CHEMICAL COMMUNICATION OF MUSTH IN CAPTIVE MALE ASIAN ELEPHANTS, *Elephas maximus*

Nancy L. Scott and L.E.L. Rasmussen*

1. INTRODUCTION

1.1 Social Systems

Asian elephants have tightly knit social systems maintained by several modes of communication (Eisenberg et al., 1971; Sukumar, 2003). Female Asian elephants group together as family units; whether these matriarchal groups coalesce into larger herds based on genetic relationships has recently been examined (Fernando and Lande, 2000). Subadult males gradually leave the familial unit. As adults, they live either as solitary elephants with indistinct home ranges or in temporary associations with other males often at the fringes of female herds (McKay, 1973; Eisenberg, 1980), where they are attracted in by preovulatory females (Rasmussen et al., in prep). The physiological phenomenon of musth in male Asian elephants apparently increases reproductive success either by increased social dominance (Eisenberg et al., 1971; Jainudeen et al., 1972a) or expanded home ranges allowing more potential encounters with females (Joshua and Johnsingh 1995). Often males accepted by females are males in musth (Sukumar, 2003).

1.2 Musth

The exact reproductive significance of musth in male Asian elephants, although documented since the stories of Buddha c. 200 BC (Lahiri-Choudhury, 1992), still remains unclear. Musth, both in the wild and in captivity, first occurs in young males who are sexually mature but socially and physically not fully developed. Musth is usually an annual event with characteristic physiological changes, but males in poor health may not exhibit musth for up to 4 years (Jainudeen et al., 1972b).

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* Nancy L. Scott, Portland State University, Portland, OR, 97207. L.E.L. Rasmussen, Oregon Health and Sciences University, Beaverton, OR, 97006.

Elevated serum testosterone levels, increased aggression between males, secretions from the paired facial temporal glands and dribbling of urine from the penile prepuce characterize musth in the Asian elephant (Jainudeen et al., 1972a; Cooper et al., 1990). Musth is usually not synchronous among males, nor is it always dependent on females in estrus. In wild Asian elephants, although musth is thought to be an annual event for each male, males in a given population tend to have non-overlapping musth periods so that throughout the year there are various males in musth (Eisenberg et al., 1971; Jainudeen et al., 1972b). Data on wild Asian elephant mating behavior are just becoming available with the advent of new genetic methods, radiotelemetry, and sophisticated recording devices and analytical techniques. For example, it is now known that during musth the home range of males expands, thus allowing encounters with more female groups (Joshua and Johnsingh, 1995). Among African savannah elephants (*Loxodonta africana*) mate choice by females and mate guarding by males appear to play crucial roles in reproductive behavior, as males in musth are more successful in competitions with subordinate males for gaining access to estrous females (Moss, 1983; Poole, 1989a). Male Asian elephants usually associate with female units when at least one female is in estrus, and only one male typically associates with a particular family unit or group of family units (McKay, 1973).

1.3 Role of Musth

We hypothesize that status in male elephants and mate guarding could be communicated by chemical signals. Asian elephants rely heavily on their chemical senses, acquiring information from chemical signals present in urine, feces, and temporal gland secretions (Rasmussen et al., 1986; Rasmussen, 1988). Previous work has shown that musth chemical signals are detected by female Asian elephants and may be important in female mate choice (Rasmussen et al., 1994; Schulte et al., 1994; Schulte and Rasmussen, 1997). Chemical signals indicative of musth could also relay the physiological status of the male elephant to male conspecifics.

Zahavi and Zahavi (1997) proposed that aggressive behavior in any species can often be avoided with "honest signals," indicating an individual's condition and rank in a hierarchy. A state such as musth that affects the physiology of an elephant could be used as an honest signal to conspecifics, especially as only well-nourished males are capable of experiencing musth (Gale, 1974). Increased serum testosterone may drive increased aggression between males. The ability of a male elephant to detect the musth state of another male could prevent aggressive interactions with a less dominant nonmusth male. Such encounters have been documented behaviorally and chemically in the wild (Rasmussen et al., 2002). Therefore, a male who is able to experience musth could be emitting reflectively honest signals to others, indicating a male of substantial condition and heightened reproductive readiness. This could temporarily increase his relative dominance among males, as seen in African savannah elephants (Poole, 1989b), and perhaps be used to assess the quality of a male by female conspecifics.

