH AMONG BULL ELEPHANTS IN CAPTIVITY IN SRI LANKA.**" Ceylon Journal of Science Biological Sciences **40**(1): 25-32.

The phenomenon of musth among Asian elephants has been known since ancient times. Musth is a temporary post-pubertal, reproductive phenomenon commonly observed in the healthy male Asian elephant (*Elephas maximus*) both in the wild and in captivity. However, the treatment of musth bulls in Asia has remained almost unchanged. The traditional way of dealing with musth bulls involves restraining the animals by tethering them to trees and reducing the food intake so as to weaken them, with the assumption that they would drop out of musth faster. But such methods can cause severe wounds on the legs from the ropes used to tie the animals, and make the bulls more aggressive and traumatic, thereby posing a serious danger to their keepers or mahouts. The alternative method described in the paper provides a strong, safe, and secure tool for the management of musth bulls in captivity. The method not only assures the safety of the bulls but ensures that of the mahouts as well. Being a predominantly Buddhist country, Sri Lanka can lead the way in promoting the bull pen as an alternative tool in the management of bulls in musth, while assuring the utmost safety of their keepers.

Sarma, K. K. (2001). **Musth in Asian Elephant**. New Delhi, India, Central Zoo Authority.

Sarma, K. K. (2003). Managing troublesome bulls with special reference to musth in captive Asian elephants. **Healthcare, Breeding and Management of Asian Elephants**. D. Das. New Delhi, Project Elephant. Govt. of India: 58-66.

Sarma, K. K. and B. Dutta (1996). "**Musth and its management in Asian elephant: a discussion based on four clinical cases.**" Zoos' Print Journal April: 21-22.

Schmidt-Burbach, J., D. Ronfot and R. Srisangiam (2015). "**Asian Elephant (*Elephas maximus*), Pig-Tailed Macaque (*Macaca nemestrina*) and Tiger (*Panthera tigris*) Populations at Tourism Venues in Thailand and Aspects of Their Welfare.**" PLoS ONE 10(9).

This study focused on determining the size and welfare aspects of Asian elephant, pig-tailed macaque and tiger populations at facilities open to tourists in Thailand. Data were gathered from 118 venues through direct observations and interviews with staff. A score sheet-based welfare assessment was used to calculate scores between 1 and 10, indicating each venue's welfare situation. Factors such as freedom of movement for the animals, access to veterinary care, environmental noise quality, hygiene standards and work intensity were included in the score sheet. 1688 elephants, 371 macaques and 621 tigers were found at the venues. 89 venues exclusively kept elephants, 9 designated 'Monkey schools' offered macaque shows, 4 venues kept primarily tigers, mostly for petting and photo opportunities, and the remaining venues kept a mix of these animals. A strong imbalance in female to male gender ratios was recorded with about 4: 1 for adult elephants and 1: 4 for adult macaques. Severely inadequate welfare conditions were common, with 75% of macaques and 99% of tigers being kept at venues with scores less than 5. 86% of elephants were kept in inadequate conditions at venues with scores between 3 and 5, but a significant number of venues with scores above 5 were found. 4.6% of elephants were provided commendable conditions, reaching assessment scores of 8 and above. 71% of venues did not offer any sort of education about animals to visitors. This study is the first to assess welfare aspects of captive wild animals at tourism venues across Thailand. It concludes that significant concerns exist about the welfare of wild animals in the tourism sector of Thailand. Urgent attention needs to be given to address these concerns and prevent further suffering. But also to ensure the demand for wild animals doesn't have a negative impact on wild populations.

Schulte, B. A. and L. E. Rasmussen (1999). "**Signal-receiver interplay in the communication of male condition by Asian elephants.**" Animal Behaviour 57(6): 1265-1274.

Signal design and meaning are dependent on the condition of the sender and receiver as well as the response of the receiver. This study examined (1) whether female Asian elephants, *Elephas maximus*, can distinguish between a conspecific male in musth and nonmusth states using urinary signals, (2) how the oestrous condition of the female affects discrimination, and (3) correlation of female responses with the testosterone level of the male. Musth is a rut-like state displayed by healthy adult male elephants. Males in musth dominate nonmusth males and may be preferred by females as mates. Urine was collected from two captive male Asian elephants during nonmusth periods and from one of these males during times of musth. Samples of musth and nonmusth urine and control liquids were placed in an elephant enclosure weekly for 16 weeks, the length of a female oestrous cycle. Primary response behaviours were approach and four trunk-tip motions, namely sniff, check, place and flehmen. Musth urine consistently elicited greater responses than nonmusth and control samples. Females were more responsive during their follicular (sexually receptive) than luteal (unreceptive) stages of oestrus. Furthermore, females appeared to be sensitive to the degree of musth as responses increased with rising serum testosterone levels of the male donor. Chemical signals from males are a likely source of honest signals related to status and reproductive condition. Female elephants appear capable of detecting differences in a male based upon urinary chemosignals.

