Chapter 7
Comparisons of State and Likelihood of Performing Chemosensory Event Behaviors in Two Populations of African Elephants (*Loxodonta africana*)[‡]

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Abstract The demonstration of a species-level chemical signal assumes that the same chemical signal serves a similar purpose across the range of the species. Yet, the response to putative chemical signals varies with social setting, environmental conditions, age, sex, and reproductive status of the individuals. Through observations and biological assays with African elephants (*Loxodonta africana*), we evaluated variation in state behaviors and the likelihood that elephants would perform specific chemosensory event behaviors at our study sites at Addo Elephant National Park South Africa and at Ndarakwai Ranch in Tanzania. We have noted similar time budgets in state behaviors. Post-pubescent ($>$ 9 y) elephants showed similar likelihoods in investigating their environment, including conspecific urine and feces. As we pursue the identity of an estrous pheromone, other chemical signals, and developmental patterns, studies with the two populations will be invaluable in assessing the generality of these findings to savanna African elephants.

7.1 Introduction

Studying the variation in time budgets and chemosensory behavior of a species across its geographic range can improve our understanding of chemical signal dynamics and the ubiquity of function for particular signals. Determining chemical

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signal activity involves performing biological assays with either parts of a relevant subject animal (e.g., electroantennograms) or whole animals. To facilitate chemical identification, bioassays often are performed in laboratories or at facilities with captive animals. These captive animals represent the first population under study. To verify activity and to elucidate the evolutionary function of the signal, field trials are implemented (Wyatt 2003). The discovery of a preovulatory pheromone, (*Z*)-7-dodecen-1-yl acetate, in Asian elephants (*Elephas maximus*) followed this protocol (Rasmussen, Lee, Roelofs, Zhang and Daves 1996; Rasmussen, Lee, Zhang, Roelofs and Daves 1997; Rasmussen 2001). While our research with African elephants is not as advanced, bioassays with male African elephants at facilities in North America have shown that males respond more to preovulatory than luteal urine from conspecific females (Bagley, Goodwin, Rasmussen and Schulte 2006). Chemical investigation is ongoing and several promising compounds, known to be pheromones in some invertebrates, have been discovered (Goodwin, Eggert, House, Weddell, Schulte and Rasmussen 2006). In preparation for field bioassays, we have been investigating the activity patterns and chemosensory behaviors of African elephants across age and sex in two populations, one in Northern Tanzania and the other in South Africa.

7.2 Objective

The purpose of the current study was to compare the state and chemosensory behaviors of African elephants at our two African study sites. While similarity in these behaviors does not guarantee that chemical signals will be identical in structure and function, the absence of large differences would suggest that such a situation is probable.

7.3 Study Sites, Elephants and Procedures

7.3.1 Study Sites

One of our field sites involves free-ranging African elephants at Ndarakwai Ranch, Tanzania. Ndarakwai Ranch is a privately owned area of ca. 4300 ha located in northern Tanzania. The habitat is a mix of grassland and mixed acacia woodland. This region typically experiences annually a short and a long wet season separated by dry seasons (Vyas 2006), similar to nearby Amboseli National Park, where rainfall averages 350 mm annually (Poole 1999).

The second field site is at Addo Elephant National Park (AENP), founded in 1931 and located in the Eastern Cape of South Africa near Port Elizabeth. The 14,000 ha fenced study area is composed of sub-tropical succulent thicket and grassland (Low and Rebelo 1996, as cited in Whitehouse, Hall-Martin and Knight 2001; Whitehouse and Hall-Martin 2000). Five main waterholes supply pumped water year round, while numerous natural pans are created during rainy periods. The average rainfall for the region is 445 mm annually (Paley and Kerley 1998).

