# ASSESSING CHEMICAL COMMUNICATION IN ELEPHANTS

Bruce A. Schulte, Kathryn Bagley, Maureen Correll, Amy Gray, Sarah M. Heineman, Helen Loizi, Michelle Malament, Nancy L. Scott, Barbara E. Slade, Lauren Stanley, Thomas E. Goodwin, and L.E.L. Rasmussen[*]

## 1. INTRODUCTION

The study of chemical communication in elephants has resulted in startling and exciting new discoveries in the past decade (Rasmussen and Schulte, 1998; Rasmussen et al., 2003). To date, the highlight of this research has been the identification of two compounds that serve as pheromones (as defined by Karlson and Lüscher, 1959). Rasmussen et al. (1996, 1997) identified (*Z*)-7-dodecen-1-yl acetate (*Z*7-12:Ac) in female Asian elephant urine collected during the pre-ovulatory period. This estrous pheromone signals approaching ovulation to conspecific males but elicits little interest from female conspecifics. The compound is not unique to elephants; *Z*7-12:Ac is a component of the mating pheromones for numerous lepidopteran species. More recently, Rasmussen and Greenwood (2003) isolated frontalin, a known aggregation pheromone in bark beetles (Kinzer et al., 1969), from male Asian elephant temporal gland secretion. Male and female Asian elephants exhibit a range of behaviors when exposed to frontalin. The responses depend on the age, sex, and status of the receiver. Male Asian elephants release temporal gland secretion profusely only during musth (Jainudeen et al., 1972a,b), suggesting that frontalin carries a musth-alerting message. Thus, two single compounds, likely acting in conjunction with other chemical components such as proteins (Lazar et al., 2002), mediate sexual and social interactions among Asian elephants.

[*] Bruce A. Schulte, Kathryn Bagley, Amy Gray, Helen Loizi, Lauren Stanley, Georgia Southern University, Statesboro, GA, 30460. Maureen Correll, College of William and Mary, Williamsburg, VA, 23186. Sarah M. Heineman, Thomas E. Goodwin, Hendrix College, Conway, AR, 72032. Michelle Malament, Miami University, Oxford, OH, 45056. Nancy L. Scott, Barbara Slade, Portland State University, Portland, OR, 97207. L.E.L. Rasmussen, Oregon Health and Sciences University, Beaverton, OR, 97006.

The success of such investigations hinges upon readily observable behaviors that reveal chemical reception, that is, a successful bioassay protocol (Mackintosh, 1985; Wyatt, 2003). Understanding independent variables, such as age, sex, and physiological status that affect receiver responsiveness enhances the repeatability of bioassay results. Elephants use their trunks extensively in the exploration of their environment. The trunk is a modified nose and upper lip with a terminus composed of tactile hairs and free nerve endings (Rasmussen and Munger, 1996). We have established a small set of easily observable and distinguishable behaviors that indicate chemosensory interest by Asian and African elephants. Over years of conducting studies with captive and wild elephants, we have related variation in expression of these significant behaviors to critical independent variables as noted above. Through intensive observations we have identified numerous additional behaviors associated with chemosignal detection and response. The expansion of our bioassay ethogram provides us with information that may expose more independent variables of importance to understanding elephant communication. Finally, these additional dependent variables, the response behaviors, provide insight into the receiver's psychological landscape (Guilford and Dawkins, 1991).

To be effective signals, chemicals must be detectable, recognizable, and remembered. Factors affecting responses by a receiver are part of its psychological landscape and thus must be considered to decipher signal meaning (Guilford and Dawkins, 1991). We are examining the variation in response behavior by elephants to assist in our interpretation of the chemical released-chemical detected-information acquired complex. This complex could easily involve multiple sensory channels because visual, vocal, and tactile components often accompany chemical signal reception and response (Rasmussen, 1988; Rowe, 1999; Langbauer, 2000). In this paper, we primarily discuss communication in elephants via chemical signals.