Schulte, B. A. and L. E. L. Rasmussen (1999). Musth, sexual selection, testosterone and metabolites. **Advances in Chemical Communication in Vertebrates 8**. R. E. Johnston, D. Muller-Schwarze and P. W. Sorenson, Kluwer Academic/Plenum Press: 383-397.

Musth is an annual, yet asynchronous, rut-like condition that is experienced by many adult African and Asian male elephants. Behaviorally, musth is characterized by heightened aggression, decreased feeding, urine dribbling, temporal gland secretion and enhanced sexual activity. Musth improves the access of a male to reproductively active females through increased mobility and a higher dominance ranking (intrasexual competition). Whether females prefer males in musth as mates is as yet uncertain (intersexual choice). Females can distinguish among the odors of males in musth and nonmusth. Although behavioral musth has been associated with greatly elevated plasma testosterone levels, a recent study in Sri Lanka shows that intensified aggressiveness follows maximal testosterone secretion and proposes that behavioral musth is a consequence of declining androgen levels. Our data from an Asian male elephant in North America suggest that either declining or rising serum testosterone may be related to "musth behaviors." Our report demonstrates that certain aspects of body physiology are greatly altered during musth. Rather than a single state, our data suggest that musth is an ever-changing condition with some typical stages. Specific chemical compounds released at different stages of musth may serve individually or in combination as honest signals of male condition.

Schulte, B. A. (2001). **Examining Ideas on the Evolution of Musth**. A Research Update on Elephants and Rhinos; Proceedings of the International Elephant and Rhino Research Symposium, Vienna, June 7-11, 2001, Schuling Verlag.

Shannon, G., B. R. Page, K. J. Duffy and R. Slotow (2006). "**The consequences of body size dimorphism: Are African elephants sexually segregated at the habitat scale?**" *Behaviour* **143**(9): 1145-1168.

Sexual segregation is a commonly observed phenomenon in dimorphic ungulates, which has been categorised into two distinct components: social segregation and habitat segregation. In this study we investigated whether elephants were sexually segregated at the habitat scale. The locations of 12 family groups and 16 males, in three distinct populations were recorded over a period of 2.5 years. Selection ratios were calculated for each habitat type and a Kendall's coefficient of concordance was used for the analyses. The habitat and foraging preferences were firstly tested for concordance within sex, and then between the sexes. Female habitat preferences showed significant concordance across all reserves and they also exhibited strong concordance in their summer foraging preferences. Their weakest association with habitat and foraging preference was during winter, which may be related to resource scarcity. Males exhibited significant concordance in their habitat preferences in two out of the three reserves. They had their weakest associations in the summer months and this may be linked to avoidance of other males in musth and the abundance of forage. There were no significant differences in habitat preference between males and females and it is likely that individual preferences vary as much within sex as between sexes. Differential habitat utilisation does not appear to be driving sexual segregation in elephants and it is postulated that sociality, divergent reproductive strategies and foraging behaviour at the plant scale play a more significant role. The results of this study highlight the importance of scale in elucidating the mechanisms involved in sexual segregation. © Koninklijke Brill NV, 2006.

Shaw, W. (1900). "**Castration of an elephant.**" Vet. J. London **2**: 151-152.

Siegel, R. K. (1984). "**LSD-induced effects in elephants: comparisons with musth behavior.**" Bull. Psychonom. Soc **22**(1): 53-56.

Musth is a condition observed in male Asiatic elephants and is characterized by aggression and temporal gland secretion. A classic and controversial 1962 study attempted to induce a musth syndrome in an elephant via treatment with LSD. Two elephants in the present study survived dosages of LSD (.003 -.10 mg/kg) and exhibited changes in the frequency or duration of several behaviors as scored according to a quantitative observational system. LSD increased aggression and inappropriate behaviors such as ataxia. Results are discussed in terms of musth and drug-induced perceptual-motor dysfunction.