7.3.2 Elephant Populations

Before 1995, only anecdotal records exist of elephants in Ndarakwai Ranch and the surrounding area. Elephants are thought to travel through the area encompassing Ndarakwai as they move between Amboseli and the West Kilimanjaro area (see Vyas 2006 for details). From 2004–6, over 230 elephants in 26 individual groups were identified, as well as 44 solitary adult males (Vyas 2006; Napora, personal communication). Year of birth was known only for animals born during the observation period. Morphological features (e.g., shoulder height and tusk length approximations) were used to estimate ages (Moss 1996) as follows: calves (0–4 y), juveniles (5–9 y), subadults or pubescents (10–19 y), and adults (> 19 y). These ages reflect the approximate time of major developmental changes for elephants (calf: nursing; juvenile: weaning; pubescent: capability of producing viable gametes and dispersal (males) or reproduction (females); adult: full reproductive status and rise in rank). This classification also was used for the elephants at AENP for comparisons.

In 1954, AENP was fenced to protect elephants and humans (Whitehouse 2001). The selective hunting of tusked elephants before this time resulted in a founder population with skewed genetics such that only a small percentage (2–3%) of the female population of elephants at AENP has tusks currently (Whitehouse 2001; personal records). The population has been cataloged in a photographic database (Whitehouse and Hall-Martin 2000; Merte 2006). In 2003, 60 elephants were moved to a new fenced section of the park (Loizi 2004). Currently, our study population in the main park consists of approximately 360 elephants in six family groups. The year of birth was estimated from photographs for older individuals (Whitehouse 2001) and the month or even day of birth is known for almost all individuals born over the past 10 years (Whitehouse 2001; Bagley 2004; Loizi 2004; Merte 2006).

Elephants from both populations were identified using characteristic ear markings, venation patterns, tusk features and other distinguishing marks such as a broken tail or scar. Photographic identification files were created for all new elephants and updated as needed for previously identified animals. Calves were identified by their association with known adult females (Moss & Poole 1983; Wittemyer, Douglas-Hamilton and Getz 2005; Archie, Moss and Alberts 2006).

7.3.3 Observational Methods

At both locations, all observations were made during the day at waterholes. Observations at waterholes permit an unobstructed view of elephants and their trunk movements. Waterholes serve as points of congregation for elephants, so chemical signals in the form of urine and feces as well as their sources (elephants) were readily available. We used continuous focal observations that ended after 20 min or when the animal went out of sight, whichever occurred first (Altmann 1974). Observations of less than 5 min were not included or were added to observations of the same individual in the same area and within a few weeks of the short observation. The order of individuals to be observed was determined by random selection without replacement for the eight age by sex categories (calf, juvenile, pubescent, adult and the two sexes). Whenever the age and sex of the elephant was not available, we watched an animal from the next age and sex category on the day's list. The particular individual observed for this age and sex was selected based on visibility (Lehner 1996).

We classified behaviors as states with measurable duration, or as chemosensory events, recorded as a frequency (Martin and Bateson 1993). The major states were drink/suckle, dust/mud/wallow, stand, walk or other. Chemosensory events were actions by the trunk tip contacting another elephant, investigating a substrate or performing actions called accessory trunk behaviors. We recorded the part of the body touched and the age and sex of the individual touched. The chemosensory events included sniff, check, place, and flehmen, and 10 accessory trunk behaviors (blow, dig, flick, horizontal sniff, periscope sniff, pinch, rub, suck, wrap and wriggle; see Schulte and Rasmussen 1999; Bagley et al. 2006; Schulte 2006; Vyas 2006).

At the Ndarakwai Ranch study site, we observed elephants from the 6 m high platform adjacent to the waterhole in 2004 and 2005. Elephants generally ignored observers who remained quiet and still while recording data. At AENP from 2003–2006, we observed from a vehicle because the elephants were acclimated to them.

