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# Factors Influencing Travel Order as Proxy for Leadership and Trade-offs in Activity Budgets in Lactating and Nonlactating African Savanna Elephants

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FACTORS INFLUENCING TRAVEL ORDER AS A PROXY FOR LEADERSHIP  
AND TRADE-OFFS IN ACTIVITY BUDGETS IN LACTATING AND  
NONLACTATING AFRICAN SAVANNA ELEPHANTS

A Thesis  
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In Partial Fulfillment  
Of the Requirements for the Degree  
Master of Science

By  
Malgorzata Wisniewska

December 2011

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Nutritional and energetic needs of female mammals depend upon size or reproductive investment and shape individual activity budgets and behavioral patterns. To maximize nutritional and energetic intake females may increase time allocated to foraging or access resources through risk-prone behaviors, represented as aggression or leadership. Conversely, to minimize nutritional and energetic spending females may engage in risk-averse activities such as resting or nonaggressive social interactions. Females with the highest needs should exhibit activities and behaviors that facilitate the greatest nutritional and energetic returns or highest metabolic savings. The propensity for risk-prone behaviors may be greater among older as well as lactating females. Older individuals tend to be larger and more experienced than younger conspecifics. Moreover, lactating females are under substantially greater energetic, nutritional and water stresses than nonlactating individuals. Therefore, to fulfill greater nutritional and energetic needs, older and lactating females may allocate more time to foraging or rest or be more assertive during search for and defense of resources. I assessed the relative effects of age, reproductive condition and sex of nursing offspring on activity budgets, the frequency of risk-prone and risk-averse behaviors such as leadership propensity, and chemosensory inspection of the surroundings in female African savanna elephants

(*Loxodonta africana africana*). To quantify activities and behavioral patterns I used focal animal sampling with continuous recording. I determined leadership by the position in a mobile herd, where the first and last positions were considered as ends, and the center was considered as a middle position. I discovered that older females stood more, were more aggressive, socialized less and traveled closer to the end of a traveling group than younger females. Females that were lactating spent more time foraging, were more aggressive and engaged in nonaggressive social interactions less frequently than their nonlactating conspecifics. Finally, females nursing female calves spent more time foraging than females nursing male calves, but the latter spent more time nursing and standing. These results elucidate how individual nutritional and energetic needs influence the activity budgets as well as the propensity to exhibit risk-prone and risk-averse behaviors in female elephants and thus add to a body of work examining mammalian female activity budgets shaped by individual differences such as age and reproductive condition.

CHAPTER I

FACTORS INFLUENCING TRAVEL ORDER AS A PROXY FOR LEADERSHIP IN  
AFRICAN SAVANNA ELEPHANTS

ABSTRACT

Individuals that frequently influence the collective behavior of group members are called leaders. Studies of group-living animals have linked leadership behavior with either the correlates of rank such as age or size or with the correlates of reproductive investment such as reproductive state or number of offspring. My goal was to assess the relative contribution of the proximate determinants of leadership behavior in female African savanna elephants (*Loxodonta africana africana*). From June to December 2010, I determined leadership behavior of each individual by position in mobile herds of African savanna elephants in Addo Elephant National Park in South Africa. To examine the effect of age on leadership behavior, I compared individual travel position by age. To explore the effect of reproductive state on female propensity to lead, I contrasted leadership behavior of lactating and nonlactating females. Lastly, to determine how calf sex affected leadership behavior, I compared travel position of mothers of female versus mothers of male calves. I recorded or photographed position and noted identity of all animals walking in single-file groups upon entry to or exit from waterholes. Age was a significant predictor of female leadership behavior. Namely, older or more experienced females traveled closer to the end of the linearly traveling group; whereas, younger and likely inexperienced females traveled closer to the middle of a linearly traveling group. Reproductive state and sex of nursing calf were not significant determinants of female

leadership. The results of my study are not fully, statistically conclusive, yet the tendency among older females to exhibit greater leadership propensity while experiencing higher nutritional and energetic needs may have biological relevance.

## Introduction

Decisions about group activities arise from interactions among individuals and are made in a shared, an unshared or an intermediate manner (Conradt and Roper 2005, Van Vugt *et al.* 2008). Individuals that consistently influence the group's collective behaviors, such as movement or synchronized feeding, are called leaders (Harcourt *et al.* 2009). In an unshared decision-making process, a single individual uses its high social rank to impose decisions on its conspecifics (Leca *et al.* 2003). Shared or intermediate group decisions are common and occur when several unequally experienced individuals make trade-offs to reach a mutually beneficial decision (Conradt and Roper 2003). Thus, leadership is distributed, and an individual's contribution to the decision outcome transposes depending on the situation (Conradt and Roper 2005, Leca *et al.* 2003). Leadership in domesticated herbivores has been assessed when group members follow a particular individual who changes activity and gradually moves away from the group (Hafez *et al.* 1969, as cited in Dumont *et al.* 2005). Studies of movements of domestic and wild ungulates reveal consistency of individual order; this suggests that leaders and followers experience different trade-offs and exhibit a different suite of physiological traits (Dunbar 1983, Zanette and Ratcliffe 1994). During group movements, leaders often access a point resource first and benefit the most; yet the risk of predation is greater for leaders than followers (Bumann *et al.* 1997, Dugatkin and Godin 1992, Dumont *et al.* 2005). If the resource is small, followers may be excluded; however, when the resource is abundant followers clearly benefit from the leaders' experience (Conradt and Roper

2003, Tilson and Hamilton 1984). Fischhoff *et al.* (2007) found that the leading individuals were more likely to drink immediately upon arrival at the waterhole than were subsequent individuals. However, an empirical study of predation risk in fish shoals showed that 83% of all predator attacks were directed at the leading individuals and that the degree of predation risk increased with the distance away from the center of the group (Bumann *et al.* 1997).

Fitness consequences of leadership have been identified as predation risk offset by the foraging prospects in a new and hypothetically dangerous area (Bumann *et al.* 1997, Beauchamp 2000). However, the relative contributions of the proximate determinants of leadership are not well understood. An individual's propensity to lead should depend upon its familiarity with the risk and resource, and its nutritional and energetic needs (Bumann *et al.* 1997). Leadership often correlates with age and size, both common measures of rank and experience (Archie *et al.* 2006a, Fischhoff *et al.* 2007, Harcourt *et al.* 2009). Decisions about where and when to forage affect the leader's individual fitness as well as fitness of all group members; therefore, leaders should rarely make mistakes, or else they may be supplanted (West-Eberhard 1969). The tendency of the most knowledgeable or high-ranking individuals to lead the group is common and likely attributable to older age. Moreover, in species with female philopatry, leadership seems to be the exclusive domain of females (West-Eberhard 1969). For example, capuchin monkey (*Cebus capucinus*) groups are characterized by female philopatry, a high level of social tolerance and distributed leadership (Fedigan



1993). Leca *et al.* (2003) showed that females of the species initiated group movements with equal frequency but more successfully than males. Female familiarity with resource distribution and conspecifics, greater than that of resident or nonresident males, exemplifies how rank determines leadership. Recent studies indicate that leadership is not a fixed property of a rank and may be influenced by intrinsic physiological factors such as reproductive state, as well as by extrinsic factors such as the sex of a nursing offspring (Archie *et al.* 2006a, Beauchmanp 2000, Peterson *et al.* 2002, Sih *et al.* 2004). Fischhoff *et al.* (2007) proposed that female leadership is dyadic in nature and should be attributed to both an individual's rank and its physiological state.

Although age limits the frequency with which inexperienced females emerge as leaders, to maximize their individual fitness, younger, breeding females may still initiate collective movements towards a resource and positively influence their own nutritional and energetic intake (Dumont *et al.* 2005). The relative costs and benefits of gestation and lactation in mammalian females are associated with the highest sustained metabolic rates in vertebrates. In particular, high caloric demands and increased mortality rates during lactation make it the most challenging reproductive state (Clutton-Brock *et al.* 1989, Gittleman and Thompson 1988, Hamel and Côté 2008, Mellish *et al.* 2000). Moreover, as male calves suckle more and more often, and have faster growth rates than female calves sustained milk production may be metabolically more challenging for mothers of male than female offspring (Lee and Moss 1986). Consequently, driven by their higher nutritional and resource needs, lactating females and females nursing male

offspring may exhibit leadership propensities similar to leadership among older females. The influence of physiological factors on leadership has been examined directly and indirectly in the context of female activity budgets, constrained by the nutritional requirements unique to different reproductive states (Clutton-Brock *et al.* 1989, Clutton-Brock *et al.* 2006). For example, lactating plains zebras (*Equus burchellii*) were more likely to initiate harem movement than nonlactating females, and harems with lactating females led the herd more frequently than harems with only nonlactating females (Fischhoff *et al.* 2007). In gelada (*Theropithecus gelada*) group movement was initiated more frequently by lactating females than by nonlactating females or resident males (Dunbar 1983). By contrast, in grey wolves (*Canis lupus*) the dominant breeding female initiated pack activities four times more often than subordinate breeding females. However, leadership propensity decreased among all breeding females soon after they became pregnant (Peterson *et al.* 2002). Clearly, female leadership across different species, reproductive states and social rank is highly heterogeneous.

In African savanna elephants (*Loxodonta africana africana*), a matrilineal unit called the family is comprised of a matriarch, typically the eldest and most dominant female, as well as females related to the matriarch and their offspring (Douglas-Hamilton 1972). Related family units coalesce into a kinship group. Within each kinship group, age- and size-ranked linear dominance hierarchy determines each individual's social rank (Wittemyer and Getz 2007). The matriarch is considered the unit's repository of social and ecological knowledge (McComb *et al.* 2001). The quality of experience the

matriarch possesses impacts per capita reproductive success of all group members. According to McComb *et al.* (2011) the matriarch makes “ecologically relevant decisions in a domain critical to survival” (p. 3270), such as response to predatory threat or group movements. In addition, the matriarch influences the intergroup dynamics as she coordinates group movement and her group’s interactions with other groups (Esposito 2008). Wittemyer *et al.* (2007) showed that during the dry season the families of dominant matriarchs traveled shorter distances, stayed within boundaries of the protected areas and accessed better quality habitats than families of subordinate matriarchs. Seasonal changes in resource quality and distribution and the degree of competition often lead to fission events. As a kinship group fissions into family units, a new leader emerges within each of these units. Often, females that were followers during fusion lead when fission occurs (Archie *et al.* 2006b). The synergistic relationship between an individual’s rank determined by age and physiological state may provide insight into how the differences in age and reproductive cost create a situation where female elephants, navigating within a very fluid social organization, experience both low and high propensities to lead (Archie *et al.* 2006b).

To determine the relative effects of age and reproductive condition on leadership behavior, I examined the individual order of free ranging female elephants traveling in nuclear families as well as in large aggregations of tens of individuals from the same kinship group. I used travel position as a proxy for leadership, where leaders would be more likely to travel in exterior positions (i.e., near the front or back of a linearly

arranged, mobile group; Dumont *et al.* 2005). I assumed that rank among female elephants was a correlate of age and did not analyze its effect on leadership behavior (Douglas-Hamilton 1972). To determine if leadership behavior varied with age, I compared individual travel position of females by age. To compare the leadership propensity of females with different reproductive state, I juxtaposed prolonged nursing against the metabolically less demanding, nonlactational period (Hamel and Côté 2008). Finally, to contrast leadership behavior in females with different costs of lactation, I compared travel position of females nursing female and male calves. I hypothesized that leadership behavior in female African savanna elephants depends upon age, reproductive state and sex of nursing calf. I predicted that older females traveled closer to the end of the linearly traveling group than younger females. Secondly, I predicted that lactating females traveled closer to the end of the line than nonlactating females. Finally, I predicted that mothers nursing female calves traveled closer to the middle of the line compared to mothers nursing male calves.

## **Methods**

This research has been approved by Western Kentucky University's Institutional Animal Care and Use Committee (Welfare Assurance # A3558-01A) and by South African National Parks (SANParks permit # SCHBA669).

### *Study Site and Population*

I conducted this study in Addo Elephant National Park (AENP), located 70 km north of Port Elizabeth in the Eastern Cape Province, South Africa. Classified as sub-

tropical succulent thicket with open, grassy plains the park receives  $\leq 450$  mm rainfall per year; rainfall is relatively evenly distributed throughout the year (Merte 2006). The vegetation consists largely of dense, thorny thicket with a variety of shrubs, herbs and grasses (Paley and Kerley 1998). The park was established in 1931 to support a nearly extirpated population of 11 elephants in the area (Whitehouse & Hall-Martin 2000). Since its establishment, the park was fenced and has undergone several expansions (Gough and Kerley 2006). At the time of this study, the park consisted of three parts: Colchester (~12760 ha), Main Camp (~12125 ha) and Nyathi (~13150 ha) sections (Adendorff, J, personal communication, November 6, 2011). The extant population of ca. 510 elephants descended from the founder population and a number of adult bulls imported from Kruger National Park (Table 1.1; Merte 2006). Longitudinal data, gathered since the park's creation, allowed scientists to define two clans and six matrilineal lines delineated by letters A, B, H, L, P and R (Whitehouse and Hall-martin 2000). Each of the matrilineal lines forms a kinship group, a basic unit of membership determination. Within those six kinship groups, 37 family associations exist in the Main Camp and Colchester sections, each with a distinguishable matriarch (Esposito 2008). Because the entire population has been identified based on apparent physical characteristics and photographically catalogued, I was able to determine age and social status of all females 10 years of age or older (Whitehouse and Hall-Martin 2000). I determined female lactation status via direct observation of nursing (N=27) or if a female had a suckling calf of up to 6 years of age (N=6; Lee and Moss 1986). Whenever a female had lost her

youngest calf but also had another offspring less than six years old (potentially suckling opportunistically) that female was considered nonlactating (N=4). I observed two cases of nonlactating females seemingly nursing a calf and a juvenile; in one instance a male calf appeared to suckle from its postreproductive grandmother. In the second instance, a juvenile male appeared to suckle from its mother. Due to the aberrant nature of these observed behaviors, I considered both of these females nonlactating.