Smit, I. P. J., C. C. Grant and I. J. Whyte (2007). "**Landscape-scale sexual segregation in the dry season distribution and resource utilization of elephants in Kruger National Park, South Africa.**" Diversity And Distributions **13**(2): 225-236.

This study compared the dry season distribution of elephant bull groups and mixed herds and the resources driving these distributions within Kruger National Park, South Africa. It is important to understand what resources drive the distribution of elephants as this may be of relevance to understanding and managing their impact. It is also important to distinguish between resource use by bull groups and mixed herds because their impact on the habitat may differ. Our results indicated that sexual segregation, both in space and in resource selection, did occur in Kruger Park. Bulls roamed more widely in the park, and although their distribution and resource use overlapped with mixed herds, they also occurred in areas that mixed herds apparently did not, or could not, utilize in the dry season. This gave rise to areas used exclusively by bulls but no areas used exclusively by mixed herds. Lower collective feeding requirements as a result of smaller group size, wider habitat tolerance, and increased mobility as a result of bigger body size, as well as conflict avoidance with musth bulls in areas with mixed herds, might have been some of the reasons for bull groups roaming more widely and for the establishment of separate bull areas. Rivers were an important resource driving both the distribution of the mixed herds and bull groups, but with the mixed herds occurring closer to these resource hot spots than the bull groups. Tree cover proved important for mixed herds, probably because of the importance of shade and the higher nutritional requirements of the smaller-sized cows and calves. Artificial waterholes might have opened up previously unutilized areas for bulls in the dry season, especially on the grassy basaltic plains in the north of the park. However, the distribution of the mixed herds suggested that they did not occur in higher densities in areas surrounding waterholes.

Somgird, C., S. Sripiboon, S. Mahasawangkul, K. Boonprasert, J. L. Brown, T. A. Stout, B. Colenbrander and C. Thitaram (2016). "**Differential testosterone response to GnRH-induced LH release before and after musth in adult Asian elephant (*Elephas maximus*) bulls.**" Theriogenology **85**(7): 1225-1232.

Bull elephants exhibit marked increases in testosterone secretion during musth, and studies have shown a heightened sensitivity of the testis to GnRH-stimulated testosterone production in musth compared to nonmusth males. However, activity of the hypothalamo-pituitary-gonadal axis before or soon after musth has not been studied in detail. The aim of this study was to evaluate LH and testosterone responses to GnRH challenge in nine adult Asian elephant (*Elephas maximus*) bulls during three periods relative to musth: premusth, postmusth, and nonmusth. Bulls were administered 80 mug of a GnRH agonist, and blood was collected before and after

injection to monitor serum hormone concentrations. The same bulls were injected with saline 2 weeks before each GnRH challenge and monitored using the same blood collection protocol. All bulls responded to GnRH, but not saline, with an increase in LH and testosterone during all three periods. The mean peak LH (1.76 ± 0.19 ng/mL; $P < 0.001$) and testosterone (6.71 ± 1.62 ng/mL; $P = 0.019$) concentrations after GnRH were higher than the respective baselines (0.57 ± 0.07 ng/mL, 3.05 ± 0.60 ng/mL). Although basal- and GnRH-induced LH secretion were similar across the stages, evaluation of the area under the curve in GnRH-treated bulls indicated that the testosterone response was greatest during premusth (2.84 ± 0.76 area units; $P = 0.019$) compared to postmusth (2.02 ± 0.63 area units), and nonmusth (2.01 ± 0.46 area units). This confirms earlier reports that GnRH stimulates LH release and subsequent testosterone production in bull elephants. Furthermore, although the hypothalamo-pituitary-gonadal axis is active throughout the year, the testis appears to be more responsive to LH in terms of testosterone production in the period leading up to musth, compared to the nonmusth and postmusth periods. This heightened sensitivity, perhaps as a result of LH receptor up-regulation, may prime the testis for maximal testosterone production, leading to the physiological and behavioral changes associated with musth.

Somgird, C., J. L. Brown and C. Thitaram (2017). "**Reproductive control in elephant: A tool for population and aggression management.**" *Thai Journal of Veterinary Medicine* **47**(1): 1-6.