## 2.   MAIN BEHAVIORS OF CHEMOSENSORY BIOASSAY

An elephant's trunk leads the animal through its habitat. Whether an elephant is standing still or in transit, the trunk moves almost constantly. Over 20 years ago, Rasmussen et al. (1982) documented a flehmen-like behavior exhibited by male Asian elephants. The frequency of this behavior over years of bioassays led to the discovery of the estrous pheromone (Rasmussen et al., 1996). Explicit proof that the preovulatory pheromone moves from a urine puddle to the male Asian elephant's vomeronasal organ (VNO) is in progress but has not been yet obtained. We do know that $Z$7-12:Ac binds to a protein in the VNO ductal mucus (Rasmussen et al., 2003). Hence, this distinctive trunk movement by elephants appears to transfer chemical signals to the VNO, so we term this behavior flehmen rather than "flehmen-like" (Schneider, 1930; Estes, 1972). Preceding a flehmen, elephants sniff and contact the chemical source (Rasmussen et al., 1986; Rasmussen, 1988). Signal detection or transfer occurs by two primary contact responses. A check response occurs when the very end of the trunk (Asian elephants have a single anterior "finger" while African elephants have anterior and posterior fingers) touches the sample. A place contact transpires when the end of the trunk flattens and forms a seal with the substrate. Olfaction and probably tactile reception accompany both behaviors. The four behaviors - sniff, check, place, and flehmen - form the major response sequence of our elephant semiochemistry bioassay (Fig. 1).

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The frequency of these four behaviors as well as the duration of time spent near the samples reflects level of interest (Rasmussen et al., 1982, 1996; Schulte and Rasmussen, 1999; Scott, 2002; Slade et al., 2003).  The sequence of response is somewhat linear in that the order of responses is often conserved and the frequency decreases from olfactory exploration (sniff) to putative VNO input (flehmen). Sniffs may provide identification of critical sample features; sometimes, no additional information seems required.  At other times, the initial information sets in motion a response sequence suggestive of a requirement for additional olfactory information, obtained via checks, places and flehmen.  However, the sequence is not invariable.  After the first bout of investigation, elephants often directly contact a sample with little hovering of the trunk over the sample.  Although olfactory input probably is still occurring, it is not as pronounced as an overt sniff.  Checks also may be reduced in frequency with places becoming more prominent (especially in females).  In some situations, the place response is omitted and the rate of check-flehmen increased (common in males if the sample is fresh such as newly released or placed urine).  The neuronal feedback loops that control the observed sequence are not well understood.  Current methods to assess sensory input, such as electroolfactograms, neural pathway analysis, and brain activity are not readily applicable to elephants (Hildebrand, 1995; Johnston, 1999; Keverne, 1999; Firestein, 2001).  Hence, we rely on a combination of chemical, molecular, biochemical, and behavioral analyses to identify signals, to determine the route of detection, and to decipher the meaning of the message.  Because signal meaning is receiver dependent, knowledge about differences in receivers is essential.
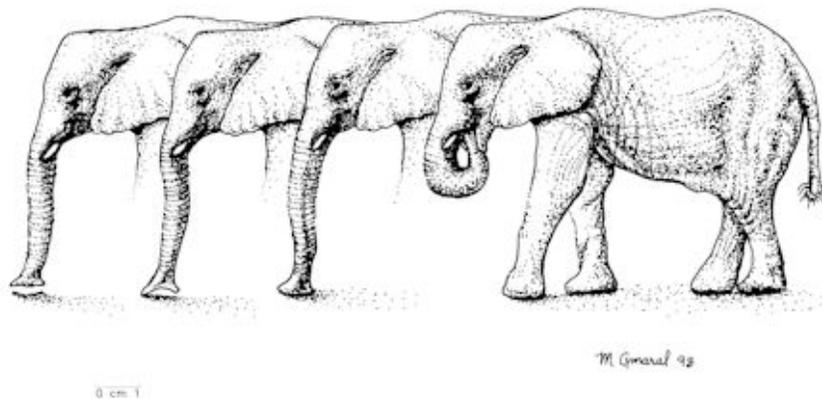


**Figure 1.**  Main sequence of chemosensory trunk responses to a putative chemical signal. From left to right, sniff, check, place and flehmen (see also Schulte and Rasmussen, 1999).  Drawing by Mary Amaral.