### *Data Collection*

Leadership data were collected from June to December of 2010, during the local hours of 08:00 to 18:00, in the Main Camp and Colchester sections of AENP. I spent 111 days in the field; this equated to 713 h or an average of 6:25 h/day ( $\pm 1.5$  h). To quantify leadership I observed groups of elephants upon arrival at or exit from waterholes or during passage across tourist roads. Following AENP guidelines, all data were collected while in a field vehicle from an approximate distance of one to 50 meters. Whenever necessary I used binoculars to collect data. I recorded or photographed position and noted identity of all animals walking in single-file group. A group was defined as a cluster of two or more related individuals, with the distance of each individual to its nearest neighbor less than three body lengths (Esposito 2008). Mean group size was 9.9 individuals ( $\pm 1.1$ ). Only groups with at least one lactating and one nonlactating female present were included in the analyses. Males 12 years of age or younger were considered as part of the traveling group, had their position and identity noted, but they, along with any older males present were not considered in the data analyses.

### *Data Analysis*

I considered the first and last positions as end positions, and the central positions as the middle positions. To account for variance in the number of members in a group, termed group size, I standardized individual travel position measures by determining the number of positions from end to middle (such that each traveling group consisted of two halves with one or two individuals occupying the middle positions, depending upon even or odd size of the group). The end was demarcated as zero. I divided each individual's position number by the number of positions from the end to the middle minus one. Therefore, the middle position was always given a value of one. All intermediate positions were labeled with their respective decimal values. For example, in a group of 10 individuals, the positions were labeled as 0, 1, 2, 3, 4, 4, 3, 2, 1, 0 (such that there were five positions from each end to the middle); the standardized scores were  $0/4=0$ ,  $1/4=0.25$ ,  $2/4=0.5$ ,  $3/4=0.75$ ,  $4/4=1.0$ . Secondly, to control for excessive variance in the group size variable and to represent an individual's travel position in a more standardized fashion, I analyzed data fitting within one standard deviation of the mean separately from the longitudinal data (Fig. 1.1). Lastly, to further investigate the individual travel position, I disregarded data for all female and male calves and juveniles traveling with the group and recalculated standardized median travel scores for only reproductively active females. I only used groups with three individuals or more, where either end and the middle positions were always occupied. I disregarded data from groups traveling with more than one matriarch, as those are aggregations of several

leaders and their discrete families traveling in close proximity. Mean group size consisted of 4.1 reproductively mature females ( $\pm 0.2$ ).

To eliminate between-subject variance, I analyzed matched pairs data for lactating and nonlactating females of the same age and for lactating parous females of similar age but with oppositely sexed calves (Table 1.2). In parametric tests, for individuals represented more than once in the dataset, I used the median value of their travel positions. In nonparametric tests, namely linear mixed effects model (LME) and randomized residual permutation procedure (RRPP), I used longitudinal data; therefore, an individual could have been represented more than once. I tested the data for normality using Shapiro-Wilk test. Data sets that were normally distribution or had a Shapiro-Wilk test statistic greater than 0.9 were analyzed parametrically. Otherwise, nonparametric tests were used.

I analyzed travel order data using R (R Core Development Team, 2009). The initial assessment of data was performed with the linear mixed effects model (LME model) in the lme4 package of R (Pinheiro and Bates, 2000). In the LME model, I examined the effects of age, reproductive state and temperature as fixed effects associated with multiple individuals. To control for pseudoreplication, I treated the individual's name nested within family as a random effect specific to individuals. Standardized travel position was used as the response variable in the LME model. The LME models, fitted with restricted maximum likelihood (REML), were evaluated using Akaike's information criterion (AIC) with lower AIC scores signifying better models.



The effects of age, age class, age of nursing calf, family, reproductive state, sex of nursing calf and temperature on standardized travel position were evaluated using parametric tests (Analysis of Variance (ANOVA), simple linear regression test, Spearman's correlation test and Student's t-test) and nonparametric tests (Kruskal Wallis one-way ANOVA, Pearson's correlation and Wilcoxon-signed rank test). Standardized travel position was used as the response variable in parametric and nonparametric tests. To provide a robust analysis of non-normal longitudinal data with unequal number of observations per individual, I performed the randomized residual permutation procedure (RRPP) without replacement on all fixed effects in the model (Anderson and Robinson 2001). For example, in each random permutation, reduced models contained random effects plus non-targeted fixed effects. I examined the effects of age, reproductive state and temperature as fixed effects. Age and social rank tend to be correlated in elephants; therefore, I did not consider social rank in this analysis. I treated the individual's name nested within family and the number of observations per individual as random effects. Standardized travel position was used as response variable. Residuals from the three possible reduced models were concatenated to preserve consistency in their random placement and shuffled randomly during iterations of the process. In each random permutation, I calculated residual sums of squares and used those to calculate coefficients of determination ( $R^2$ ) as the test statistic. Thus, p-values indicate the probability of finding as extreme of an  $R^2$  value for each effect, by chance, with respect to other model effects. All statistical tests used  $\alpha$  of 0.05.

## Results

Age and reproductive state variables had some effect on travel position when model selection was conducted on longitudinal data for group sizes from four to 32 individuals. The best-fit model for travel position was a two-factor one, consisting of reproductive state and temperature variables. The best single-factor model included age. The AIC scores for the two-factor model and single-factor model differed marginally. Overall, the best models always included either age or reproductive state variables alone or their additive or interactive effect with a second fixed variable (Table 1.3).

Age was a significant predictor of the standardized median travel position ( $R^2 = 0.008$ ,  $p_{\text{slope}} = 0.014$ ). Among adult females older females traveled closer to the end of the traveling group than younger adult females ( $R^2 = -0.09$ ,  $p_{\text{slope}} = 0.04$ ; Fig. 1.2 and Table 1.4). Age was not a significant predictor of the standardized median travel position in subadult females. Nor was age a significant predictor of the standardized median travel position when lactating ( $R^2 = -0.019$ ,  $p_{\text{slope}} = 0.19$ ) and nonlactating ( $R^2 = -0.071$ ,  $p_{\text{slope}} = 0.106$ ) females were analyzed separately (Fig. 1.3 and Table 1.4). However, analysis of data fitting within one standard deviation of the mean variable (including groups with six to 11 members) revealed that the predictive value of age on the standardized median travel position in both lactating and nonlactating females approached significance ( $p_{\text{slope}} < 0.1$ , Table 1.4). The predictive value of age on the standardized median travel position in mothers nursing female calves approached significance ( $R^2 = 0.095$ ,  $p = 0.094$ ) and was not significant in mothers nursing male

calves ( $R^2 = -0.05$ ,  $p_{\text{slope}} = 0.68$ ). Analysis of the effect of age on the standardized median travel position among reproductively mature females, when all calf and juvenile individuals of either sex were excluded from the travel order data, did not reveal new statistically significant findings.

Adult and subadult females did not differ significantly in their standardized median travel position ( $F = 0.23$  df (1, 44),  $p = 0.63$ ). Likewise, the standardized median travel position was not different for lactating and nonlactating females ( $F = 1.91$ , df (1, 44),  $p = 0.17$ ; Fig. 1.4 and Table 1.5). There was a significant interaction between reproductive state and kinship ( $F = 2.61$ , df (5, 44),  $p = 0.038$ ; Table 1.5). The travel pattern by the R elephant kinship groups appeared most divergent when compared to the travel patterns of other kinship groups (Fig. 1.5). Comparison of standardized median travel position between females of different age classes, reproductive state and nursing differently sexed offspring, when all calf and juvenile individuals of either sex were excluded, did not reveal new statistically significant findings.

To investigate the effect of age on female travel position relatively independently of reproductive state, I analyzed a subgroup of parous, lactating females, all with a suckling calf of up to four years of age. Adult and subadult parous, lactating females did not differ in their standardized median travel position (K-W  $\chi^2 = 0.085$ , df = 1,  $p = 0.77$ ). Mothers nursing female and male calves did not show significant divergence in their standardized median travel position (K-W  $\chi^2 = 0.511$ , df = 1,  $p = 0.48$ ). Lactating, parous

females of different kinships did not differ significantly in their standardized median travel position (K-W  $\chi^2 = 8.7$ ,  $df = 5$ ,  $p = 0.12$ ; Table 1.6).

To investigate further the relationship between reproductive state and travel position, I compared the standardized median travel position of subadult, lactating and nonlactating females. The age difference between the females in each pair was equal to or less than one year. There was no significant difference in the standardized median travel position between subadult, lactating and nonlactating females of similar age ( $t = 0.58$ ,  $df = 5$ ,  $p = 0.59$ ; Fig. 1.6). A matched pairs comparison with equal variance between similarly aged mothers of female versus male calves showed no significant difference in their standardized median travel position ( $t = 0.23$ ,  $df = 11$ ,  $p = 0.82$ ; Fig. 1.7).

Results from RRPP were consistent with parametric tests and the LME model; age, reproductive state and temperature had no significant effect on the standardized travel position. The model targeting age factor appeared to explain the greatest amount of variance in the observed results ( $R^2 = 0.038$ ,  $p = 0.14$ ). The models targeting temperature ( $R^2 = 0.006$ ,  $p = 0.23$ ) and reproductive state ( $R^2 = 0.003$ ,  $p = 0.41$ ) factors explained less than one percent of variance in the observed results (Table 1.7). Overall, the permuted model, obtained through the RRPP estimating three null distributions of the variance components ( $R^2$  for 10000 permutations where age, reproductive state or temperature were the effects of interest) was not significant for any effect of interest.

This indicated that none of the effects of interest was a strong predictor of the standardized median travel position in female elephants (Fig. 1.8).

## **Discussion**

Leadership behavior in group-living mammals has been associated with correlates of rank such as age or size and with correlates of reproductive investment such as reproductive state or sex of offspring (Fischhoff *et al.* 2007, Peterson *et al.* 2002). Although fitness consequences of leadership are well understood, less is known about the relative contribution of its proximate determinants. I investigated how age and reproductive condition related to the position in a traveling group of female African savanna elephants at AENP South Africa. Age was a significant predictor of travel position in female elephants, but when considered by age class, adult ( $\geq 20$  y) and subadult (10-19 y) females did not show statistically significant difference in their travel position. Similarly, travel position between lactating and nonlactating females was not statistically different. Further, in a subsample of similarly aged females travel position did not differ between females of different reproductive states. There was a significant interaction between reproductive state and kinship. Namely, in the R kinship group, lactating females traveled closer to the end of a linearly traveling group and nonlactating females traveled closer to the middle of the line. Lastly, similarly aged mothers nursing female and male calves did not differ significantly in their standardized median travel position, but the predictive value of age on the standardized median travel position in mothers nursing female calves approached significance.

Bumann *et al.* (1997) showed that the peripheral positions of a linearly traveling group are more dangerous than the core positions. A common strategy to minimize the individual and group risks of predation or wrong navigation decisions involves having the most experienced individuals as the group leaders (Dumont *et al.* 2005). However, in zebra finches dominant and subordinate individuals frequently arrived at food source simultaneously; thus, the authors concluded that dominance status was not a strong predictor of leadership (Beauchamp 2000). Dominance relationships among female elephants should ensure that the oldest and most experienced females are typically in the position of leadership (Archie *et al.* 2006a, McComb *et al.* 2001). In this study, travel position in female elephants was weakly predicted by age. Still, relative to other effects of interest, age was the best determinant of female travel position. Namely, older adult females, except in the R kinship group, traveled closer to the ends of a mobile group more often than younger adult females. Age in long-lived social mammals indicates ecological and social knowledge, imperative for skillful navigation and antipredator protection, so leadership in female elephant is at least in part determined by age (Wittemyer *et al.* 2007). The low predictive value of age on female travel position may be explained because elephants rely on widely distributed resources with relatively constant phenology; thus, younger and less experienced individuals may have a functional knowledge of when and where to forage and seek water and may at times emerge as leaders or at least by their location give the semblance of leaders (Archie *et al.* 2006b, Beauchamp 2000). In the present study, R kinship group showed the most

anomalous pattern with older lactating females occupying core positions. However, data were obtained from this group in only two instances, and it is not possible to determine if this reveals a meaningful pattern or an aberration.

Besides age or experience, reproductive state often circumstantiates leadership propensity in female ungulates (Fischhoff *et al.* 2007). Females with the highest nutritional and resource needs may initiate movement or lead their group members towards a foraging ground or water point (Clutton-Brock *et al.* 1989, Dunbar 1983). In addition, by positioning themselves near the periphery of a mobile group, females with the greatest resource needs may better control timing and direction of travel and gain better access to the forage or water (Fischhoff *et al.* 2007). Among different reproductive states, lactation is generally considered to be the most challenging one (Bartošová *et al.* 2011, Gittleman and Thompson 1988, Mellish *et al.* 2000). In some primate species with prolonged lactation and late weaning of offspring, lactating females initiate group movement more frequently than nonlactating females or resident males (Dunbar 1983). In my study, reproductive state alone was not a significant determinant of female leadership. Age also was not a significant predictor of travel position between pairs of similarly aged, lactating and nonlactating females. However, in the reduced data set including groups with six to 11 individuals, the predictive value of age approached significance in both lactating and nonlactating females. Although not significant, the effect of age on travel position among lactating and nonlactating females was similar to the pattern seen in adult and subadult females. The seemingly parallel effects of age and

reproductive state on female travel behavior may be due to the synergistic relationship between those factors. Alternatively, it may be a reflection of age-specific reproductive state, when older females are commonly parous and lactating, but younger females may still be nulliparous and nonlactating.