Although Asian elephant is listed among the endangered species, the number of populations is over the carrying capacity in some areas, resulting in human-elephant conflict, as well as African elephants. High aggression associated with musth and female reproductive pathology are observed in captive elephants. Thus, population and aggression management through reproductive control is an alternative method for mitigating these problems. This article reviews methods of reproductive control in both Asian and African elephants with an overview of male and female reproductive physiology. Hormonal control and immunocontraception, i.e. porcine zona pellucida and gonadotropin releasing hormone (GnRH), are described for the control of reproduction, musth and reproductive pathology.

Somgird, C., S. Sripiboon, S. Mahasawangkul, K. Boonprasert, J. L. Brown, T. A. E. Stout, B. Colenbrander and C. Thitaram (2016). "**Differential testosterone response to GnRH-induced LH release before and after musth in adult Asian elephant (*Elephas maximus*) bulls.**" *Theriogenology* **85**(7): 1225-1232.

Bull elephants exhibit marked increases in testosterone secretion during musth, and studies have shown a heightened sensitivity of the testis to GnRH-stimulated testosterone production in musth compared to nonmusth males. However, activity of the hypothalamo-pituitary-gonadal axis before or soon after musth has not been studied in detail. The aim of this study was to evaluate LH and testosterone responses to GnRH challenge in nine adult Asian elephant (*Elephas maximus*) bulls during three periods relative to musth: premusth, postmusth, and nonmusth. Bulls were administered $80 \mu\text{g}$ of a GnRH agonist, and blood was collected before and after injection to monitor serum hormone concentrations. The same bulls were injected with saline 2 weeks before each GnRH challenge and monitored using the same blood collection protocol. All bulls responded to GnRH, but not saline, with an increase in LH and testosterone during all three periods. The mean peak LH (1.76 ± 0.19 ng/mL; $P < 0.001$) and testosterone (6.71 ± 1.62 ng/mL; $P = 0.019$) concentrations after GnRH were higher than the respective baselines (0.57 ± 0.07 ng/mL, 3.05 ± 0.60 ng/mL). Although basal- and GnRH-induced LH secretion were similar across the stages, evaluation of the area under the curve in GnRH-treated bulls indicated that the testosterone response was greatest during premusth (2.84 ± 0.76 area units; $P = 0.019$)

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Somgird, C., P. Homkong, S. Sripiboon, J. L. Brown, T. A. E. Stout, B. Colenbrander, S. Mahasawangkul and C. Thitaram (2016). "**Potential of a gonadotropin-releasing hormone vaccine to suppress musth in captive male Asian elephants (*Elephas maximus*)**." *Animal Reproduction Science* **164**: 111-120.

Musth in adult bull elephants is a period of increased androgen concentrations ranging from a few weeks to several months. For captive elephant bull management, musth presents a serious challenge because of the aggressive behavior of musth bulls toward people and other elephants. Commercially available GnRH vaccines have been shown to suppress testicular function by interrupting the hypothalamo-pituitary-gonadal (HPG) axis in many species. The aim of this study was to test the efficacy of a GnRH vaccine in elephant bulls for suppressing the HPG axis and mitigating musth-related aggressive behavior. Five adult Asian elephant bulls (22-55 years old) were immunized with a GnRH vaccine starting with an initial injection 2-4 months before the predicted musth period, and followed by three boosters at approximately 4-week intervals. Blood samples were collected twice weekly for hormone and antibody titer analysis. An increase in GnRH antibody titers was observed in all bulls after the second or third booster, and titers remained elevated for 2-3 months after the final booster. Musth was attenuated and shortened in three bulls and postponed completely in two. We conclude that GnRH vaccination is capable of suppressing symptoms of musth in adult bull elephants. With appropriate timing, GnRH vaccination could be used to control or manage musth and aggressive behavior in captive elephant bulls. However, more work is needed to identify an optimal dose, booster interval, and vaccination schedule for complete suppression of testicular steroidogenesis. © 2015 Elsevier B.V.

Stoeger, A. S. and A. Baotic (2016). "**Information content and acoustic structure of male African elephant social rumbles**." *Sci Rep* **6**: 27585.