7.3.4 Data Analysis

State behaviors were recorded as duration, while event behaviors were converted from frequency to rate (frequency/hour). These data were analyzed as proportion of time spent in a state or proportion of elephants performing a behavior using a Fisher Exact Test (Sokal and Rohlf 1995). Because of the distance between the observer and the elephant, it was sometimes difficult to distinguish sniff, check and place, and flehmens were not common, so the main chemosensory behaviors were analyzed as a single response variable (SCPF) (Schulte and Rasmussen 1999). The chemosensory behaviors were placed into two categories depending on the substrate type: environmental (general substrate) or elephant origin (conspecific, urine or feces). For consideration of age by sex effects, elephants were classified as either pre-puberty (< 10 y) or post-puberty (≥ 10 y) to increase sample size.

7.4 African Elephant Behavior at Northern Tanzania and AENP

The main state behaviors for elephants of all ages at the waterholes in both populations were walk, stand, drink/suckle and bathing in the mud. At Ndarakwai Ranch in Tanzania, these behaviors comprised 90% of the state activities at the waterhole (Fig. 7.1a). In AENP, the same behaviors comprised 97% of the state activities at the various waterholes (Fig. 7.1b). The elephants at Ndarakwai spent somewhat more time drinking and suckling than standing, which was reversed at AENP, but for the

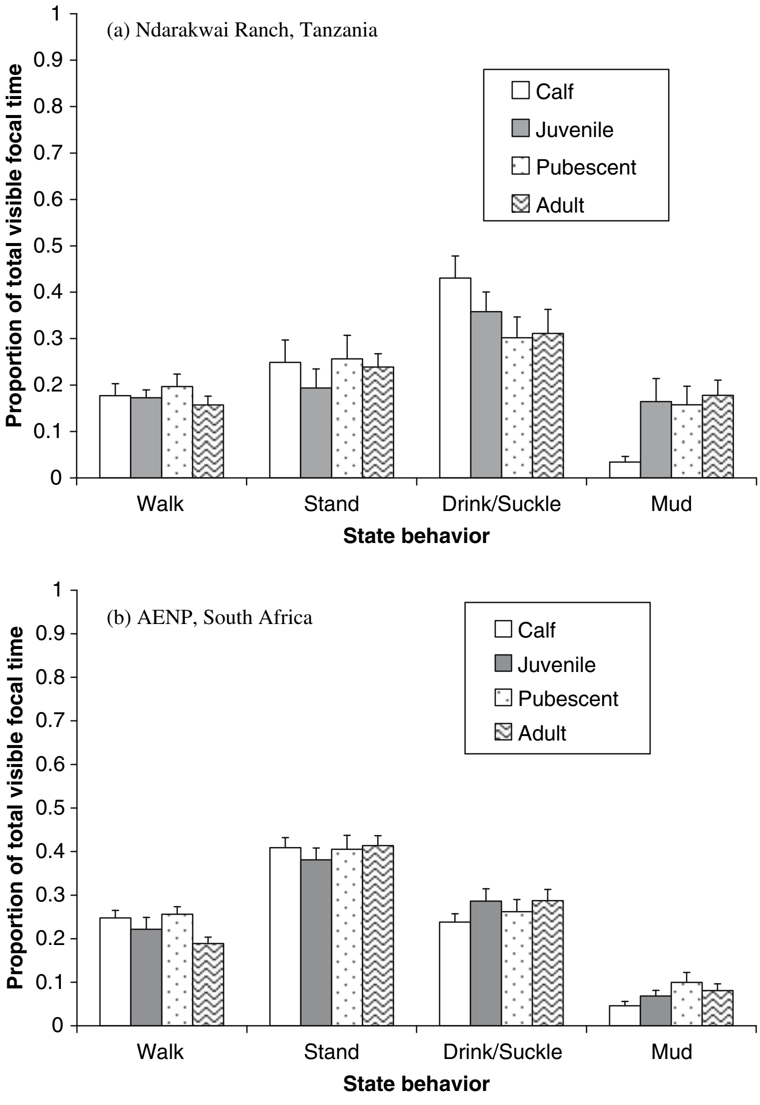

Fig. 7.1 Comparison of the proportion of total time visible that elephants spent in the four major states (a) at Ndarakwai Ranch, Tanzania (90% of all time in all states; sample size was 29, 19, 20 and 32 by age class per behavior from left to right.) and (b) at AENP, South Africa (97% of all time in all states, sample size was 37, 37, 34 and 43 from left to right

two populations these two behaviors comprised 60% and 67%, respectively, of the time at the waterholes. Elephants are not only acting in a similar fashion at waterholes in these two regions, but their activity provides them with similar opportunities to investigate the environment at and around waterholes.