Among lactating females, mothers nursing female versus male calves may be subject to different metabolic demands. Published evidence has shown that male calves grow faster, nurse more, wean at later age and when malnourished have lower survivorship than female calves (Lee and Moss 1986, Reinhardt and Reinhardt 1981). Consequently, sustained milk production may be metabolically more challenging for mothers of male than female calves and may be manifested by divergent behaviors (Lee and Moss 1986). Although the influence of offspring sex on mothers' activity patterns has been examined in various species, I know of no published studies elucidating the relationship between the sex of a nursing offspring and mother's leadership behavior (Clutton-Brock *et al.* 1989, Hamel and Côté 2008). In my study, mothers of female and male calves did not exhibit divergent travel patterns. However, the predictive value of age on the travel position in mothers of female calves approached significance. The mean age in these two groups of females was not significantly different nor was mean age of female and male calves; therefore, the observed difference was likely related to the sex of nursing calves. Although wellness of offspring of either sex depends upon maternal care, the reproductive success of daughters depends more on their own reproductive investment than on their size at puberty (Graeme *et al.* 2008). On the



contrary, the reproductive success of sons depends heavily on their competitive ability, which is determined by size (Hollister-Smith *et al.* 2007). Because sons have greater potential reproductive success than do daughters and because offspring fitness indirectly affects maternal fitness, mothers should invest more in their sons than daughters (Clutton-Brock *et al.* 1981). In matrilineal societies after puberty, daughters often continue to share their mothers' home ranges and as allomothers may contribute to the successful rearing of their younger siblings (Bradshaw *et al.* 2005, Lee 1987). In elephants, daughters may stay with their mothers for a lifetime and maintain life-long cooperative bonds with their sisters (Douglas-Hamilton 1972). To enhance their own fitness, mother elephants may be equally strongly committed to investing in their sons and their daughters. In sum, the dual nature of maternal investment in elephants may help reconcile the lack of clear divergence in leadership propensities in mothers of female versus male calves.

The evidence gathered in this study does not provide strong support for my predictions that age and reproductive condition shape females' leadership propensity. Although my analyses did not reveal statistically significant divergence in travel patterns in females of different age class, reproductive state and nursing oppositely sexed calves, I noted that older adult females traveled closer to the periphery of a traveling group more often than younger adult females. This finding partly supports my prediction and shows that age and ecological knowledge may be the strongest determinants of female leadership (Peterson *et al.* 2002). However, the effects of reproductive condition on

individual travel patterns remain inconclusive. These results may have been affected by the fact that different subsets of females were studied under a semblance of one reproductive state. For example, among lactating females there was a relatively large age disparity. Likewise, similar consideration of travel order in small families as well as in large aggregations of elephants may have exaggerated the importance of the end and the middle positions and neglected the biological importance of distance away from each of these positions. My attempts to eliminate excess variance by considering only similarly sized groups (6-11 group members) or only reproductively mature females may not have been sufficient. Therefore, future studies should focus on deriving more sensitive methods to investigate travel order in uniformly sized groups and should attempt to stratify sampling among females by age (Šárová *et al.* 2010).

**Table 1.1.** Female group organization of living elephants in Main Camp of AENP

Clan	1			2		
Kinship	A	B	H	P	L	R
Oldest Matriarch (year born)	AND (1956)	TAN (1951)	HEI (1972)	MEG (1965)	LLT (1968)	REB (1964)
# Individuals	81	73	21	95	44	49
# Families	8	7	1	10	3	6
Matriarch (year born)	AND (1956)	TAN (1951)	HEI (1972)	MEG (1965)	LLT (1968)	REB (1964)
	ALO (1961)	BEV (1970)		PAU (1969)	LAU (1972)	RUT (1971)
	ALI (1963)	CAT (1970)		TIP (1973)	LUL (1984)	RIT (1973)
	AMA (1969)	BLU (1976)		MOL (1981)		ROZ (1975)
	ALI (1972)	BON (1980)		MON (1981)		ROS (1981)
	APP (1975)	BRI (1980)		PHY (1981)		RON (1984)
	AMB (1977)	BHU (1986)		PUM (1984)		
	ANN (1985)	BYR (1986)		MEL (1987)		
				MOR (1990)		
				MAD (1991)		

\*B kinship has seven families and eight matriarchs because Tania and Beverly led the same individuals; six months after the conclusion of this study Tania was presumed dead.

\* Whitehouse & Hall-Martin 2000

**Table 1.2.** Sample size distribution for age class (adult vs. subadult), reproductive state (lactating vs. nonlactating) and social rank (matriarch vs. non-matriarch) for (a) elephant groups with four to 32 and six to 11 members, and (b) lactating, parous females.

(a) Group Size

Age Class	Social Rank	Reproductive State	Group Size 4-32	Group Size 6-11
Adult	Matriarch		37	21
			17	12
	Non-matriarch	Lactating	13	10
		Nonlactating	4	2
			20	9
			19	8
	Nonlactating	1	1	
Subadult	Non-matriarch		28	22
			28	22
		Lactating	8	7
		Nonlactating	20	15

(b) Parous Females

Age Class	Social Rank	Reproductive State	Parous Female	
			Female calf	Male calf
Adult	Matriarch		16	16
			8	5
	Non-matriarch	Lactating	8	5
			8	11
		Lactating	8	11
Subadult	Non-matriarch		5	3
			5	3
		Lactating	5	3

**Table 1.3.** Linear mixed effects model comparison using AIC. Age, reproductive state and temperature were fixed effects; name nested within family was a random effect. Standardized travel position was a response variable. The best overall model is denoted with †; the best single-factor model is denoted with ‡. Only parameters and interactions with significant p-values and  $AIC\Delta \leq 2$  relative to the null model are presented.

Model	df	AIC	BIC	logLIK	$\chi^2$	$\chi^2$ df	Pr ( $>\chi^2$ df)
Null	4	131.49	143.51	-61.75			
‡Age	5	126.90	141.91	-58.45	3.61	0	2.2e-16*
RState+Age	6	128.40	146.42	-58.2	6.213	1	0.013*
Age+Temp	6	127.73	145.75	-57.87	0.666	0	2.2e-16 *
Age*Temp	7	127.22	148.25	-56.611	6.285	1	0.012 *
†RState*Temp	7	126.38	147.41	-56.191	3.485	0	2.2e-16 *

**Table 1.4.** Regression analysis results compared the effect of age on standardized median travel position in elephants of different age class, reproductive state and nursing calves of different sex, for groups with six to 11 members and four to 32 members.

Group	Regression Variables	$\alpha+\beta\text{Age}$	$R^2$	p	F(df)
6-11	Age~Position	0.48-0.003	-0.015	0.55	(1,41)=0.36
6-11	Age~PositionA	0.5-0.01	-0.027	0.497	(1,19)=0.49
6-11	Age~PositionSA	0.7-0.02	-0.012	0.399	(1,20)=0.74
6-11	Age~PositionL	0.67-0.01	-0.103	0.065•	(1,23)=3.77
6-11	Age~PositionNL	0.2+0.02	0.159	0.057•	(1,16)=4.22
4-32	Age~Position	0.6-0.01	0.08	0.014*	(1,63)=6.364
4-32	Age~PositionA	0.76-0.013	-0.09	0.043*	(1,35)=4.39
4-32	Age~PositionSA	0.9-0.04	0.077	0.083	(1,26)=3.248
4-32	Age~PositionL	0.55-0.01	0.02	0.192	(1,38)=1.762
4-32	Age~PositionNL	0.62-0.01	0.07	0.106	(1,23)=2.826
parous	Age~Position	0.55-0.01	0.02	0.192	(1,38)=1.762
parous	Age~PositionF	0.74-0.01	0.095	0.094	(1,19)=3.088
parous	Age~PositionM	0.21-0.003	-0.05	0.683	(1,17)=0.173
parous	AgeF1~Position	0.48 -0.06	0.02	0.202	(1,38)=1.687

\*  $p \leq 0.05$

•  $p < 0.1$

**Table 1.5.** ANOVA results for the effect of age class (adult or subadult), reproductive state (lactating or nonlactating) on standardized median travel position for groups of elephants with six to 11 members, and for all sized groups ranging from four to 32 members, in AENP.

Group	ANOVA Variables	df	Sum Sq	Mean Sq	<i>F</i> value	Pr(> <i>F</i> )
6-11	RState	1, 23	0.15	0.15	1.304	0.27
6-11	AClass	1, 23	0.04	0.04	0.359	0.56
6-11	Kinship	5, 23	0.24	0.05	0.417	0.83
6-11	RState:AClass	1, 23	0.53	0.53	4.54	0.044*
6-11	RState:Kinship	5, 23	1.12	0.22	1.921	0.13
6-11	AClass:Kinship	3, 23	0.38	0.13	1.362	0.28
6-11	RState:AClass: Kinship	4, 23	0.1	0.03	0.223	0.92
4-32	RState	1, 44	0.18	0.18	1.913	0.17
4-32	AClass	1, 44	0.02	0.02	0.233	0.63
4-32	Kinship	6, 44	0.32	0.05	0.557	0.76
4-32	RState:AClass	1, 44	0.05	0.05	0.553	0.46
4-32	RState: Kinship	5, 44	1.24	0.25	2.61	0.038*
4-32	AClass: Kinship	4, 44	0.56	0.14	1.47	0.23
4-32	RState:AClass: Kinship	2, 44	0.02	0.01	0.089	0.91

\*  $p \leq 0.05$

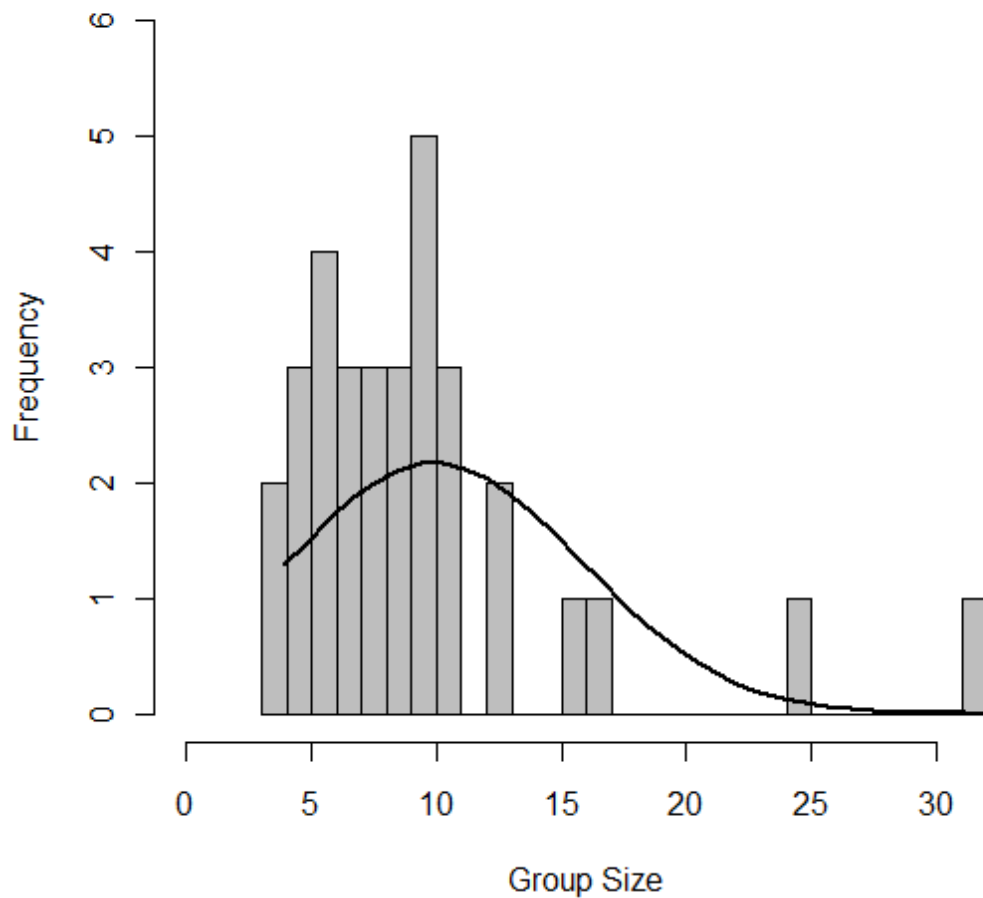
**Table 1.6.** Kruskal Wallis one-way ANOVA results of comparison of standardized median travel position in lactating parous females; sample sizes for the six kinship groups were as follows: A=10, B=8, H=4, L=2, P=13, R=2.