Until recently, the prevailing theory about male African elephants (*Loxodonta africana*) was that, once adult and sexually mature, males are solitary and targeted only at finding estrous females. While this is true during the state of 'musth' (a condition characterized by aggressive behavior and elevated androgen levels), 'non-musth' males exhibit a social system seemingly based on companionship, dominance and established hierarchies. Research on elephant vocal communication has so far focused on females, and very little is known about the acoustic structure and the information content of male vocalizations. Using the source and filter theory approach, we analyzed social rumbles of 10 male African elephants. Our results reveal that male rumbles encode information about individuality and maturity (age and size), with formant frequencies and absolute fundamental frequency values having the most informative power. This first comprehensive study on male elephant vocalizations gives important indications on their potential functional relevance for male-male and male-female communication. Our results suggest that, similar to the highly social females, future research on male elephant vocal behavior will reveal a complex communication system in which social knowledge,

companionship, hierarchy, reproductive competition and the need to communicate over long distances play key roles.

Stokke, S. and J. G. duToit (2002). "**Sexual segregation in habitat use by elephants in Chobe National Park, Botswana.**" Afr. J. Ecol **40**: 360-371.

We report on a study conducted on free-ranging African elephants in the woodlands of northern Botswana. We compared bull groups and family units with regard to (1) their patterns of habitat use and (2) their ranging distances from perennial water sources. During the dry season, adult males frequented more habitat types than family units, whereas family units used a wider diversity of habitats than bulls during the wet season. Bulls roamed widely (>10 km) from perennial drinking water in the dry season, when family units congregated within 3.5 km of the rivers. During the wet season, when ephemeral pans were abundant, all elephant groups were found at intermediate distances (5 km) from the rivers. The spacing of elephants in the dry season is consistent with sexual segregation but we reject the hypothesis that this is an outcome of indirect competition for food, because our concurrent studies on elephant feeding ecology found no evidence for intraspecific competition. Instead, we propose that most adult male elephants space themselves to avoid conflict with musth bulls and roam widely in the dry season between discretely distributed feeding 'hotspots'. The small proportion of males that are in musth remain close to family units to maximize mating opportunities, and family units are unable to range far from water in the dry season. This is due to (1) comparatively high rates of water turn-over among juveniles and lactating cows and (2) the reduced mobility of neonates.

Taya, K. (1993). "**The reproductive physiology of the elephant.**" Journal of Reproduction and Development **39**(6): 77-91.

A discussion. In the females the vagina opens ventrally, ovarian cycles average 15-17 weeks in length, the gestation period is 22 months, and the ovary has a number of corpora lutea, although elephants are monovular. In males, there are permanent intra-abdominal testes, there is no distinct epididymis, but instead there is an extremely tortuous and convoluted duct which connects the testes to the openings of the seminal vesicles, the accessory organs are extremely well developed, especially the seminal vesicles and the bulbo-urethral glands. During musth, adult bulls become disobedient, aggressive and extremely dangerous, often attempting to kill their mahouts, or anybody else who comes within range. Bulls in musth have high testosterone levels and show urine dribbling and swollen temporal glands.

Thakuria, D. B. and T. Barthakur (1996). "**Management of musth in a male African elephant by chemical sedatives in the Assam state zoo, Guwahati.**" Indian Veterinary Journal **73**(3): 339-340.

Thurber, M. I., C. E. O'Connell-Rodwell, W. C. Turner, K. Nambandi, C. Kinzley, T. C. Rodwell, C. T. Faulkner, S. A. Felt and D. M. Bouley (2011). "**Effects of rainfall, host demography, and musth on strongyle fecal egg counts in African elephants (*Loxodonta Africana*) in Namibia.**" Journal of Wildlife Diseases **47**(1): 172-181.

Wild African elephants (*Loxodonta africana*) are commonly infected with intestinal strongyle parasites. Our objective was to determine baseline fecal strongyle egg counts for elephants in the northeast region of Etosha National Park, Namibia and determine if these numbers were affected by annual rainfall, elephant demography (age of individuals and composition of groups), and hormonal state of males. We found that matriarchal family group members have significantly higher fecal egg counts than male elephants (bulls). Among family group members,

strongyle egg counts increased with age, whereas among bulls, strongyle egg counts decreased with age. Years of higher rainfall were correlated with decreased numbers of strongyle eggs among bulls. Finally, bulls were not affected by their physiologic (hormonal) status (musth vs. nonmusth). These results suggest that infection by strongyle parasites in Namibian African elephants is a dynamic process affected by intrinsic and extrinsic factors including host demography and rainfall. © Wildlife Disease Association 2011.