## 3.  RECEIVER VARIATION

Reproductive condition, sex, age, experience, and dominance status (i.e., receiver "states") are some of the primary variables that affect receiver behavior when exposed to a chemical signal (Doty and Ferguson-Segal, 1989; Schulte and Rasmussen, 1999). Alteration in behavior with state could result for one of two reasons.  First, the receiver cannot detect the signal except in certain states (e.g., some combination of the above variables).  Hypothetically, a male elephant in musth with highly elevated testosterone levels might detect chemicals or concentrations that males not in musth cannot detect. Second, detection occurs but signal relevance changes.  In this case, the nonmusth male may perceive that the signal is from a receptive female, but his relatively lower competitive condition may obviate high interest in the signal source.  Some results suggest the latter may be applicable (Rasmussen et al., 1997).  To distinguish among these hypotheses, more definitive records of behavioral responses are required because the lack of detectable behavioral response will not permit resolution between these two factors.  However, the observation of particular responses excludes hypothesis one.  The challenge is to determine what variables are responsible for reduced or different subsequent behaviors upon confirming detection.

Experiments using *Z*7-12:Ac show that Asian male elephants detect the chemical signal but exhibit very different responses depending on breeding experience or dominance (Rasmussen et al., 1997).  Experienced and generally more dominant males displayed high flehmen rates and sometimes exhibited erections.  However, sexually inexperienced males, generally considered subordinate, typically sniffed then backed away.  Referring to the two hypotheses above, in the absence of signal detection, males would continue their forward movement.  The avoidance responses by these males support hypothesis two.  For captive female Asian elephants, differences in behavior to conspecific female urine reflect stage of the estrous cycle (Slade et al., 2003).  Only females in the follicular phase responded more to follicular than luteal stage urine (Fig. 2).  Females in the follicular phase demonstrated greater interest in follicular urine by both greater rates of sniffs and checks and by the occurrence of place and flehmen responses.  Females in their follicular compared to luteal phase also were more responsive to male urine, especially from a male in musth (Schulte and Rasmussen, 1999).

Our standard control in these studies is vanilla extract in water.  The control generally elicits a low level of interest, mainly sniffs and checks.  We interpret this as interest in an odor source but not one with a meaningful signal (i.e., with evolutionarily evolved meaning).  Female Asian elephants often show about the same interest in luteal urine as our control.  However, luteal urine does evoke place and flehmen response on occasion, whereas, the control does not (Slade et al., 2003).  Luteal urine probably contains cues on sender identity, but chemicals either specific to or more abundant in follicular urine reveal reproductive readiness.

For female to female communication, the relevance of these chemicals appears restricted to follicular phase females.  However, reproductive state is not an on-off condition.  Hormone levels change cyclically and so responses are likely to be graded rather than discrete.  The frequency of the main behaviors and the duration of time near the sample provide some degree of graded responsiveness.  Yet, individual variation in these main response behaviors and the quantification of additional behaviors related to