Group	Kruskal Wallis ANOVA Variables	K-W $\chi^2$	df	p
Parous	AClass	0.09	1	0.77
Parous	SexF1	0.51	1	0.48
Parous	Kinship	8.69	5	0.12

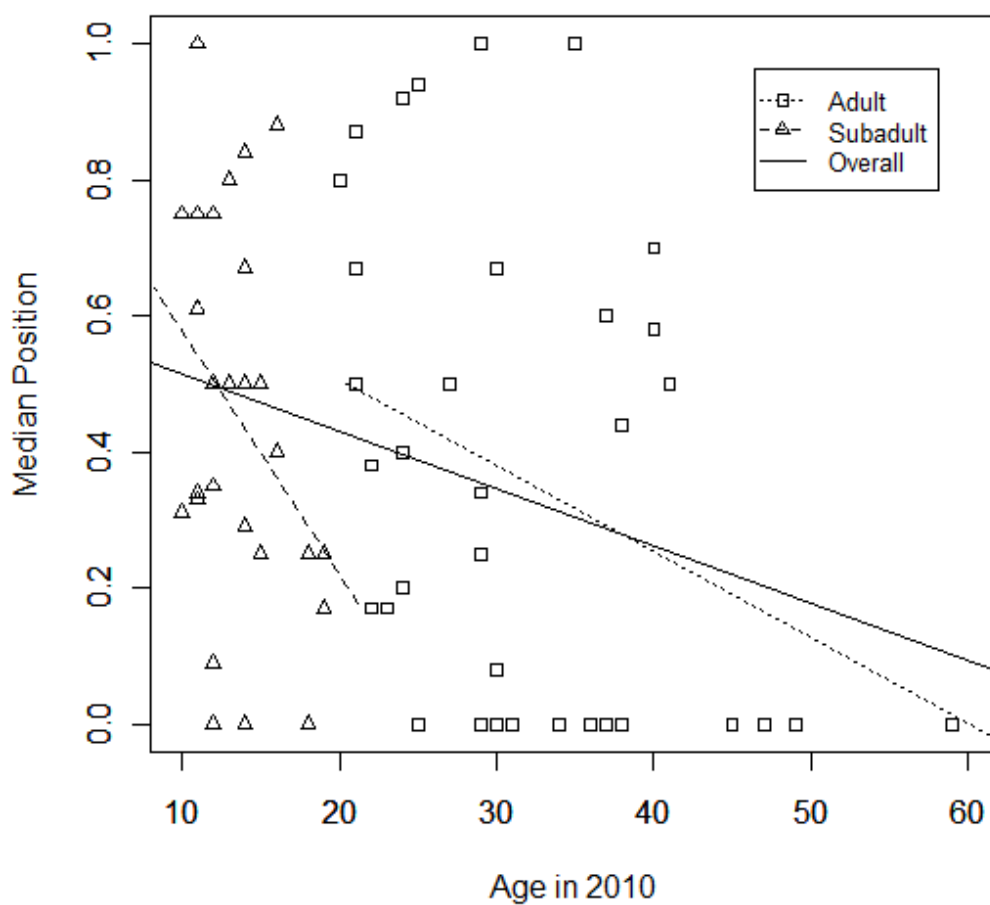


**Table 1.7.** Randomized residual permutation of 10000 trials comparing the effect of age, reproductive state and temperature on standardized travel position for elephant groups with four to 32 members.

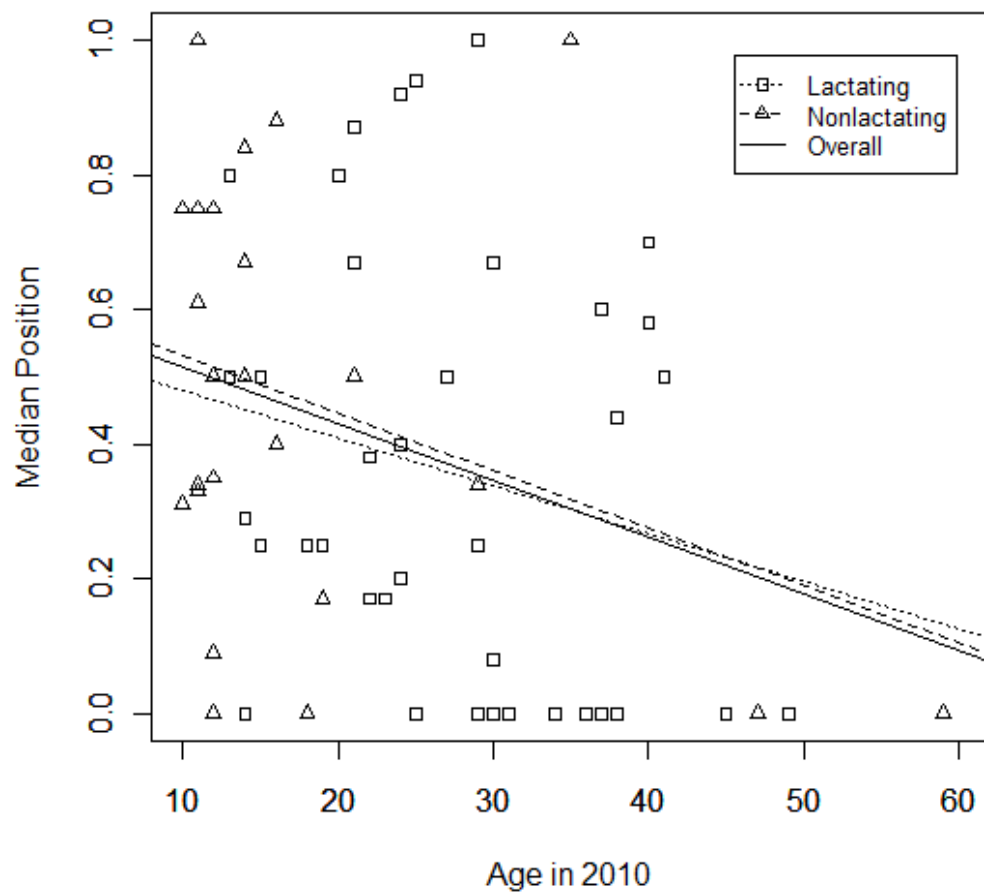
Fixed Variable	Sums of Squares	R <sup>2</sup>	p
Temperature	0.13	0.006	0.23
Age	0.795	0.038	0.14
Reproductive State	0.06	0.003	0.41



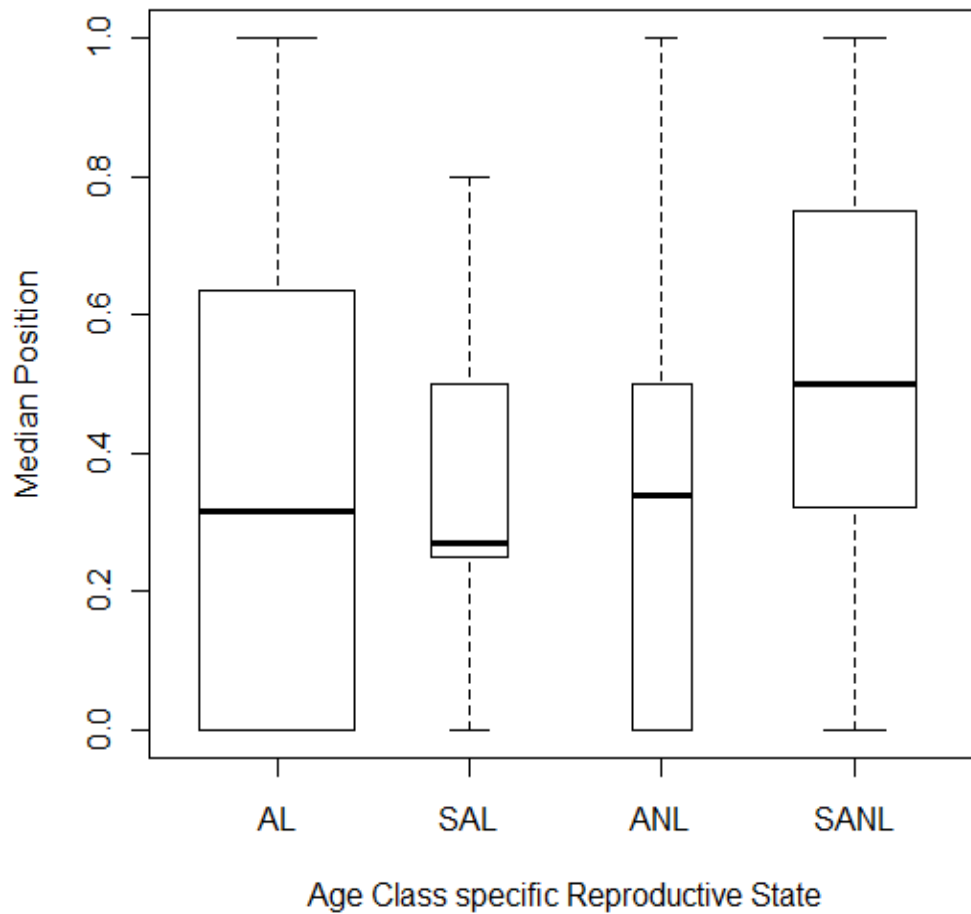
**Figure 1.1.** Group size distribution while traveling in single file for families of African savanna elephants in Addo Elephant National Park South Africa: (min=4, 1<sup>st</sup>quartile=6, median=9, 3<sup>rd</sup>quartile=11, max=32,  $N_{4-32}=32$ ,  $N_{6-11}=25$ ).



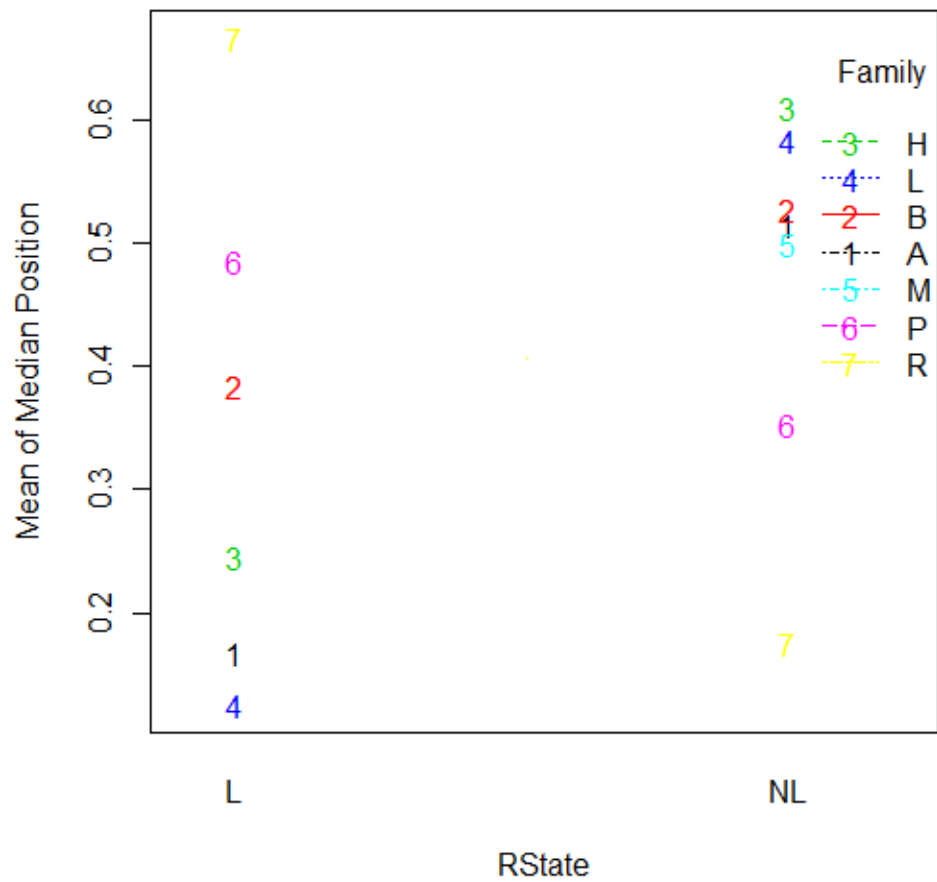
**Figure 1.2.** Linear regression of age on the standardized median travel position with separate trendlines for adult and subadult females: adult ( $N = 37$ ) and subadult ( $N = 28$ ), and an overall trendline for the combined data. For statistical analyses refer to Table 1.3.



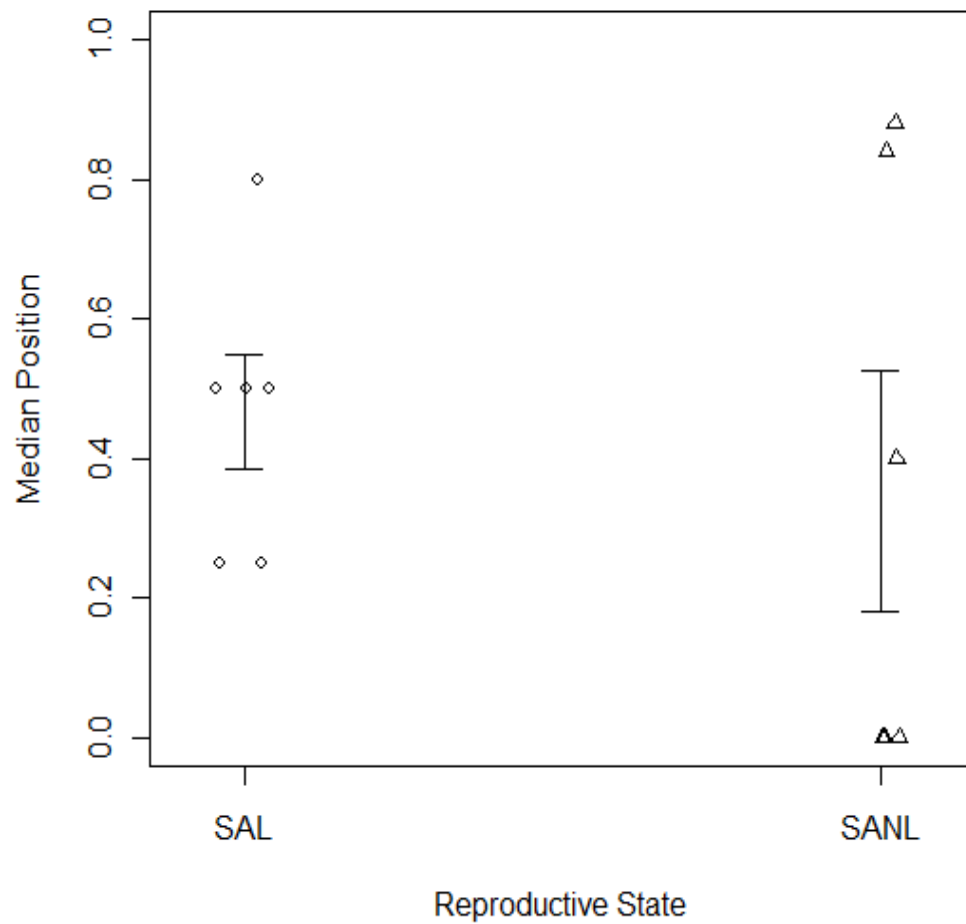
**Figure 1.3.** Linear regression of age on the standardized median travel position with separate trendlines for lactating and nonlactating females: lactating (N = 40) and nonlactating (N = 25). For statistical analyses refer to Table 1.3.