During musth, males rub the sides of their faces against trees, leaving temporal gland secretions as stationary olfactory markers that other conspecifics investigate (Eisenberg et al., 1971; Rasmussen et al., 2002). The temporal glands are larger and more active during musth than nonmusth in the male Asian elephant (Gale, 1974). As demonstrated in other mammals, this sexually dimorphic trait suggests a reproductive function (Thiessen and Rice, 1976). The enlargement of the glands in male Asian elephants prior to external secretions (Gale, 1974) coincides with emission of volatile chemical compounds just prior to the onset of musth (Rasmussen et al., 1990; Rasmussen and Perrin, 1999). Analyses of these compounds have shown that the glands become active days before the other signs of musth are apparent (e.g., urine dribbling and temporal gland secretion) (Rasmussen and Perrin, 1999).

In addition to temporal gland secretions (TGS), males in musth also dribble urine. Rasmussen (1988) showed that constituents of musth urine elicit visible chemosensory responses (e.g., the flehmen response) in elephants. Chemical signals present in musth urine may be used to indicate physiological status and relative dominance rank. In several mammalian species, males scent-mark conspecific females with urine or secretions during courtship or mating, e.g., goats, *Capra* spp., (Shank, 1972; Coblentz, 1976); Gray's waterbuck, *Kobus megaceros*, (Walther, 1979); and badgers, *Meles meles*, (Kruuk et al., 1984). This scent marking is thought to discourage other males from mating with the female long enough to ensure that the female's ova are fertilized only by the male that marked her (Jewell et al., 1986). Reindeer, *Rangifer tarandus*, also dribble urine on their hind legs as a male-repellent and female-attractant. The self-urine-marking in reindeer is thought to occur because the male himself constitutes the center of his moving territory (Espmark, 1964).

Dribbling of urine while in musth could also function as a scent marker for male Asian elephants. The inner sides of the hind legs of musth males are often stained with pungent-smelling urine. During the mating act, odiferous compounds could be transferred to females, thus signaling other males that a recent mating occurred by a musth male who may still be nearby, ready to defend his mate. The urine is also dribbled in a trail behind the musth male elephant as he walks and may be later detected by another male who encounters the urine even in the absence of the musth male. The chemosensory information obtained by another male may indicate the dominance, musth status, health, and age of the scent-marking male. Since males in musth are more aggressive and defend estrous females from other males, subordinate males may benefit from discriminating between musth and nonmusth males *via* chemical cues in the urine.

1.4 Chemical Senses

Elephants have a highly developed chemosensory system consisting of the main olfactory (MO) and vomeronasal organ (VNO) systems (Boas and Pauli, 1925; Eales, 1926; Rasmussen et al., 1986; Rasmussen and Hultgren, 1990). In most terrestrial mammals, MO is used for detecting airborne, volatile substances whereas the VNO system is used for detecting liquid substances such as urine and glandular secretions (Stoddart, 1980; Keverne, 1982), although increasing evidence shows crossovers between the two sensory systems. The two systems each have characteristic receptors and discrete neuronal pathways to the olfactory and accessory olfactory bulbs, respectively (Stoddart, 1980; Barlow and Mollon, 1982; Farbman, 1992). In elephants, sensory epithelia for the primary olfactory system primarily cover the well-developed ethmoturbinals (Rasmussen and Hultgren, 1990; Rasmussen et al., 1993). Airborne substances pass over the surface of these deeply protected bipolar sensory neurons after the inspired air has been well warmed. The trunk of an elephant has several important sensory roles: it transports chemical signals to the openings of the VNO ducts, thus carrying VNO-destined information; it acts as a conduit for inhalant air that will pass into the turbinate area of the main olfactory system; and the high density of several types of tactile and pressure sensory corpuscles in its tip demonstrates the tip is a major region of sensory epithelium (McKay, 1973; Rasmussen and Munger, 1996; Rasmussen et al., 2003). Elephants place this finger-like projection at the end of the trunk into a substance and then transfer the material from the trunk tip to the openings of the VNO (located on the palate), a behavior termed the "flehmen" response (Rasmussen, 1982). In the elephant the vomeronasal organ is a paired tubular structure containing both sensory and respiratory epithelium; many mucous glands are associated; long, convoluted paired ducts from the VNO open into dorsal anterior mouth cavity (Rasmussen and Hultgren, 1990; Johnson and Rasmussen, 2002). Thus, the muscular trunk acts both as a vehicular tube to allow airborne volatiles access to the olfactory turbinal bones and as the mechanical transfer agent to place liquid substances on the openings of the vomeronasal ducts during the flehmen response.