Turczynski, C. J. (1993). **The endocrinology of musth in the male Asiatic elephant (*Elephas maximus*): Serum estradiol, serum LH and serum, fecal and urinary testosterone.** College Station, TX, USA, Texas A&M University. **PhD.**

Vidya, T. N. C. and R. Sukumar (2005). "**Social and reproductive behaviour in elephants.**" Current Science **89**(7): 1200-1207.

We present a review of studies on elephant social and reproductive behaviour. While the social organization of the African savannah elephant (*Loxodonta africana africana*) has been intensively studied, that of the African forest elephant (*Loxodonta africana cyclotis*) and the Asian elephant (*Elephas maximus*) are poorly understood. Noninvasive molecular methods are useful in combination with behavioural data in understanding social organization and dispersal strategies. The ecological determinants of social organization, and the importance of matriarchal leadership to social groups, and relative importance of different forms of communication under various ecological conditions remain interesting topics that await investigation. Reproductive behaviour also has been examined in detail only in the African savannah elephant, although rigorous chemical analyses continue to be carried out using captive elephants of both species. Improved laboratory techniques may enable future work on reproductive signalling in free-ranging elephants, allowing for comprehensive studies of male-male interactions and mate choice by females.

von Elke Scheurmann, G. and M. R. Jainudeen (1972). ""**Musth**" beim asiatischen elefanten, *Elephas maximus*." Zool. Gart **42**: 131-142.

von Elke Scheurmann, G. (1977). "**Musth**" in the Asiatic elephant. Giessener Beitr. Entwicklungforsch "**Musth**" beim Asiatischen Elefanten. **1**: 87-92.

West, L. J. and C. M. Pierce (1962). "**Lysergic acid diethylamide: Its effects on a male Asiatic elephant.**" Science **138**: 1100-1103.

Summary: Researchers gave LSD to a zoo elephant in order to "induce a behavioral aberration that might resemble the phenomenon of going on musth." Elephant cause of death was asphyxiation secondary to laryngeal spasm.

Wheeler, J. W., L. E. Rasmussen, F. Ayorinde, I. O. Buss and G. L. Smuts (1982). "**Chemical constituents of temporal gland secretion of the African elephant, *Loxodonta africana*.**" J. Chem. Ecol **8**(5): 821-835.

Temporal gland secretion (TGS), obtained from 15 different mature African elephants in Kruger National Park was analyzed for volatile constituents. Only five volatile components were present. p-Cresol was present in all samples, but phenol was found as an appreciable component of only one sample and as trace amounts in six others. Three sesquiterpenes were identified, the latter two being new natural products: E-farnesol, farnesol hydrate (3,7,11-trimethyl-2,10-dodecadien-1,7 diol), and farnesol dihydrate

(3,7,11-trimethyl-2-dodecen-1,7,11-triol). These sesquiterpenes represent the first isolated from mammals. Ten samples of TGS, serum, and saliva were assayed for cholesterol, urea, and proteins including several enzymes.

Whitehouse, A. M. and D. S. Schoeman (2003). "**Ranging behaviour of elephants within a small, fenced area in Addo Elephant National Park, South Africa.**" *African Zoology* **38**(1): 95-108.

The elephant population (n = 324, December 2000) in Addo Elephant National Park (AENP), South Africa, is restricted to an area (103 km²) considerably smaller than most elephant ranges. The Addo elephants' ranging behaviour was studied in order to determine whether natural patterns of male and female ranging behaviour can be maintained within a confined area. Radio-tracking was used to facilitate measurements of hourly distances travelled, larger scale directional movements, home range sizes, centres of activity and associations. Female home ranges overlap, and interactions between family groups are frequently observed. Females and non-musth males travel similar distances and speeds on an hourly basis, but female core range sizes are larger, presumably because bigger areas are needed to satisfy the nutritional requirements of their young. Contrary to expectations, Addo males do not travel further and faster on an hourly basis when they are in musth in comparison to when they are not in musth. However, the movement of males in musth is more directional, so that they cover a greater area of the park. Males associate more frequently with females when in musth than when non-musth. Unlike in other populations, non-musth 'male retirement areas' in AENP are not exclusive, as there is spatial and temporal overlap with female ranges, and hence with the ranges of males in musth. It is suggested that the resulting increased frequency of contact between musth and non-musth males may result in elevated mate competition, and this could contribute to the high levels of aggression observed between Addo bulls.

Wilson, J. C. C. (1922). "**The breeding of elephants in captivity.**" *J. Bombay Nat. Hist. Soc* **28**: 1128-1129.