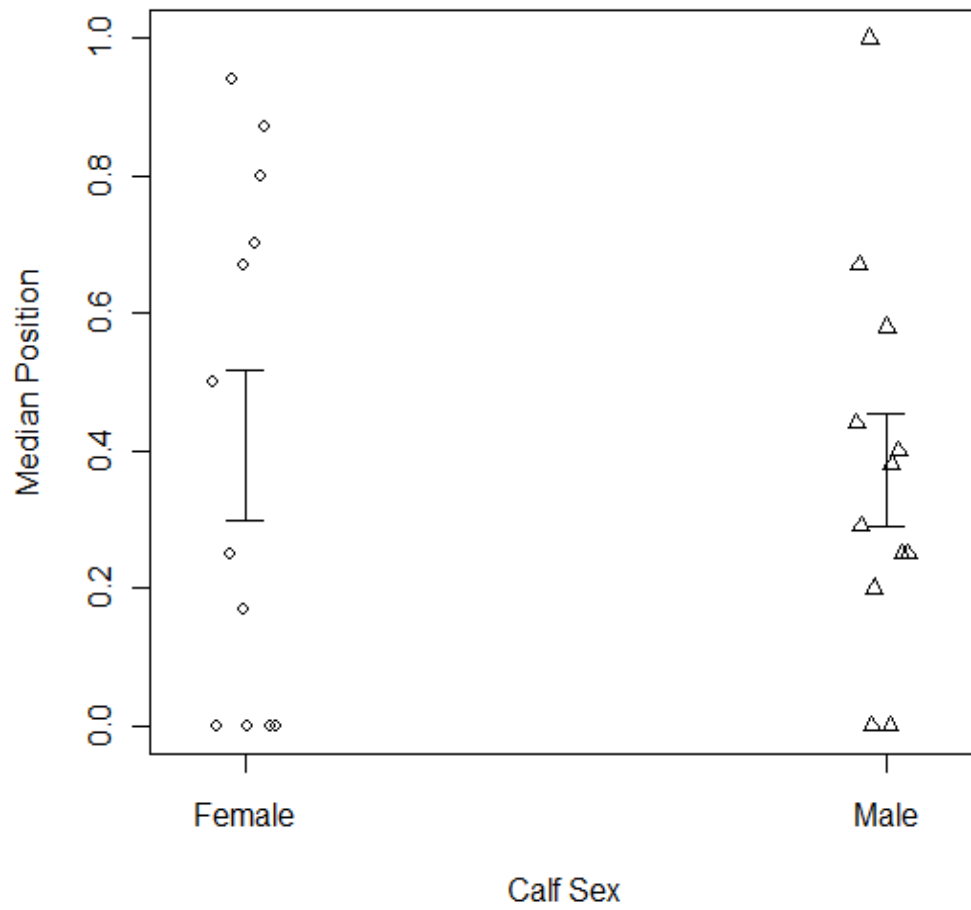
**Figure 1.4.** Comparison of the standardized median travel position in lactating and nonlactating females of specific age classes: adult lactating (AL) (N = 32), subadult lactating (SAL) (N = 8), adult nonlactating (ANL) (N = 5) and subadult nonlactating (SANL) (N = 2). For statistical analyses refer to Table 1.5.



**Figure 1.5.** The simple effect of reproductive state and kinship on the standardized median travel position: A = 6, B = 6, H = 4, L = 2, P = 11, R = 2. For statistical analyses refer to Table 1.5.

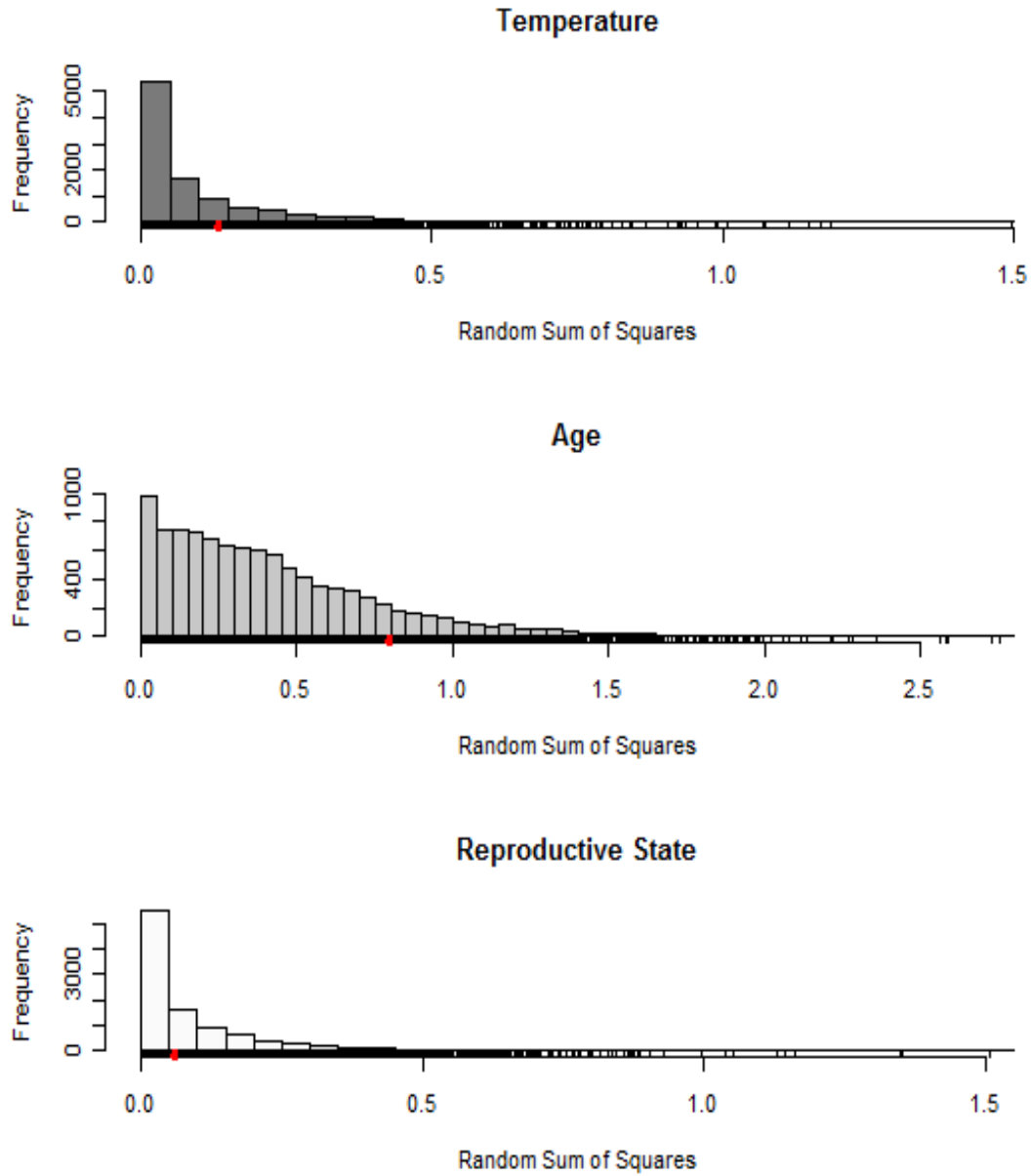


**Figure 1.6.** Comparison of the standardized median travel position in subadult lactating (SAL) and nonlactating (SANL) females of similar age (N = 6 pairs); the age difference between females in each pair was equal to or less than one year; the black lines signify mean  $\pm$  1SEM.



**Figure 1.7.** Comparison of the standardized median travel position in lactating mothers of female versus male calves (N = 12 pairs); the age difference between lactating mothers in each pair was equal to or less than one year; black lines signify mean  $\pm$  1SEM.





**Figure 1.8.** Result of randomized residual permutation procedure from 10000 trials comparing the effects of age, reproductive state and temperature on the standardized travel position, for data spanning groups of 4 to 32 individuals. The red line represents the probability of  $R^2$  statistic for each fixed effect (age, reproductive state and temperature) with respect to the remaining fixed effects in the model. The method of simulation of the data is described in the text. For statistical analyses refer to Table 1.7.

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## CHAPTER II

### TRADE-OFFS IN ACTIVITY BUDGETS IN LACTATING AND NONLACTATING AFRICAN SAVANNA ELEPHANTS

#### ABSTRACT

Nutritional and energy needs of female mammals depend upon allometric and physiological factors such as size or reproductive condition and shape individual activity budgets and behavioral patterns. Females with the greatest nutritional and energy needs should engage in activities and exhibit behaviors that facilitate the greatest net nutritional returns or the highest metabolic savings. To maximize nutritional and energy returns, females may increase time allocated to foraging or access resource through risk-prone behaviors, represented as heightened aggression. Conversely, to minimize nutritional and energy requirements females may spend time engaged in facile activities such as resting or avoid conflict by exhibiting risk-averse behaviors such as nonaggressive interactions or sensory inspection of the stimuli. I examined the effects of age, reproductive condition and sex of nursing offspring on activity budgets and frequency of risk-prone and risk-averse behaviors in female African savanna elephants, using focal animal sampling, with continuous recording. I hypothesized that the activity budgets and the frequency of risk-prone and risk-averse behaviors depended upon age, reproductive state and sex of nursing offspring. I determined that adult females and mothers of male calves spent more time engaged in nursing and standing than subadult females and mothers of female calves.

Lactating females and mothers of female calves foraged longer than nonlactating females and mothers of male calves. I also discovered that older and lactating females directed more aggression and fewer nonaggressive social behaviors towards conspecifics; whereas, younger and nonlactating female were subject to more frequent aggression and they exhibited nonaggressive social behaviors more frequently than the former. The findings of my research elucidate how individual needs influence activity budgets and specific behaviors in female African savanna elephants and thus add to the body of work examining mammalian female activity budgets shaped by individual differences such as size or age and reproductive condition.

## Introduction

The activity budgets of female mammals are functions of allometric and physiological variations (Gittleman and Thompson 1988). Foraging, resting, socializing and traveling constitute the majority of ungulates' daylight and nocturnal activities (Brockett *et al.* 1999, Rees 2009). To maximize nutritional and energy intake, females may increase time allocated to foraging or access resources through risk-prone behaviors, represented as heightened aggression (Fischhoff *et al.* 2007, Week *et al.* 2000). Conversely, to minimize nutritional and energy requirements females may spend time engaged in facile activities such as resting or avoid conflict by exhibiting risk-averse behaviors such as nonaggressive social interactions or sensory inspection of conspecifics or the surroundings (Altman 1986, Creel 2001, Schulte and Rasmussen 1999). The relative degree of risk-prone and risk-averse behaviors and the difference in time allocated to vital activities should vary with individual differences such as size and reproductive condition (Hamel and Côté 2008). In matrilineal societies with clearly defined, linear dominance hierarchies, females have to trade-off maintaining social and spatial cohesion with competing for resources (Slade *et al.* 2008). The advantages of stable dominance hierarchies are amelioration of conflict and enhancement of fitness for group members, especially when ecological knowledge comes from the most experienced and most dominant conspecifics (Archie *et al.* 2006, McComb *et al.* 2001). Still, individual needs for nutritional and energy intake may trigger social conflict and cause



markedly different activity and behavioral patterns among individuals (Isbell and Young 1993).

Because nutritional and energetic requirements play a key role in determining activities and behavioral patterns, females with the greatest needs should engage in activities and exhibit behaviors that facilitate the greatest nutritional and energetic returns or the highest metabolic savings (Gittleman and Thompson 1988). As time is always a constraint, the benefits of time allocation to different activities should outweigh their costs (Mooring *et al.* 2006, Wolf *et al.* 2007). First, the extent of the compensation between activities often depends upon individual size or age (Gittleman and Thompson 1988). Larger individuals may have greater absolute nutritional and energetic requirements, but Graeme *et al.* (2008) noted that individuals with smaller body size may have higher mass-specific metabolic requirements and lower digestive efficiency. Therefore, smaller or younger individuals may allocate their time differently and exhibit different activities and behaviors compared to their larger conspecifics. Second, in sexually dimorphic species, female reproductive success depends more on reproductive investment than on their size at puberty. Reproduction can be compartmentalized into pre- and postpartum events, such as mating, gestation, lactation and provision of extended care to offspring (Gittleman and Thompson 1988). Lactation results in up to 180% increase in metabolic requirement and it inflates mortality rates; therefore, it is considered the most challenging reproductive state (Bartošová *et al.* 2011, Clutton-Brock *et al.* 1989, Mellish *et al.* 2000). Moreover, as male calves suckle more and have faster

growth rates than do female calves, sustained milk production may be metabolically more challenging for mothers of male than female calves (Lee and Moss 1986). Consequently, in order to fulfill their nutritional and energetic requirements, lactating females may exhibit activities and behavioral patterns that diverge from those of nonlactating females.

Wild population studies measuring activity patterns in lactating and nonlactating females reveal heterogeneity in reproductive strategies (Clutton-Brock *et al.* 2006). Across mammalian taxa, lactating females forage more or rest more than nonlactating females (Komers *et al.* 1993, Neuhaus and Ruckstuhl 2002). Hamel and Côté (2008) found that lactating mountain goats (*Oreamnos americanus*) traded lying for foraging and ruminating and spent eight percent more time foraging than their nonlactating conspecifics. The authors also found that mothers of male offspring foraged more than did mothers of female offspring. Lactating chimpanzees, regardless of their dominance rank, consume higher quality resources than do nonlactating females (Murray *et al.* 2009). However, solitary pregnant polar bears (*Ursus maritimus*) fast during eight-months-long pregnancy and hibernate during their four-months-long postimplantational period (Atkinson and Ramsay 1995). Evidently, lactation causes female mammals to reallocate energy from relatively auxiliary to vital activities. However, an individual female's choice to exhibit different rates of risk-prone aggression and risk-averse nonaggressive social interactions may also optimize resource acquisition. For example, lactating, female black-tailed prairie dogs (*Cynomys ludovicianus*) engage in infanticide in order to access burrows near better foraging grounds (Hoogland 1995). To increase

time allocated to feeding, female gelada (*Theropithecus gelada*) frequently relinquish their resting time but rarely forego time spent socializing as the latter may have important fitness benefits (Dunbar and Dunbar 1988). In bighorn ewes (*Ovis canadensis*), weaning success positively correlates with boldness (measured as frequency of trapping); this in turn suggests that bolder ewes are more successful mothers than their shy conspecifics (Réale *et al.* 2000).