2. URINE BIOASSAYS WITH MALE ASIAN ELEPHANTS

2.1 Overview

To begin the assessment of possible chemical messages between male Asian elephants, responses of captive males to conspecific musth and nonmusth urine were measured. Some obvious disadvantages of captive studies are substantially offset by some real advantages: (1) close, accurate behavioral observations in a limited-size enclosure, (2) precise placement of test samples on substrate free of conflicting signals, (3) safe collection of test samples of elephant origin from males whose hormonal status can subsequently be determined.

2.2 Sample Collection

For this study 500 ml urine samples were collected both during musth and nonmusth periods from two mature male Asian elephants and frozen for subsequent tests. Concurrent serum samples retroactively established circulatory testosterone concentrations of the donor male pertinent to the collected urine aliquots (Table 1) by Dr. David Hess of the Oregon Regional Primate Center using a previously described methodology (Rasmussen et al., 1984).

2.3 Bioassay Procedure

Our previous studies established that a 150 ml aliquot is sufficient to elicit chemosensory responses (Scott et al., 1997). For a bioassay series, two 500 ml aliquots—one from a male in musth and the second from a male not in musth—were thawed at 20°C and then subdivided into three equal volumes. These sub-aliquots were subsequently presented to one male at a time, as paired samples, plus the water control for a total of three samples per assay. Thus, presentations were aliquots of musth urine, nonmusth urine, and tap water, a visual control. Logistically we did not have the financial resources to freeze the urine collected at –80°C. Freezing at –20°C certainly maintained the integrity of most bioactive urinary compounds, and the purpose of this study was to compare responses to musth versus nonmusth urine. The tight control

Table 1: Musth states and their parameters.

	Serum Testosterone	Temporal Gland Secretion	Urine Dribbling
Nonmusth	< 20 ng/ml	No	No
Pre-musth	> 20 ng/ml	Yes/No	No
Musth	> 20 ng/ml	Yes	Yes
Post-musth	> 20 ng/ml	No	No
Moda Musth*	>20 ng/ml*	Yes*	No

*The first several musth episodes of young teenage adult males (usually between age 10–18 y in captivity and age 14–19 y in the wild) are characterized by widely fluctuating testosterone levels, sporadic temporal gland secretions that often smell like honey (Rasmussen et al. 2002). Two of the test males were approaching the onset of this moda age.

exerted over the unfreezing process insured the equivalency of the samples. In the future, as specific classes of compounds are targeted for study, lower temperature freezing conditions will be utilized. Thus bioassays, which tested urine for bioactivity, were performed by presenting paired samples (musth and nonmusth) of previously frozen urine and a water control to each test animal.

The three samples were each presented in discrete areas 1m apart on a rinsed concrete slab. These urine bioassays were performed when the ambient temperature was 5–25°C to avoid freezing or rapid evaporation of samples. From the time of sample placement and subsequent release of the test animal, each bioassay was performed for the duration of one hour with a single focal animal. The subject was not present when the samples were placed. In addition, the elephant could not see the observer, thus preventing any bias in behavior that might be caused by the observer's presence. The visible physiological state of the elephant and weather conditions were recorded for each bioassay. Each elephant's behavior was videotaped as he approached the sample areas and while he was within a body length either of the urine samples or the water control sample.

Chemosensory responses indicated by trunk interaction with the sample were recorded for all occurrences (Table 2). The sequence of behaviors for each bout was recorded, as was the duration of time spent at each sample. Separate bouts of chemosensory investigation were distinguished when the trunk tip was greater than 0.5 m distant from the sample for longer than 5 s. Each behavior required the trunk to touch the sample or to be within 0.5 m of it.

Bioassays were performed in 1995, 1996, and 1998. Test males included the two donor males (age 33–36 y), an immature male familiar with the donors (age 12–13 y) and two males at different locations (age 10 and 26 y). Three of the test males, (age 26–36 y) experience musth once annually. Two young teenage males (age 10–13 y) had not yet experienced their first musth episode.