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signal detection (dependent variables) are likely to reveal even more about signal meaning for particular types of receivers (independent variable).
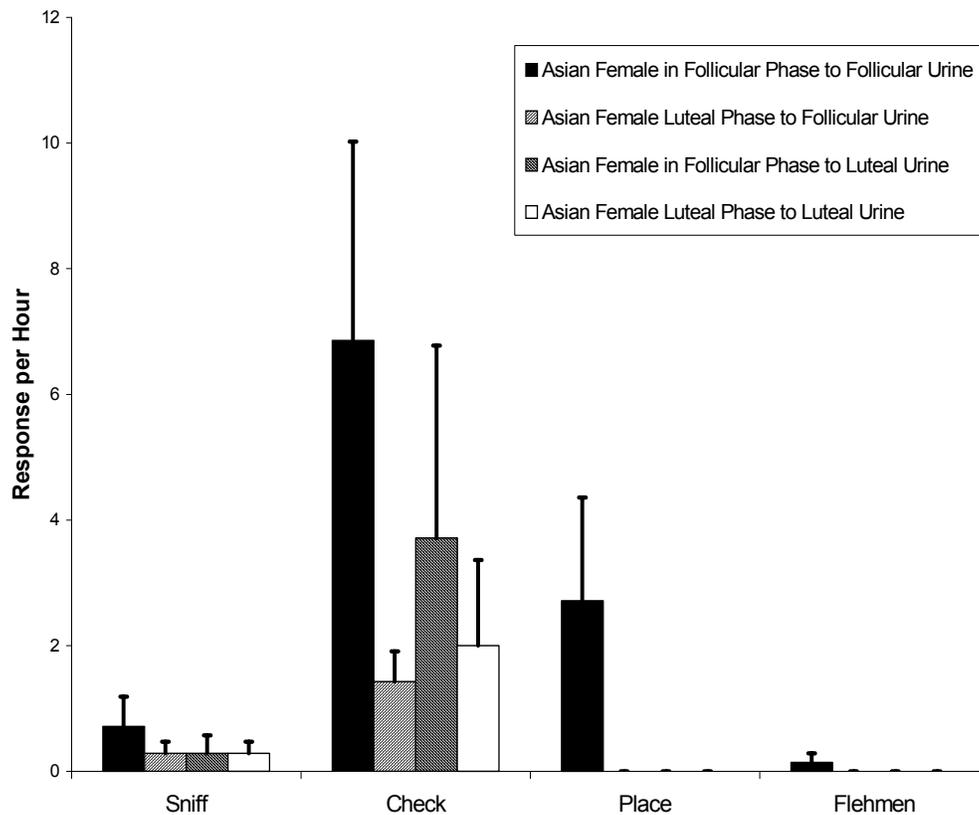


**Figure 2.** Main chemosensory responses (see Fig. 1) by captive female Asian elephants in their luteal and follicular stages of the estrous cycle to luteal and follicular urine from a conspecific female (see Slade et al., 2003).

## 4. ADDITIONAL BEHAVIORS: EXPANDING THE ETHOGRAM

The flehmen trunk movement is easy to differentiate from other trunk movements irrespective of elephant species or sex. Variation in the duration and frequency of flehmen may be dependent on the chemical sample or perhaps on the particular style of an individual elephant (Rasmussen, unpubl. data). Check and place responses also are distinct. Because African elephants have two trunk tip fingers, compared to one for the Asian species, checks can be more variable for the African species (i.e., anterior, posterior or simultaneous checks are possible). Behaviorally, the multiple positions in which the trunk moves for sniffing are perhaps the most intriguing types of variation. As

defined for a bioassay scenario, a sniff occurs when the trunk hovers over a sample that we place on the ground (Fig. 1). This is the most direct means by which an elephant can intake headspace over the sample, however, air intake can occur using other trunk positions.