Female African savanna elephants (*Loxodonta a. africana*) are social and live in matrilineal units with age- and- size-ranked dominance hierarchies, where dominant females are highly tolerant of subordinate individuals (Douglas-Hamilton 1972). The oldest and most dominant female, known as the matriarch, is also the unit's repository of ecological knowledge and influences per capita reproductive success of all group members (McComb *et al.* 2001; Esposito 2008). To meet their nutritional and energetic requirements, female elephants access abundant but widely distributed resources by relying on information exchange facilitated by social cohesion, relative activity synchrony and infrequent aggression (Graeme *et al.* 2008, Wittemyer and Getz 2007). However, females with different nutritional and energetic requirements may exhibit divergent activity budgets and rates of risk-prone and risk-averse behaviors. Graeme *et al.* (2008) showed that female elephants spent more time foraging than male elephants but did not investigate the differences in activity budgets by different types of females (e.g., age, reproductive state). Moreover, one extensively studied measure of risk-prone behavior is aggression and, although infrequent, aggressive contests are typically initiated

and won by older, larger or otherwise more dominant female elephants (Archie *et al.* 2006). Still, I know of no published research that elucidates the differences in activity patterns between female elephants of different reproductive conditions. Likewise, with the exception of Slade *et al.* (2008), who reported that rates of aggressive behaviors in Asian elephants increased as the senders approached ovulation, little is known about heightened rates of risk-prone and risk-averse behaviors in lactating and nonlactating females. Ovulation is theoretically a more expensive state than an anovulatory stage of estrus; therefore, it is also likely that activity budgets and behavioral patterns vary across reproductive states (Gittleman and Thompson 1988).

Female elephants must balance their energy needs between their own survival and survival of their offspring. Elephant calves are born after twenty-two months of gestation, the longest of all terrestrial vertebrates (Douglas-Hamilton 1972). According to Lee and Moss (1986) for the first three months of their lives, elephant calves rely solely on their mothers' milk. Male calves suckle more often and consume more milk than female calves. Weaning occurs when calves are approximately five years of age, and male calves are weaned at later age than female calves (Lee and Moss 1986). Lactating female elephants are subject to high sustained nutritional, mineral and water requirements, much higher than nonlactating females (Smith and Buss 1973). Moreover, sustained milk production may be metabolically more challenging for mothers of male than female calves (Lee and Moss 1986). Therefore, individual differences brought about by different size and reproductive condition may influence behaviors involved in

resources acquisition and consumption. One way to meet nutritional and energy requirements may be to allocate more time to foraging and increase nutritional intake. Alternatively, by engaging in risk-prone behaviors, such as aggressive interactions, females may access better quality resource. Yet another strategy may be to avoid risk and divert energy to priority functions such as growth or reproduction by engaging in social cooperation and resource shearing or assessing their surroundings via chemosensory inspection.

My aim was to examine the effects of age and reproductive condition on activity budgets and the frequency of risk-prone and risk-averse behaviors in female African savanna elephants. I made three assumptions based upon the literature: 1) absolute metabolic needs increase with age, or its correlate size, 2) lactation in elephants is metabolically the most challenging reproductive state; and 3) age correlates with dominance (Archie *et al.* 2006, Strier 2005). To determine if activity budgets and frequency of risk-prone and risk-averse behaviors varied with age, I compared state and event behaviors of females by age. To compare activity and behavioral patterns of females of different reproductive states, I juxtaposed prolonged nursing against the metabolically less demanding nonlactational period (Hamel and Côté 2008). Finally, I compared activity patterns and risk-prone-and-averse behaviors of females nursing female versus male calves. I hypothesized that the activity budgets and the frequency of risk-prone and risk-averse behaviors in female elephants depended upon age, reproductive state and sex of nursing offspring. I predicted that older females would

have different activity budgets and would exhibit higher rates of risk-prone behaviors than younger females. I also predicted that lactating females would allocate their time differently and exhibit higher rates of risk-prone behaviors than nonlactating females. Lastly, I predicted that mothers of male calves would show higher rates of risk-prone behaviors and would exhibit different activity budgets when compared to mothers nursing female calves.

## **Methods**

This research has been approved by Western Kentucky University's Institutional Animal Care and Use Committee (Welfare Assurance # A3558-01A) and by South African National Parks (SANParks permit # SCHBA669).

### *Study Site and Population*

I conducted this study in Addo Elephant National Park (AENP), located 70 km north of Port Elizabeth in the Eastern Cape Province, South Africa. Classified as sub-tropical succulent thicket with open, grassy plains, the park receives  $\leq 450$  mm rainfall per year; rainfall is relatively evenly distributed throughout the year (Merte 2006). The vegetation consists largely of dense, thorny thicket with a variety of shrubs, herbs and grasses (Paley and Kerley 1998). The park was established in 1931 to support a nearly extirpated population of 11 elephants in the area (Whitehouse and Hall-Martin 2000). Since its establishment, the park was fenced and has undergone several expansions (Gough and Kerley 2006). During this study, the park consists of three parts: Colchester (~12760 ha), Main Camp (~12125 ha) and Nyathi (~13150 ha) sections (Adendorff, J,

personal communication, November 6, 2011). The extant population of ca. 510 elephants descended from the founder population with a number of adult bulls imported from Kruger National Park (Table 2.1; Merte 2006). Longitudinal data, gathered since the park's creation, allowed scientists to define two clans and six matrilineal lines delineated by letters A, B, H, L, P and R (Whitehouse and Hall-Martin 2000). Each of the matrilineal lines forms a kinship group, a basic unit of membership determination. Within those six kinship groups, 37 family associations exist in the Main Camp and Colchester sections, each with a distinguishable matriarch (Esposito 2008). Because the entire population has been identified based on apparent physical characteristics and photographically cataloged, I was able to determine age and social status of all females 10 years of age or older (Whitehouse and Hall-Martin 2000). I determined female lactation status via direct observation of nursing (N = 60) or if a female had a suckling calf of up to 6 years of age (N = 6; Lee and Moss 1986). Whenever a female had lost her youngest calf but also had another calf less than 6 year old (potentially suckling opportunistically), that female was considered nonlactating (N=15). I observed two cases of nonlactating females seemingly nursing a calf and a juvenile; in one instance a male calf appeared to suckle from its postreproductive grandmother. In the second instance, a juvenile male appeared to suckle from its mother. Due to the aberrant nature of these observed behaviors, I considered both of these females nonlactating.

#### *Data Collection*

Behavioral data were collected from June to December 2010 between the local

hours of 08:00 and 18:00, in the Main Camp and Colchester sections of AENP. I spent 111 days in the field; this translated to 713 h or an average of 6:25 h/day ( $\pm 1.5$  h). To quantify activity and behavioral patterns I observed individual elephants engaged in natural activities at eight permanent reservoir-fed waterholes (90.6%, N = 242) or near tourist roads (9.4%, N = 25). The elephants were habituated to tourist traffic and vehicles, even at close vicinity. Following AENP guidelines, all data were collected from field vehicle from an approximate distance of one meter to 50 meters. Whenever necessary I used binocular to collect data. I recorded 267 instances of focal animal sampling with continuous recording on 109 reproductively active females (Table 2.2; Altman 1974). My goal was to collect focal observations from as many females as possible as well as multiple data recordings per female. Therefore, upon encountering a family with multiple females, I preferentially collected data from individuals for whom I had the least amount of focal observations first (min = 1 focal observation, mean = 2.4 observations per female, max = 6, SD = 1.2, SE = 0.01). The duration of sampling periods varied with the length of visible period per focal female in minutes (max = 29, min = 5.2, mean = 14.9, SD = 5.8, SE = 0.01). Before each focal observation, I recorded location, social context and weather conditions. To quantify activity and behavioral patterns I recorded state and event behaviors. I measured duration of state behaviors in seconds and frequency of event behaviors as rate per hour. State behaviors are long lasting activity patterns such as standing or walking (Table 2.3); event behaviors are short lasting and exemplified by aggressive and chemosensory trunk behaviors towards



conspecifics or substrate (Table 2.4; Martin and Bateson 2007). For all aggressive, chemosensory and nonaggressive social behaviors involving the focal animal and its conspecific, I recorded the sender and the receiver as well as the relationship between them. Similar event behaviors were grouped together to form general types of behaviors, including sent and received aggressive contact behaviors, sent and received aggressive noncontact behaviors, chemosensory behaviors, excretion related behaviors, other behaviors and sent and received nonaggressive social behaviors. Sent and received aggressive contact and noncontact behaviors were combined into grand sent and received aggressive behaviors (Table 2.4).

#### *Data Analysis*

I analyzed behavioral data using R (R Core Development Team, 2009). I tested the data for normality using Shapiro-Wilk tests. Data that were normally distributed or had Shapiro-Wilk test statistics greater than 0.9 were analyzed parametrically; otherwise, nonparametric tests were used. Total state behaviors were analyzed as proportion of total duration of visible focal time per female (N = 109). The true duration of the first and last behaviors of focal observations as well as behaviors preceding and following nonvisible time could not be determined. Therefore, I removed these behaviors from the analyses of bout behaviors. Therefore, bout behaviors included only uninterrupted activities observed from start to finish (Martin and Bateson 2007). They were analyzed as mean bout duration of visible focal time per focal female (N = 108). The initial assessment of state behaviors was performed with principal components analysis (PCA, Hamel and

Côté 2008). I chose PCA analysis because it is a robust method for analyzing data where the proportions of time spent in each of the state behaviors are not independent. In addition, PCA analysis allowed me to reduce the dimensions of my data set to three orthogonal axes. I used the three sets of eigenvalues derived from PCA analysis in factorial analysis of variance (ANOVA) to assess the influence of age, reproductive state and sex of nursing offspring on females' activity budgets. Age and social rank tend to be correlated in elephants; therefore, I did not consider social rank in this analysis. The effects of age, reproductive state and sex of nursing offspring on the original values representing females' activity budgets also were evaluated using parametric tests (pairwise comparison with Bonferroni correction, regression analysis and Student's t-test) and nonparametric tests (Kruskal Wallis one-way ANOVA, Pearson's correlation and Wilcoxon-signed rank test). Event behaviors were analyzed as rates by dividing their frequency by total duration of visible focal time per female ( $N_{\text{females}} = 109$ ). The effects of age, reproductive state and sex of nursing offspring on the original values representing females' rates of specific event behaviors were evaluated using parametric tests (regression analysis) and nonparametric tests (Kruskal Wallis one-way ANOVA, Pearson's correlation and Wilcoxon-signed rank test). All statistical tests used  $\alpha$  of 0.05.

## **Results**

The results are presented in two sections based on the two major response variables, namely state behaviors and event behaviors, to examine the effects of age, reproductive state and sex of nursing offspring on the behaviors of reproductively active

female African savanna elephants. The mean length of visible focal observation was 14.8 min ( $\pm$  SE = 0.39) with significant difference between lactating (L mean = 15.6 min  $\pm$  0.5 SE) and nonlactating females (NL mean = 13.1 min  $\pm$  0.6 SE,  $t = 3.3$ ,  $df (3, 80)$ ,  $p = 0.001$ ). In addition, a difference in focal observation duration was evident for mothers with or without nursing calves ( $F = 11.1$ ,  $df (1, 107)$ ,  $p = 0.001$ ). Pairwise comparison with Bonferroni correction showed that the significant difference in mean visible focal observation time was between female elephants nursing female (female calf mean = 16.3 min  $\pm$  0.7 SE) calves and females without calves (no calf mean = 13.3 min  $\pm$  0.5 SE,  $p = 0.001$ ). There was no difference in median visible focal observation time between females nursing differently sex calves (male calf mean = 14.8 min  $\pm$  0.7 SE).

#### *State Behaviors*

The first three axes of the PCA explained 89% of the variability in female activity budgets (Fig. 2.1, Table 2.5). As shown by the eigenvectors of the behaviors, the first PCA axis contrasted time spent standing (+) to time spent eating (-). The second PCA axis differentiated time spent eating (+) and time spent drinking (-). The third PCA axis opposed time spent walking (+) against time spent drinking (-). I tested the PCA scores of all three axes with factorial ANOVA (Table 2.6). Calf sex had a significant effect on PCA axis one ( $F = 6.22$ ,  $df (1, 107)$ ,  $p = 0.014$ ). Pairwise comparison with Bonferroni correction showed that there was a significant difference in the first PCA axis between mothers of females and mothers of males ( $p = 0.006$ ) and between mothers of females and females without calves ( $p = 0.007$ ). The difference in the first PCA axis between

mothers of males and nonlactating females was not statistically different ( $p = 0.95$ ). The effect of reproductive state on the first PCA axis approached significance ( $F = 2.79$ ,  $df (1, 103)$ ,  $p = 0.09$ ); whereas, age class had no significant effect on the first PCA axis ( $F = 1.55$ ,  $df (1, 103)$ ,  $p = 0.2$ ). Factorial ANOVA of the second and third PCA axes did not reveal any significant differences. Biplots of eigenvalues for the first two PCA axes with respect to age class and reproductive state (Fig 2.2) and with respect to sex of nursing calf did not reveal any grouping patterns (Fig 2.3).