3. RESULTS

The relative amount of time each elephant spent investigating samples with visible olfactory behaviors was compared to overall investigation time. This resulted in a relative

Table 2: Monitored olfactory behaviors

Main Olfaction: SNIFF: trunk tip directed towards sample and hovering within centimeters of it; inhalation of sample volatiles BLOW: forced exhalation from trunk TRUNK SHAKE: trunk movement back and forth, often accompanied by exhalation
Contact/Olfaction (pre-flehmen): CHECKS: dorsal trunk tip projection placed in contact with sample PLACE: entire distal surface of trunk tip placed in contact with sample SCRUB: movement within the sample with the entire distal surface of trunk tip placed in contact with sample SUCK: inhalation of sample into trunk with the entire distal surface of trunk tip placed in contact with sample
Flehmen: dorsal trunk tip projection is placed in sample and then the trunk swings to bring the tip into contact with the VNO ducts

rate of olfactory investigation for each of the three samples (musth, nonmusth urine, and water). The pooled results for the three familiar male elephants show that they spent significantly more time investigating musth urine (68.6%) than nonmusth urine (31.0%) or water (0.4%) (Figure 1; Sign test, $p<0.05$). While both musth and nonmusth urine elicited observable olfactory behavioral responses, the water control was rarely investigated by the elephants.

To monitor vomeronasal organ system responses, we examined the rate of flehmen responses relative to each approach to the samples. Flehmen responses per approach to each of the urine samples by subadults (n=2) and the adults (n=3) in the study were compared. The subadults performed flehmens at a greater rate to musth compared to nonmusth urine and at an overall greater rate compared to the adult responses (Figure 2).

The subadult presented with urine form an unfamiliar donor performed several-fold more olfactory and pre-flehmen responses than did the subadult who was familiar with the urine donor (Figure 3). The range of responses from the adult presented with unfamiliar urine was greater than the 2 familiar adults, although the means for both groups were similar.

4. DISCUSSION

Results from the relative time spent investigating each sample demonstrate that the captive male Asian elephants in this study used chemical signals in urine to distinguish between musth and nonmusth urine. The males spent more time investigating the musth urine samples, perhaps to assess the relative dominance of the donor and status as a potential competitor for mates. Olfactory investigation of nonmusth urine shows that there are additional chemical signals other than those related to musth state present in excretions.

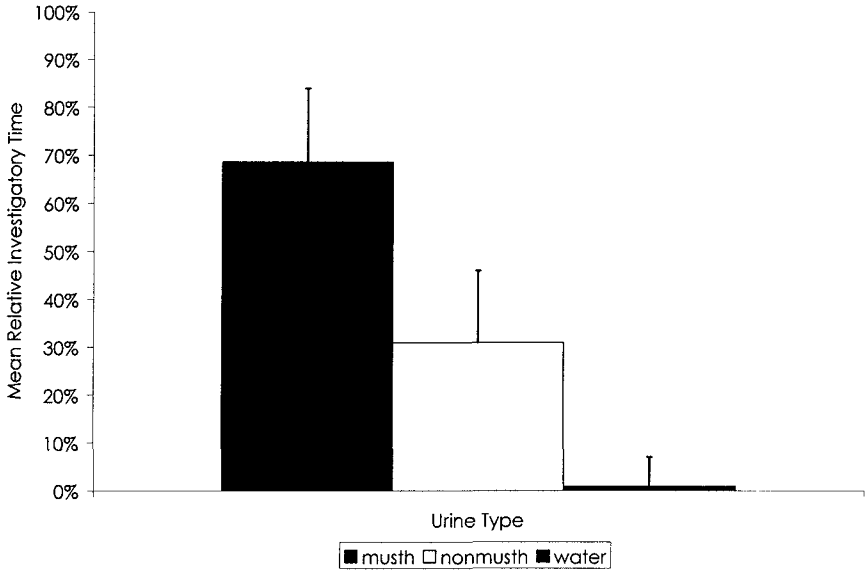

Figure 1: Mean relative percent of bioassay time spent investigating *familiar* urine samples; pooled results for 1 subadult male and 2 adult male Asian elephants (+/- SE)