Urine and feces represent a small portion of the total substrate available at a waterhole (Merte 2006), yet they are a source of chemical signals. At both study sites, approximately 50% of the elephants observed investigated the general

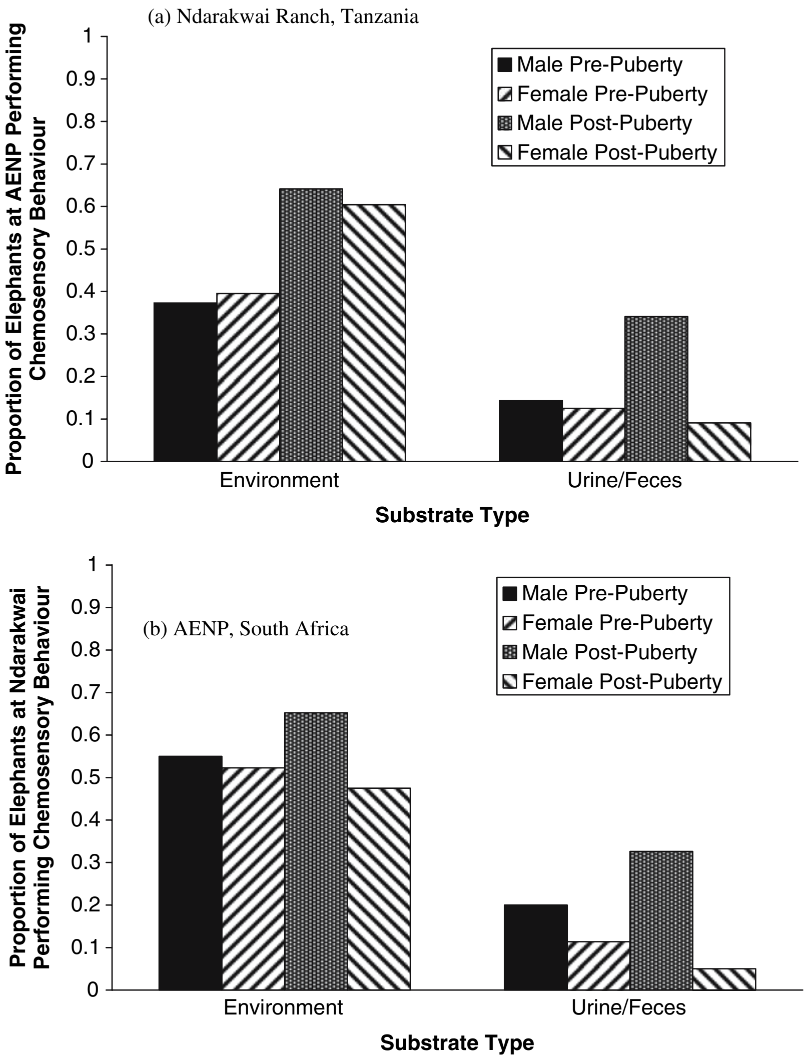

Fig. 7.2 Comparison of the proportion of elephants responding with chemosensory behaviors to the general substrate (environment) and to urine/feces for pre- and post-pubescent males and females. (a) Ndarakwai Ranch, Tanzania; sample size of different elephants from left to right for environment and to urine/feces: 40, 44, 46 and 40. The same animals were observed for response to urine/feces as to the environment. (b) Addo Elephant National Park South Africa; sample size from left to right for environment: 59, 43, 53 and 48. Many of the same animals were observed for response to urine/feces as to the environment. Sample sizes to urine/feces from left to right: 49, 32, 44 and 44

environment with their trunk tip, while 10-30% specifically examined urine or feces. Elephants at the two locations showed very similar trends in their likelihood to investigate. At Ndarakwai, 65% of post-pubescent males performed chemosensory behaviors to the environment, slightly higher than the other age and sex groups (Fig. 7.2a). At AENP, this value was 64% of the post-pubescent males (Fig. 7.2b).