The posture of the trunk may reflect the most efficient means of detecting odors from different locations. Chemical signals may emanate from urine, feces, temporal gland secretion or other bodily fluid on a horizontal or vertical substrate, as well as from visible conspecifics or distant individuals. We describe a number of trunk positions and discuss sample intake and potential functional significance beyond airflow to and from the lungs. An elephant may reach directly out toward the nearby object of interest (reach). The elephant looks larger as it thrusts out its trunk, a formidable weapon as well as a passageway to the main olfactory system. To sample air currents, elephants commonly raise their trunk in a periscopic fashion (Poole, 1999; pers. obs.). This position places the trunk above the body height of nearby elephants, potentially sampling cues from a distance. The posture almost shows a disinterest in the immediate surroundings and appears non-threatening. When elephants are within tens of meters of objects, their trunk position becomes enigmatic. The trunk may curl over (overpass), under (underpass), sideways (side door), or around in a helical fashion (roundabout). The purpose of these various postures is unclear. The elephant may be investigating itself (e.g., during an underpass the trunk tip is pointed up toward the elephant's own head), but typically the trunk tip points toward an object such as an observer or another elephant. The curvature exhibited by the trunk may be beneficial for retaining volatile compounds by allowing longer association /disassociation times with the proteinaceous compounds of the truncal mucus. The trunk position also may convey a behavioral message to a receiver. For instance, a direct reach posture may imply a potential threat in addition to improving the efficiency of air sampling. The curled postures may be less hostile or even provide a dishonest signal of pretended friendliness. Elephants may appear to leave the area only to move around behind the object of interest and approach from a vantage position that is potentially more informative. We are tracking the use of different trunk postures to assess potential communicative function to their use. Not only are behaviors after signal detection important, but receiver psychology may be decoded by careful scrutiny of the means of signal reception.

Events related to sensory reception involve both the intake of putative chemical signals and other intricate processes. We have documented at least ten distinct, additional behaviors that occur during sample investigation (Table 1). For some of these behaviors, the purpose seems apparent but not quantitatively proven. The trunk tip may dig into, blow on, suck up or rub around in urine soaked dirt or dried feces to locate liquid bound chemicals or release volatile chemicals. The tip can pinch shut as if to close off additional odor intake and to isolate odors already acquired into the trunk. The trunk may shake back and forth after touching a sample and this may precede flehmen (Scott, 2002; Rasmussen and Greenwood, 2003). Some of these same behaviors also may serve to clear the trunk of odor or particles. Blow, flick, and shake are all behaviors that release material from the trunk. Audible behaviors such as blow might communicate to others, either intentionally or through eavesdropping (Bradbury and Vehrencamp, 1998). Vocalizations are more likely to be purposeful responses to chemical message reception. We have observed elephants dusting themselves with chemical samples, such as dilute acetic acid or musth urine. Such anointing occurs in other species such as moose to facilitate mate attraction (Miquelle and Van Ballenberghe, 1985), but the purpose in

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elephants is uncertain. At times, an elephant appears to be performing a flehmen but the trunk tip stops at about chin level. In some cases, the animal seemed to be distracted but in other instances, a loss of interest would be a more appropriate explanation. In the latter circumstances, processing of olfactory reception may break off the chemical transfer to the VNO openings in the palate.

**Table 1.** Possible function and description of elephant trunk behaviors related to chemical signal reception.

| Possible function | Behavior | Operational definition |
| --- | --- | --- |
| Increase sample detection | Dig | Trunk tip moves substrate, creating a hole |
| | Blow | Forceful audible exhalation often accompanied by particle release and sometimes substrate movement |
| | Pinch | End of trunk closes in or above sample |
| | Rub or Scrub | End of trunk flattens and moves around in sample |
| | Shake | Trunk is off substrate and lower half or more of the trunk swings up and often around in a corkscrew pattern |
| | Suck | Strong inhalation with trunk on substrate accompanied by observable, muscular, truncal contractions |
| Clearance | Blow | See above |
| | Flick | End of trunk (<ca. 25 cm) moves back and forth similar to a human wrist motion |
| | Shake | See above |
| Anoint | Dust | Trunk grabs substrate containing chemical sample and distributes substrate on elephant |
| Respond to signaler or others | Blow | See above |
| | Vocalize | Audible or infrasonic sound production while investigating sample |
| Lose interest or distracted | Aborted flehmen | Trunk exhibits a check or place response (Fig. 1) and curls to chin level and then is dropped before entering palate |

Numerous other behaviors can vary among elephants upon detecting a particular chemical signal. Males exhibit several penis-involved behaviors such as unsheathing, erection, belly hitting, and trunk touching. Changes in body positions include anterior elevations in stature, pinna of ears assuming a 90-degree position to main axis of body, and ear(s) flapping or waving. The directional movement of the elephant also may change. An individual may back up, become motionless, depart at an angle to its original direction, or go around and then forward. Each behavior potentially reveals something about signal meaning to the individual receiver.