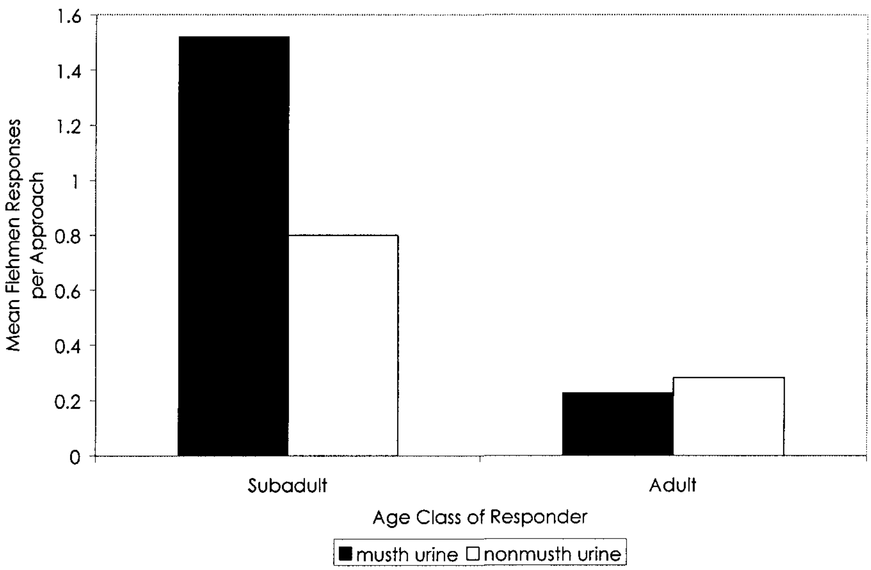

Figure 2: Mean flehmen responses per approach to musth and nonmusth urine by two age classes of male elephants

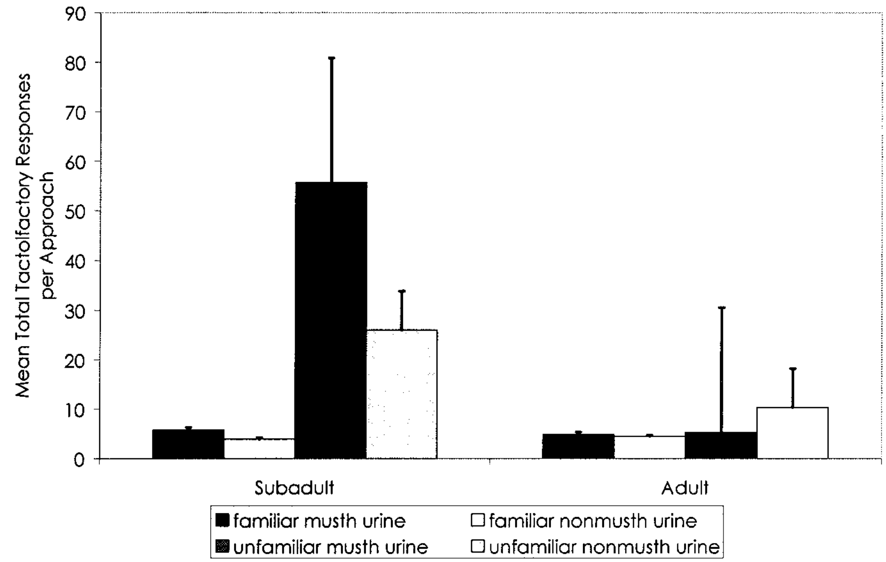

Figure 3: Mean sum of olfactory responses (C+P+F) per approach to musth and nonmusth urine from *familiar* and *unfamiliar* donors and a control by 2 subadult and 3 adult male elephants (+/- SE)

Subadult males may perform more flehmen responses than adults as they acquire information for their olfactory memory and learn more of their surroundings. Adult males may easily recognize the urinary chemical signals indicative of musth, while subadult males need repeated exposure to their VNO system to fully assess a urine sample for the musth state and identity of the donor.

In addition to musth state, chemical signals may include individual recognition or recognition of familiarity. Responders unfamiliar to the urine donor performed more olfactory and pre-flehmen responses than familiar responders. This was most dramatic in the subadult age class. Future research could examine how long this increased response is maintained before the responses decrease to the response frequencies observed to familiar urine. Further examination of urine bioactivity could reveal any influence a male's own musth state has on his olfactory interest in musth urine from male conspecifics. The temporary increase in relative dominance acquired by a male in musth may alter a male's olfactory investigation of musth urine compared to when he is not in musth.

5. ACKNOWLEDGEMENTS

This research was made possible by a generous grant from Disney's Animal Kingdom and support from Biospherics Research Corporation. Many thanks to the participating facilities: Oregon Zoo (Portland, OR), Riddle's Elephant and Wildlife Sanctuary (Greenbrier, AR), and Tulsa Zoo and Living Museum (Tulsa, OK). None of this research would have been possible without the support and assistance of all of the elephant keepers and handlers at these facilities. Thanks to Dr Bruce Schulte (Georgia Southern University) for design advice and inspiration. Eternal gratitude to Sharon Glaeser for her assistance with transcribing data from video tapes. Sincere appreciation to Dr Deborah Duffield and my graduate committee at Portland State University.

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