Wingate, L. and B. Lasley (2000). **The Significance of Musth in Bull Elephants: Is It a Reproductive Event?** Elephants: Cultural, Behavioral, and Ecological Perspectives; Program and Abstracts of the Workshop.

Wingate, L. and B. Lasley (2001). **Is Musth a Reproductive Event: An Examination of Arguments For and Against this View.** A Research Update on Elephants and Rhinos; Proceedings of the International Elephant and Rhino Research Symposium, Vienna, June 7-11, 2001, Schuling Verlag.

Wittemyer, G. (2001). "**The elephant population of Samburu and Buffalo Springs National Reserves, Kenya.**" *African Journal of Ecology* **39**(4): 357-365.

A 21-month individual identification project on the Samburu and Buffalo Springs National Reserves' elephant population was conducted between November 1997 and July 1999. The free ranging population, of at least 767 elephants, which relied heavily on areas outside the reserves, was individually identified. The numbers of elephants observed per day fluctuated but were greater during dry periods than wet. However, the sizes of aggregations were greater during wet periods. Preliminary investigation suggested that the population could be divided into two groups, which were designated resident and non-resident family units. The groups comprised approximately equal numbers of cows and calves, but temporally had different reserve use patterns and calving peaks. The daily numbers of males and musth males were correlated with numbers of females. The reserves appeared to be a focal area for calving, indicating that the

study area was of reproductive importance to the population. Demographic data indicated a female biased population sex ratio, with over twice the number of mature females to males. The observed sex skew was greatest for older age classes, and the density of musth bulls in the study area was low. The population was affected by poaching. Continued monitoring will assist conservation efforts by alerting authorities of major demographic or range use changes.

Wyse, J. M., I. C. W. Hardy, L. Yon and M. Mesterton-Gibbons (2017). "**The impact of competition on elephant musth strategies: A game-theoretic model.**" *Journal of Theoretical Biology* **417**: 109-130.

Mature male African Savannah elephants are known to periodically enter a temporary state of heightened aggression called "musth", often linked with increased androgens, particularly testosterone. Sexually mature males are capable of entering musth at any time of year, and will often travel long distances to find estrous females. When two musth bulls or two non-musth bulls encounter one another, the agonistic interaction is usually won by the larger male. However, when a smaller musth bull encounters a larger non-musth bull, the smaller musth male can win. The relative mating success of musth males is due partly to this fighting advantage, and partly to estrous females' general preference for musth males. Though musth behavior has long been observed and documented, the evolutionary advantages of musth remain poorly understood. Here we develop a game-theoretic model of male musth behavior which assumes musth duration as a parameter, and distributions of small, medium and large musth males are predicted in both time and space. The predicted results are similar to the musth timing behavior observed in the Amboseli National Park elephant population, and further results are generated with relevance to Samburu National Park. We discuss small male musth behavior, the effects of estrous female spatial heterogeneity on musth timing, conservation applications, and the assumptions underpinning the model. © 2017 Elsevier Ltd

Yon, L., J. Chen, P. Moran and B. Lasley (2007). "**An analysis of the androgens of musth in the Asian bull elephant (*Elephas maximus*).**" *Gen Comp Endocrinol* **Mar 24**; [Epub ahead of print].

During musth in bull elephants, the androgens testosterone (T), dihydrotestosterone (DHT), and androstenedione all increase significantly. Given the unusual endocrine physiology that has been discovered in female elephants, it is also possible that bull elephants produce some unusual androgens. A cell-based androgen receptor assay was used to explore this possibility using two different methods. The first method compared the level of T measured by radioimmunoassay (RIA) with the level of androgen receptor (AR) activity measured in the serum of eight bull elephants during musth and non-musth periods. A ratio was calculated for T/AR activity for non-musth and musth, to determine if there was a change in the ratio between these two states. The second method used HPLC to separate two pooled serum samples (one non-musth and one musth) into fractions using a protocol which separates known androgens into specific, previously identified fractions. Each fraction was then tested with the AR assay to determine the androgenicity of any compounds present. This was done to determine if there were any fractions which had androgenic activity but did not contain any previously identified androgens. Results from the first analysis indicated no change in the T/AR ratio between non-musth and musth states. Clearly whatever active androgens are present during musth, they increase proportionately with T. Findings from the second analysis suggested that the only bioactive androgen present in the serum of non-musth Asian bulls is a low level of T. During musth, the only bioactive androgens detected were T and DHT; of these, T was by far the predominant active androgen present. Taken together, these two analyses suggest that T is by far the predominant active androgen present during musth in Asian bull elephants, and that no

previously unidentified bioactive androgen is present.