The challenge lies in documenting the occurrence of these various additional behaviors to understand better the sender-receiver interaction. We are doing this through field observations and more tightly controlled biological assays with elephants. We can select elephants with specific attributes and in particular conditional states for bioassay subjects and for donors of chemical samples, such as urine. Chemical samples can vary

from the same sender in numerous ways, including amount of deposition, substrate, time of deposition, and condition of the sender.  Because chemical signals can be received in the absence of the sender, variation of response behaviors to the same chemical sample reflects attributes of the receiver, alterations in environmental conditions or a combination of the two.

**5.   USING VARIATION TO UNDERSTAND RECEIVER PSYCHOLOGY**

The ability to detect chemical signals clearly varies with environmental conditions such as temperature, relative humidity, wind velocity and direction.  We are recording such important environmental variables to correlate them with measures of response. Currently, we are most interested in variation in receiver responses that cannot be explained by abiotic environmental factors.  Of special interest is the influence of group composition, sex, and learning on response patterns.  We are examining the development of chemosensory responses to particular types of chemical samples, namely urine from female elephants at different periods in their reproductive cycle (e.g., luteal and follicular phase of estrous).  We have documented conspecific adult patterns of behavior to urine from Asian elephants (Rasmussen et al., 1982, 1996; Schulte and Rasmussen, 1999; Scott, 2002; Slade et al., 2003) and are collecting data on responses to African urine.  At some point in maturation, elephants respond in an appropriate fashion to a specific signal. The type and degree of response shown by adults has an ontogenetic history that we are trying to map.

Our expanded ethogram provides greater information on the developmental pattern for understanding variation among adults to a specific chemical signal, such as an estrous pheromone.  Male and female elephants mature at similar ages physiologically, but females are able to mate at a much younger age than most males because of social factors (Laws, 1969; Eisenberg, 1980; Hildebrandt et al., 1998; Poole, 1999; Moss, 2001). Males enter their first full musth during their early twenties and are not generally able to mate females until this age.  Male Asian elephants experience a moda musth during their teenage subadult years (Rasmussen et al., 2002), but until they are larger cannot compete with older males for access to females.  We predict that direct assessment of follicular urine and an estrous pheromone through our main bioassay behaviors (Fig. 1) will vary with maturation and social status (e.g., see Rasmussen et al., 1997).  In addition, we are examining if additional behaviors will show a complementary pattern that elucidates receiver psychology.  We present one hypothetical example to illustrate.

Male elephants with the greatest ability to mate with females should exhibit the greatest interest in urine from reproductively ready females (Fig. 3).  If we suppose that males elephants reach their reproductive peak during their forties (Poole, 1987, 1989a,b; Moss, 2001), then these males would show the greatest rates of flehmen.  Inexperience and a lower social status would inhibit males at a younger age from fully responding to the urinary signal.  High response rates could be especially dangerous if the female's signal has a priming type effect, making the male more amorous and likely to be confronted by larger males in musth.  The reduced condition of extremely old males could dampen their responsiveness to the urinary signal, or lengthy experience could quicken inspection.