Only the state behaviors with proportions of duration greater than one percent were analyzed and included the following states: drink, eat, mud, nurse, stand and walk. For analysis of the states of drink and mud only focal observations that had been collected near waterholes were analyzed. For analysis of the state of nurse only lactating females were considered. When water was available female elephants spent on average 18 % of their time drinking, 10 % eating, 4 % mudding, 3 % nursing, 46% standing and 19 % walking. However when water was not available females allocated on average 78% of their time to eating, 2% to nursing, 4% to standing and 17% to walking. State behaviors of chase, dust, play, spar and trunk wrestle were omitted from the analyses because of their low prevalence.

Age had a significant effect on the proportion time spent eating ( $R^2 = 0.07 + 0.003$ ,  $p_{\text{slope}} = 0.042$ , Fig. 2.4). Older, nonlactating females spent a greater proportion of their time feeding than younger, nonlactating females. The proportion of time spent eating decreased with an increase in age in mothers of female calves. Mothers of male

calves spent similar proportion of time feeding regardless of their age (Fig. 2.5). Such disparity by age for eating was not apparent in lactating females. Age did not have a significant effect on the proportion of time spent drinking, mudding, nursing, standing or walking. When mean state bout behaviors were analyzed there was no effect of age on any of them (Table 2.7).

When total state behaviors were considered, adult females stood proportionally less than subadult females ( $t = -2.2$ ,  $df = 107$ ,  $p = 0.032$ , Fig. 2.6). Lactating and nonlactating females differed significantly in their proportion of time spent eating ( $W = 1567$ ,  $p = 0.048$ ; Fig. 2.7). Namely, lactating females allocated significantly more time to foraging than their nonlactating conspecifics. Finally, lactating mothers of female calves spent a greater proportion of their time spent eating ( $W = 889$ ,  $p = 0.011$ ) compared to mothers of male calves. Mothers of male calves nursed ( $W = 449.5$ ,  $p = 0.014$ ) and stood ( $W = 463.5$ ,  $p = 0.005$ ; Fig. 2.8, Table 2.8 and Table 2.9) proportionally more than mothers of female calves.

The analysis of mean bout behaviors did not show significant differences between adult and subadult females. There were no significant differences in bout durations between lactating and nonlactating females for any states. Mothers of female and male calves differed significantly in their mean bouts of drinking ( $W = 779.5$ ,  $p = 0.002$ ), eating ( $W = 764$ ,  $p = 0.008$ ) and nursing ( $W = 394.5$ ,  $p = 0.03$ ; Fig. 2.9 and Table 2.10). In particular mothers of female calves drank and ate proportionally more than mothers of male calves, but the latter spent a greater proportion of their time nursing. There was no

significant difference in the mean bout of mudding, standing and walking between mothers of female and male calves.

To further investigate the effects of reproductive state and sex of nursing calf on female activity budgets, I compared proportion of time spent drinking, eating, mudding, nursing, standing and walking in subadult lactating and nonlactating females. This allowed me to draw a comparison in activity budgets between groups with smaller variance in age. I considered lactating mothers of female and male calves and nonlactating females between twelve and nineteen years of age. The only difference between lactating and nonlactating subadult females was in the proportion of time they spent eating ( $W = 220.5$ ,  $p = 0.02$ ). Lactating subadult females allocated more time to eating than nonlactating subadult females. Likewise, subadult mothers of female spent significantly greater proportion of their time eating than did subadult mothers of male calves ( $W = 52$ ,  $p = 0.03$ ; Table 2.11). Age did not have a significant effect on the proportion of time spent in any of the states (Table 2.12).

### *Event Behavior*

Event behaviors were pooled into the following categories: aggressive sent, aggressive received, chemosensory, excrete, other, nonaggressive social sent and nonaggressive social received. Two of the behaviors, excrete and other, did not reveal significant differences among groups. Adult females exhibited significantly greater rates of sent aggressive behaviors ( $W = 1878.5$ ,  $p = 0.005$ ) than subadult females. On the contrary, subadult females had significantly higher rates of sent nonaggressive social

behaviors ( $W = 896.5$ ,  $p = 0.0004$ ) and received nonaggressive social behaviors ( $W = 1161$ ,  $p\text{-value} = 0.018$ ; Fig. 2.10). Lactating and nonlactating females differed significantly in their rates of sent aggressive behaviors ( $W = 1775$ ,  $p = 0.0006$ ), chemosensory behaviors ( $W = 841$ ,  $p = 0.005$ ) and sent social behaviors ( $W = 746$ ,  $p = 0.0002$ , Fig. 2.11). Lactating females sent aggressive behaviors at higher rates than nonlactating females. On the other hand, nonlactating females exhibited higher rates for both chemosensory and sent nonaggressive social behaviors. Mothers of female versus male calves did not differ significantly in their rates of any event behavior (Fig. 2.12, Table 2.13). However, differences in received aggressive behaviors by mothers of female compared to mothers of male calves approached significance ( $W = 818.5$ ,  $p = 0.09$ ).

The effect of age on the rates of sent aggressive behaviors approached significance ( $R^2 = 0.018 + 0.0008$ ,  $p_{\text{slope}} = 0.074$ ). Age had a significant effect on the rates of sent nonaggressive social behaviors ( $R^2 = 0.025 + 0.0004$ ,  $p_{\text{slope}} = 0.01$ ). Younger nonlactating females sent nonaggressive social behaviors at higher rates than older nonlactating females. Such disparity was not apparent in lactating females (Fig 2.13). Younger mothers of male calves sent nonaggressive social behaviors at higher rates than did older mothers of male calves. Mothers of female calves sent social behaviors at similar rates regardless of their age (Fig. 2.14). Finally, age did not have a significant effect on the rates of received aggressive, chemosensory or received nonaggressive social events (Table 2.14).

To investigate the effects of reproductive state and sex of nursing offspring on the rates of event behaviors, with less dependence on the age variable, I analyzed data for lactating mothers of female versus male calves and nonlactating females between 12 and 19 years of age. I compared rates of aggressive sent and received behaviors, chemosensory behaviors and nonaggressive social sent and received behaviors. Nonlactating subadult females exhibited higher rates for both chemosensory ( $W = 93$ ,  $p = 0.05$ ) and sent nonaggressive social behaviors ( $W = 43.5$ ,  $p = 0.0005$ ) when compared to lactating subadult females. There was no significant difference in the rates of any of the event behaviors between subadult mothers of female and male calves (Table 2.15). Age had a significant effect on the rate of sent aggressive behaviors ( $R^2 = 0.11$ ,  $p_{\text{slope}} = 0.032$ ; Table 2.16). Older subadult mothers of male calves sent aggressive behaviors at higher rates than younger subadult females. The higher frequency of sent aggression was apparent in older subadult mothers of female calves, when compared to younger females nursing female calves (Fig. 2.15).

## **Discussion**

Nutritional and energetic needs play a key role in determining activity budgets and behavioral patterns in female mammals. Therefore, time allocated to different activities and behaviors may depend upon individual size or age and reproductive condition (Gittleman and Thompson 1988, Fischhoff *et al.* 2007). At AENP, adult female African elephants allocated a smaller proportion of their time to standing, and they exhibited higher rates of aggression towards conspecifics compared to subadult



females. In contrast, subadult females were involved in nonaggressive social behaviors, both as senders and receivers, more frequently than adult females. Subadult females exhibited some aggressive behaviors directed at other group members, the frequency of which was greater in older subadult females. Lactating females allocated greater proportion of their time to eating and sent aggression at higher rates than nonlactating females. In nonlactating females the proportion of time spent eating increased with age. Nonlactating females also exhibited higher rates of chemosensory behaviors and engaged in nonaggressive social interactions more frequently than lactating females. Older, nonlactating females socialized less frequently than younger, nonlactating females. Additionally, mothers of female calves spent a greater proportion of their time eating and had longer drinking and eating bouts than mothers of male calves. The latter spent a greater proportion of their time nursing and standing and had longer bouts of nursing. While time allocated to nursing was stable in differently aged mothers of males, older mothers of female spent less time nursing than younger mothers.

In some species, age and size correlate positively with metabolic activity as well as nutritional and energetic demands (Graeme *et al.* 2008). A decision to spend time in a particular activity disallows simultaneous engagement in another activity; therefore, behavioral trade-offs should favor time allocation to activities or behaviors that most benefit the actors, in regards to their current needs (Hamel and Côté 2008). Due to their larger body size, older females may require more resources to meet their nutritional and energetic needs. They can fulfill these demands through increased foraging or by being

more assertive during finding or defending a resource (Thouless 1990). In this study, only time allocated to the activity of standing differed between adult and subadult females. Still, there were apparent disparities in the frequency of aggressive and nonaggressive social behaviors exhibited by adult and subadult females (Hamel and Côté 2008). Female elephants have well-defined age- and- size-ordered dominance hierarchies, and older individuals win more aggressive interactions than younger ones (Archie *et al.* 2006). Adult females in this study directed aggressive behaviors towards group members more frequently and socialized less frequently than subadult females. These findings suggest that instead of investing more time in foraging, larger, older or otherwise more dominant females may be able to access better quality resources and do it more efficiently than younger individuals by using their superior ecological knowledge or by aggressively defending a resource (Hamel and Cote 2008, McComb *et al.* 2001). In contrast, higher rates of nonaggressive social behaviors assumed by subadult females, who seldom win aggressive interactions, may be the default mode to avoid a contest, learn about foraging opportunities and partake in consuming forage (Beauchamp 2000, Dugatkin 2009).

Another common determinant of nutritional and energetic requirements in female animals is their reproductive condition (Gittleman and Thompson 1988). Pre-partum and postpartum events such as gestation and lactation carry significant costs for females; however, lactation is more costly as it poses challenges to females' physiological health and survival (Clutton-Brock *et al.* 1989 Gittleman and Thompson 1988, Mellish *et al.*

2000). To fulfill their nutritional and energetic needs, when compared to nonlactating females, lactating females in many species allocate more time to foraging and frequently engage in energy saving activities such as resting or reduced travel (Hamel and Côté 2008, Komers *et al.* 1993, Link *et al.* 2006, Neuhaus and Ruckstuhl 2002). Furthermore, to compensate for the energy demands imposed by lactation, females frequently engage in either risk-prone aggressive behaviors or risk-averse nonaggressive social interactions, both as means of finding and protecting or sharing allotted resources (Hoogland 1995, Patriquin *et al.* 2010). In AENP, lactating elephants spent a greater proportion of their time eating and they showed less frequent rates of chemosensory and nonaggressive social behaviors, but higher rates of aggressive behaviors than nonlactating females. Nevertheless, older nonlactating females spent more time eating than younger ones. These findings suggest that both lactation and age may motivate females to increase their time spent foraging. Increased rates of chemosensory and nonaggressive social behaviors in nonlactating females may be explained in two ways. First, chemosensory and social behaviors may help females locate resources and share them without conflict. Second, investigative and nonaggressive social behaviors may provide young, nonlactating females with knowledge about resource phenology and help them build cooperative social networks (Conradt and Roper 2003, Dunbar and Dunbar 1988).

Nutritional and energetic needs in mammalian females are greater for mothers nursing male than those female offspring. This is particularly true in sexually dimorphic species with polygamous breeding systems and female philopatry where males leave

natal units to search for breeding opportunities elsewhere (Lee and Moss 1986). The size and competitive ability of males influence their lifetime reproductive success (Hollister-Smith *et al.* 2007). In ungulates, male condition at dispersal often is predetermined by the quality and duration of nursing received as calf (Reinhardt and Reinhardt 1981). Because sons have greater potential reproductive success than do daughters, and because fitness of offspring indirectly affects mother's fitness, mothers have an incentive to invest more in their sons than daughters (Clutton-Brock *et al.* 1981). Published evidence has shown that male offspring grow faster, nurse more frequently, consume more milk and wean at later age than female offspring (Lee and Moss 1986, Reinhardt and Reinhardt 1981). Consequently, sustained milk production may be metabolically more challenging for mothers of male than female offspring and should reflect in their respective activity budgets (Lee and Moss 1986). However, in my study, mothers of female calves foraged and drank proportionally more than mothers nursing male calves. In addition, although statistically insignificant, the rates of received aggression were higher in mothers of female calves. The stress of subordination or the inability to defend resources may have caused mothers of female calves to allocate more time to foraging as was found in bison (Mooring *et al.* 2006). In addition, elephant mothers of male calves in AENP nursed and stood more than mothers of female calves. Time allocated to standing and an age-related decrease in social interactions among mothers of males might have compensated for energy lost to lactation. And lastly, since mothers of female calves foraged more they might have been able to forfeit their time resting while standing

My findings add to the body of work examining mammalian female activity budgets shaped by individual differences such as size or age and reproductive condition. I observed different activity budgets and behavioral patterns in female African savanna elephants of different age, reproductive state and nursing differently sexed calves. I found evidence for different time allocation to daily activities as well as risk-prone and risk-averse behaviors in lactating mothers of female and male calves and nonlactating females from 10 to 60 years of age. My analyses revealed that females with different nutritional and energetic needs use distinctive strategies to maximize energy acquisition and metabolic savings. Akin to heterogeneous strategies used by females across a number of mammalian taxa, female elephants appear to allocate more time to foraging in order to increase nutritional intake. Alternatively, female elephants engage in risk-prone behaviors to locate, defend or share better quality resources. If unable to independently find or defend resources, females may assume risk avoidance manifested by submission and thus divert energy to growth and reproduction. To better our understanding of how individual variation affects female elephants' daily activities and behavioral patterns and to further research on animal behavioral tendencies, future studies should examine fine scale differences among individuals exhibiting a suite of similar behaviors across different situational contexts (Dall *et al.* 2004).