Yon, L., S. Kanchanapangka, N. Chaiyabutr, S. Meepan, F. Z. Stanczyk, N. Dahl and B. Lasley (2007). "**A longitudinal study of LH, gonadal and adrenal steroids in four intact Asian bull elephants (*Elephas maximus*) and one castrate African bull (*Loxodonta africana*) during musth and non-musth periods.**" Gen. Comp Endocrinol **151**(3): 241-245.

During their annual musth cycle, adult African and Asian bull elephants have increased gonadal androgens (testosterone [T], dihydrotestosterone [DHT], androstenedione [A4]). Because musth is a physiologically and psychologically stressful time, this study was conducted to investigate whether the adrenal glands (stimulated by stress) increase production of both glucocorticoids and androgens during musth. Weekly serum samples were taken for 11-15 months from four intact adult Asian bull elephants, and from a castrate African bull elephant who exhibits musth. Testosterone, androstenediol (A5), A4, luteinizing hormone (LH), cortisol, and dehydroepiandrosterone (DHEA) were measured in each sample. In three of the four intact bulls, all hormones measured increased during musth. Adrenal androgens were strongly correlated with LH and testicular androgens, though not to cortisol. None of the hormones measured in the castrate bull increased during his musth cycles. While the significance of adrenal activity in the elephant during musth has yet to be determined, this study provides evidence that the adrenal gland actively produces both glucocorticoids and androgens during musth in the Asian elephant

Yon, L., S. Kanchanapangka, N. Chaiyabutr, F. Stanczyk, S. Meepan and B. Lasley (2007). "**ACTH stimulation in four Asian bull elephants (*Elephas maximus*): an investigation of androgen sources in bull elephants.**" Gen. Comp Endocrinol **151**(3): 246-251.

The phenomenon of musth is a very stressful event, both behaviorally and physiologically. An ACTH stimulation test was conducted in four adult Asian bull elephants to investigate the possibility that the classical hypothalamic-pituitary-adrenal (HPA) axis is active during musth, resulting in an increase in adrenally produced steroids. Serum cortisol, testosterone (T), androstenedione (A4), androstenediol (A5), and dehydroepiandrosterone (DHEA) were measured. Cortisol increased 3-10 times above baseline in response to ACTH stimulation, and DHEA doubled. A4 and A5 were erratic, while testosterone decreased significantly in all bulls. The pattern of results suggests that the adrenal steroid increase which occurs during musth results from some mechanism other than the classical HPA axis

Yon, L., J. Chen, P. Moran and B. Lasley (2008). "**An analysis of the androgens of musth in the Asian bull elephant (*Elephas maximus*).**" General and Comparative Endocrinology **155**(1): 109-115.

During musth in bull elephants, the androgens testosterone (T), dihydrotestosterone (DHT), and androstenedione all increase significantly. Given the unusual endocrine physiology that has been discovered in female elephants, it is also possible that bull elephants produce some unusual androgens. A cell-based androgen receptor assay was used to explore this possibility using two different methods. The first method compared the level of T measured by radioimmunoassay (RIA) with the level of androgen receptor (AR) activity measured in the serum of eight bull elephants during musth and non-musth periods. A ratio was calculated for T/AR activity for non-musth and musth, to determine if there was a change in the ratio between these two states. The second method used HPLC to separate two pooled serum samples (one non-musth and one musth) into fractions using a protocol which separates known androgens into specific, previously identified fractions. Each fraction was then tested with the AR assay to

determine the androgenicity of any compounds present. This was done to determine if there were any fractions which had androgenic activity but did not contain any previously identified androgens. Results from the first analysis indicated no change in the T/AR ratio between non-musth and musth states. Clearly whatever active androgens are present during musth, they increase proportionately with T. Findings from the second analysis suggested that the only bioactive androgen present in the serum of non-musth Asian bulls is a low level of T. During musth, the only bioactive androgens detected were T and DHT; of these, T was by far the predominant active androgen present. Taken together, these two analyses suggest that T is by far the predominant active androgen present during musth in Asian bull elephants, and that no previously unidentified bioactive androgen is present. © 2007 Elsevier Inc. All rights reserved.