Rates of response for the main chemosensory behaviors may be a somewhat large grain measure of variation by age.  By incorporating additional behaviors, we might gain

insight on finer grain developmental patterns (Fig. 3). For instance, younger elephants, especially those pre-musth, would be predicted to move away from pre-ovulatory urine sooner, vocalize more, and blow more readily to vent the odor. These behaviors would curtail as males mature and have greater opportunity to mate. Other behaviors may increase with age, such as remaining motionless at the urine, possibly with ears erect in a listening stance, as well as digging and sucking at the sample to enhance uptake. By developing general patterns of response, we can better understand the status and social history of particular individuals. Comparisons across populations could be revealing for conservation purposes. If the hypothetical pattern illustrated in Figure 3 was documented, then the relative age for peaks in behaviors may show differences in demographics and breeding success among populations. For example, a heavily poached population might show a strong leftward shift in the pattern. The benefit of introducing older males could be assessed by the shift in behaviors over time.
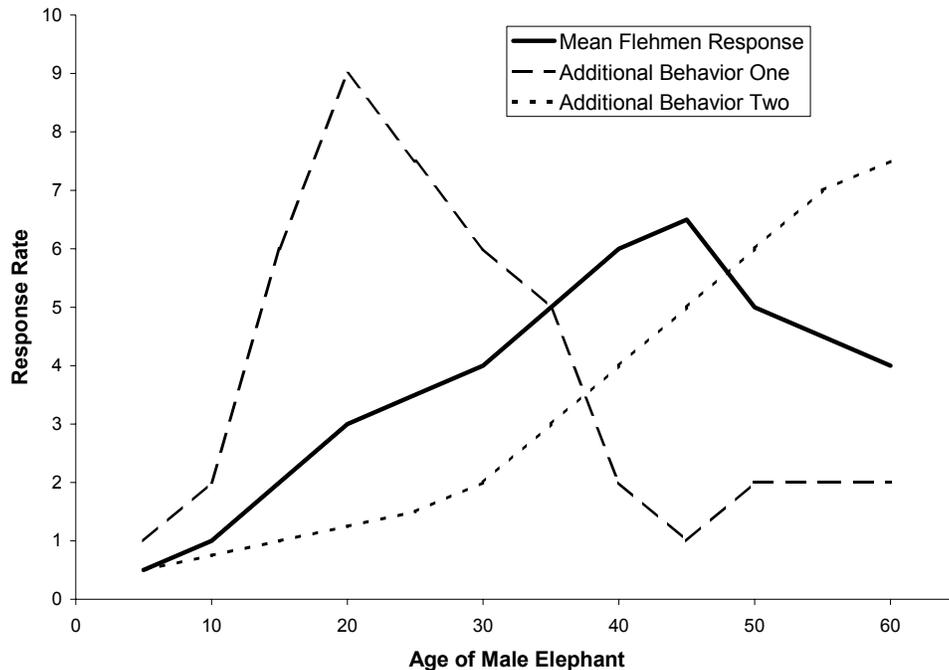


**Figure 3.** Hypothetical responses of male elephants at different ages to pre-ovulatory urine that contains an estrous pheromone. The main response of signal detection is flehmen. Additional behaviors may reveal aspects of receiver condition, status, and experience. Behavior one might include moves away, vocalize, and blow. Behavior two might include motionless with ears erect, dig, and suck. Ages are estimates and would vary with populations and their histories of human intrusion and poaching.

The primary benefit of including more behaviors in a standard bioassay, especially those done in the field, is to determine the relevant sender-receiver complex for chemical signals and their meaning. A particular chemical may have evolved under a singular selective pressure and thus have a singular meaning to one type of receiver (i.e., the intended receiver). Yet, for many animals, this meaning may change with age, reproductive state, social status, and the like. The suites of behaviors that accompany the primary receptive responses are likely to expose the role of such signals across a wide range of receiver types. In Chaos Theory, slight variation in initial conditions, such as the flapping of a butterfly's wings, can have a profound effect on the observed outcome, such as weather patterns a thousand kilometers away (hence, known as the butterfly effect, Lorenz, 1963). The release of a chemical signal may signify the flapping butterfly of communication in elephant and other animal societies.

## 6.  ACKNOWLEDGEMENTS

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