Significantly more pre-pubescent animals investigated the environment with chemosensory behaviors at Ndarakwai (53.5%) than at AENP (38.2%) (Fisher Exact Test, $P = 0.04$), but no such difference existed for post-pubescent elephants (57% and 62%, respectively, $P = 0.46$). The likelihood of performing chemosensory behaviors to urine or feces did not differ between the populations for pre-pubescent ($P = 1.0$) or post-pubescent elephants ($P = 0.85$). The same trends were evident if only the main trunk chemosensory behaviors (SCPF) were considered

7.5 Conclusions and Continuing Research

In the first study by one of our group at AENP (Loizi 2004), we showed that calf activity patterns were similar to those of calves in Amboseli National Park, Kenya (Lee 1986). The results from the current study broaden these findings. In general, the time budgets at waterholes and the likelihood of performing chemosensory behaviors to the environment or to urine and feces did not differ for elephants at the Tanzania and South African study sites. The pre-pubescent elephants at the Ndarakwai Ranch waterhole were more likely to investigate the environment using chemosensory behaviors than this age class of elephants at AENP. Some of the elephants at Ndarakwai are residential in the region, while others are transitory. In either case, the elephants do not visit the waterhole regularly throughout the year. In addition, conflict between humans and elephants occurs in this region, although not on the study site property. Finally, a wide range of other wildlife visit the waterhole, some of which also are transitory (Vyas 2006). In contrast, at AENP the elephants visit the waterholes more regularly. Human-elephant conflict is virtually non-existent and other wildlife is residential. Thus, the younger elephants may have a greater opportunity to experience new odors from conspecifics, potential predators and other organisms at the Ndarakwai waterhole. Interestingly, the likelihood of investigating urine and feces showed very similar patterns across the age and sex classes at the two populations (compare Figs. 7.2a and 7.2b). This pattern was similar whether all chemosensory behaviors or just the main trunk chemosensory behaviors were considered. A comparable pattern was reported for male African elephants at facilities in North American when they were presented with conspecific female urine (Bagley et al. 2006). The main and the accessory trunk chemosensory behaviors showed identical trends in response to luteal and estrous urine. While such results support the contention that African elephants use chemosensory behaviors similarly across their geographic range, until we identify a pheromone in African elephants we will not be able to determine fully the influence of population variation on a specific response.

Our search for an estrous pheromone continues (see Goodwin, Brown, Eggert, Evola, House, Morshedi, Weddell, Chen, Jackson, Aubut, Eggert, Schulte and Rasmussen, this volume). In light of the sexual dimorphism in elephants, we are examining the development of chemosensory behaviors through social play, social interactions and chemosensory exploration (Schulte, Bagley, Correll, Gray, Heineman, Loizi, Malament, Scott, Slade, Stanley, Goodwin and Rasmussen 2005; Meyer 2006; Vyas 2006). Further, at the Tanzanian field site, we are studying elephant-related effects on terrestrial vertebrate biodiversity, the woody habitat and crops (Schulte, Napora, Vyas, Goodwin and Rasmussen 2006). One application of this research may be to use natural chemical signals to reduce human-elephant conflict (Rasmussen and Riddle 2004). Our recent discovery of multiple known insect pheromones in female African elephant urine (Goodwin et al. 2006) has set the stage for future bioassays in North America and in Africa. Identifying such a signal would provide us with a tool to examine further the development of chemosensory behavior and the functional relevance of the signal in two populations of African elephants. The similarities in these two populations of elephants support our hypothesis that they are using chemosensory signals and behaviors for similar purposes.

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