**Table 2.1.** Female group organization of living elephants in Colchester and Main Camp sections of AENP.

Clan	1				2	
Kinship	A	B	H	P	L	R
Oldest Matriarch (year born)	AND (1956)	TAN (1951)	HEI (1972)	MEG (1965)	LLT (1968)	REB (1964)
# Individuals	81	73	21	95	44	49
# Families	8	7	1	10	3	6
Matriarch (year born)	AND (1956)	TAN (1951)	HEI (1972)	MEG (1965)	LLT (1968)	REB (1964)
	ALO (1961)	BEV (1970)		PAU (1969)	LAU (1972)	RUT (1971)
	ALI (1963)	CAT (1970)		TIP (1973)	LUL (1984)	RIT (1973)
	AMA (1969)	BLU (1976)		MOL (1981)		ROZ (1975)
	ALI (1972)	BON (1980)		MON (1981)		ROS (1981)
	APP (1975)	BRI (1980)		PHY (1981)		RON (1984)
	AMB (1977)	BHU (1986)		PUM (1984)		
	ANN (1985)	BYR (1986)		MEL (1987)		
				MOR (1990)		
				MAD (1991)		

\*B kinship has seven families and eight matriarchs because Tania and Beverly lead the same individuals; 6 months after the conclusion of this study, Tania was presumed dead.

\* Whitehouse & Hall-Martin 2000.

**Table 2.2.** Sample size distribution for age class (adult vs. subadult) reproductive state (lactating vs. nonlactating) and social rank (matriarch vs. non-matriarch) for (a) data including all focal females (global), and (b) lactating parous females.

(a) All Focal Females (global)

Age Class	Social Rank	Reproductive State	Total State Duration	Bout State Duration
Adult	Matriarch		64	64
			30	30
	Non-matriarch	Lactating	25	25
		Nonlactating	5	5
			34	34
		Lactating	33	33
		Nonlactating	1	1
Subadult	Non-matriarch		45	43
			45	43
		Lactating	17	17
		Nonlactating	28	26

(b) Parous Females

Age Class	Social Rank	Reproductive State	Mother of Female	Mother of Male
Adult			31	26
	Matriarch	Lactating	16	8
	Non-matriarch	Lactating	15	18
Subadult	Non-matriarch		7	9
		Lactating	7	9

**Table 2.3.** Ethogram of state behaviors (lasting longer than 5 s) performed by reproductively active female elephants during continuous focal observations at AENP.

<b>State Behavior</b>	<b>Definition</b>
Chase	One elephant is pursuing another
Drink	Take water into the trunk and immediately place water into the mouth
Dust	Use the foot or trunk to place dirt particles on the body
Eat	Take nutrients into the mouth via the trunk
Lay	One side of the torso in contact with the ground
Mud	Use the trunk to throw mud particles on the body or moving body rapidly in a mud hole
Nurse	Stand and nurse calf for longer than 30 s of time
Not Visible	Elephant has moved out of sight or its head cannot be seen
Other	Behavior not defined in ethogram
Play	Contact between individual in an equivalent manner (pushing rub, roll or climb on another
Sparring	Trunks down, heads together and if animal has tusks they will be interlocked and pushing against another (trunks not intertwined)
Stand	Remain in the same location for at least two seconds with none of the following trunk behaviors observed
Trunk Wrestle	Push against another individual while trunks are intertwined
Walk	Leave location while all four legs are moving in a steady pace

\*State behavior definitions derived from Loizi *et al.* 2009



**Table 2.4.** Ethogram of event behaviors performed by reproductively active female elephants during continuous focal observations at AENP.

Behavior	Definition
<b>Aggressive Contact Behavior</b>	
Head Butt	Quickly use the head to make contact with the body of another individual
Kick	Use legs to strike at another
Push	Use the body to displace another elephant from its location
Trunk Hit	Quickly use the trunk to make contact with the body of another individual
Tusk	Use the end of the tusks to push another animal with or without piercing its skin
<b>Aggressive NonContact Behavior</b>	
Back Away	Walk backwards while facing another elephant
Back Into	Intentionally walk backwards into the body of another individual
Displace	Cause another individual to move from its current location and take that position instead, or cause displacement within one body length
Ears Flat	Ears flat against body or extended less than 90°
Ears Wave	Ears extended out and rapidly brought back to the body
Present	Turn backside toward another (with or without urination and defecation)
Supplant	Cause another individual to turn away (not move away) while walking towards that individual
Tail Into	Purposefully walk backwards with tail horizontally placed and touch other animal
Threat	Head up, ears out, trunk thrown up and sideways
<b>Chemosensory Behavior</b>	
Check	Touch substrate with tip of trunk with either trunk finger

Dig	Use trunk tip or foot to displace substrate
Flehmen	Tip of trunk touches another individual or substrate and places in the VNO* ducts in the roof of the mouth
Flick	Rapid up and down movement of distal end of trunk, after inspection of substrate
Horizontal Sniff	Either the distal end or the entire trunk is elevated up to parallel to the ground and pointed away from the elephant
Place	Flatten entire trunk tip on a substrate
Sniff	Hover trunk over substrate without contact
Object Play	Use trunk to draw substrate forwards or back across the ground
Periscope Sniff	Trunk is raised to air above parallel to the ground level up to above head level and held for at least 2s (trunk forms S shape)
Trunk Wriggle	Twisting and untwisting of trunk at a moderate pace, usually after substrate inspection

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#### Social Behavior

Body Rub	Use the torso to brush against another individual's torso
Head Into	Lean on other animal with head, w/o pushing
Lean	Place body weight on the body of another individual
Mount	Stand on hind legs, forelegs resting on body of a standing elephant
Trunk over Back	Place the entire length of the trunk across back and holding position for at least 2s
Trunk to Body	Torso or area not listed
Trunk to Feet	Area below ankles
Trunk to Genitals	Vulva or penis
Trunk on Head	Place the entire length of the trunk overhead and holding position for at least 2s
Trunk to Head	Forehead and superior most point of head
Trunk to Mouth	Trunk tip inserted into mouth
Trunk to Tail	Touch or grab tail

Trunk to Temporal Gland	Contact with temporal gland or secretion
Trunk to Trunk	Portion of trunk starting from mouth area, down to tip
Trunk Wrap	Physical contact between distal end of trunk with distal end of conspecific's trunk

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**Excrete Behavior**

Defecate	Release feces
Urinate	Release urine

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**Other Behavior**

Follow Lead	Start walking after one individual's movement for longer than 10 sec, after having stood in one location for longer than 3 sec
Interspecies Social	Physical contact, threat, or mock charge involving another species
Lead	Initiate movement that results in more than one individual of the family unit/kinship group following for longer than 10 sec
Vocalize	Vocalize (trumpet or rumble) while approaching or in physical contact with another individual or group of individuals
Wait	Wait until another elephant leaves before approaching water point/foreign object/fecal or urine sample

\* Chemosensory definitions derived from Schulte & Rasmussen 1999.

\* Vomeronasal organ

**Table 2.5.** Eigenvectors derived from PCA of reproductively active female elephants' state behaviors (N = 109).

State Behavior	Eigenvector 1 (49 %)*	Eigenvector 2 (30 %)*	Eigenvector 3 (10 %)*
Mudding	0.014	-0.04	0.09
Chasing	0.0008	-0.0007	0.001
Drinking	-0.1	<b>-0.8</b>	<b>-0.43</b>
Dusting	0.002	0.01	0.02
Eating	<b>-0.6</b>	<b>0.5</b>	-0.3
Nursing	0.007	0.04	0.01
Other	0.00007	-0.0005	0.0003
Play	-0.0075	-0.02	0.05
Sparring	-0.0002	0.0006	0.004
Standing	<b>0.8</b>	0.3	-0.3
Trunk Wrestling	0	0	0
Walking	-0.4	-0.1	<b>0.8</b>

\* percentages represent the variation in activity budgets explained by each PCA axis

**bold** values represent most opposite marginal behaviors

**Table 2.6.** Factorial ANOVA testing the effects of age class (correlate of age), reproductive state and sex of nursing offspring on each of the three PCA axes of female elephants' activity budgets expressed as total state behaviors ( $N_{\text{global}} = 109$ ,  $N_{\text{parous}} = 73$ ). Age class was adult or subadult. Reproductive state was lactating or non-lactating. Sex of nursing calf was female, male or none.

Eigenvector	Variables	df	SS	MS	<i>F</i> value	Pr(> <i>F</i> )
1	AClass	1, 107	0.09	0.09	1.55	0.22
1	RState	1, 107	0.17	0.17	2.79	0.09
1	Calf Sex	1, 107	0.37	0.37	6.22	0.01*
1	AClass:RState	1, 107	0.17	0.17	2.84	0.09
1	AClass:Calf Sex	1, 107	0.005	0.005	0.08	0.78
2	AClass	1, 103	0.07	0.07	2.17	0.14
2	RState	1, 103	0.01	0.01	0.32	0.57
2	Calf Sex	1, 103	0.02	0.02	0.75	0.39
2	AClass:RState	1, 103	0.02	0.02	0.57	0.45
2	AClass:Calf Sex	1, 103	0.04	0.04	1.19	0.28
3	AClass	1, 103	0.0001	0.0001	0.008	0.93
3	RState	1, 103	0.04	0.04	3.23	0.08
3	Calf Sex	1, 103	0.03	0.03	2.41	0.12
3	AClass:RState	1, 103	0.003	0.003	0.22	0.64
3	AClass:Calf Sex	1, 103	0.0004	0.0004	0.03	0.86

\*  $p \leq 0.05$

**Table 2.7.** Regression analysis testing the effects of age on female elephants' activity budgets expressed as total state behaviors ( $N_{\text{global}} = 109$ ,  $N_{\text{parous}} = 73$ ) and bout behaviors ( $N_{\text{global}} = 108$ ,  $N_{\text{parous}} = 67$ ). For analysis of drinking and mudding only observations near water were considered. For analysis of nursing only lactating females were considered.

State	Variables	$\alpha + \beta \text{Age}$	$R^2$	p	F(df)
total	Age~%DR	0.147+0.001	0.004	0.23	(1,106)=1.45
total	Age~%E	0.07-0.003	0.029	0.04*	(1,107)=4.24
total	Age~%M	0.06-0.0009	0.015	0.1	(1,106)=2.7
total	Age~%NR	0.07-0.001	0.03	0.07	(1,73)=0.269
total	Age~%ST	0.5-0.003	0.02	0.069	(1,107)=3.38
total	Age~%W	0.18-6e <sup>-05</sup>	-0.009	0.94	(1,101)=0.05
bout	Age~%DR	1.1+0.02	0.002	0.28	(1,95)=1.2
bout	Age~%E	1.3+0.005	-0.01	0.8	(1,96)=0.68
bout	Age~%M	0.6-0.008	0.007	0.2	(1,95)=1.7
bout	Age~%NR	0.96+0.02	0.02	0.1	(1,67)=2.7
bout	Age~%ST	2.8+0.02	-0.006	0.5	(1,96)=0.4
bout	Age~%W	1.3+0.005	-0.007	0.6	(1,96)=0.2

\*  $p \leq 0.05$

**Table 2.8.** Wilcoxon-signed rank test testing the effects of age class (correlate of age), reproductive state and sex of nursing offspring on female elephants' activity budgets expressed as total state behaviors ( $N_{\text{global}} = 109$ ,  $N_{\text{parous}} = 73$ ,  $N_{\text{nursing}} = 75$ ). Age class was adult or subadult. Reproductive state was lactating or nonlactating. Sex of nursing calf was female or male. For analysis of drinking and mudding only observations near water were considered. For analyses of nursing only lactating females of different age class were considered.

State Behavior	Variables	W	p
Drink	AClass	1636	0.17
Drink	RState	1201.5	0.71
Drink	Calf Sex	772	0.7
Eat	AClass	1553.5	0.47
Eat	RState	1567	0.048*
Eat	Calf Sex	889	0.011*
Mud	AClass	1592.5	0.25
Mud	RState	1412.5	0.3
Mud	Calf Sex	669.5	0.8
Nurse	AClass	405	0.25
Nurse	Calf Sex	449.5	0.014*

\*  $p \leq 0.05$

**Table 2.9.** Student's t-test testing the effects of age class (correlate of age), reproductive state and sex of nursing offspring on female elephants' activity budgets expressed as total state behaviors ( $N_{\text{global}} = 109$ ,  $N_{\text{parous}} = 73$ ). Age class was adult or subadult. Reproductive state was lactating or nonlactating. Sex of nursing calf was female, male or none.

State Behavior	Variables	t	df	p
Stand	AClass	-2.2	107	0.032*
Stand	RState	-1.1	107	0.28
Stand	Calf Sex	-2.7	71	0.009*
Walk	AClass	-0.78	107	0.43
Walk	RState	-1.62	107	0.12
Walk	Calf Sex	-0.52	71	0.61

\*  $p \leq 0.05$



**Table 2.10.** Wilcoxon-signed rank test testing the effects of age class (correlate of age), reproductive state and sex of nursing offspring on female elephants' activity budgets expressed as mean bout behaviors ( $N_{\text{global}} = 108$ ,  $N_{\text{parous}} = 73$ ;  $N_{\text{nursing}} = 75$ ). Age class was adult or subadult. Reproductive state was lactating or nonlactating. Sex of nursing calf was female or male. For analysis of drinking and mudding only observations near water were considered.

Bout Behavior	Variables	W	p
Drink	AClass	1290	0.3
Drink	RState	1011	0.8
Drink	Calf Sex	779.5	0.002*
Eat	AClass	1229.5	0.6
Eat	RState	1150	0.2
Eat	Calf Sex	764	0.008*
Mud	AClass	1301	0.2
Mud	RState	1111	0.3
Mud	Calf Sex	595.5	0.5
Nurse	AClass	349	0.18
Nurse	Calf Sex	394.5	0.03*
Stand	AClass	1159	0.9
Stand	RState	1214.5	0.1
Stand	Calf Sex	524	0.6
Walk	AClass	1083	0.5
Walk	RState	823	0.17
Walk	Calf Sex	691	0.1

\*  $p \leq 0.05$

**Table 2.11.** Wilcoxon-signed rank test testing the effects of reproductive state and sex of nursing offspring on subadult female elephants' activity budgets expressed as total state behaviors. Reproductive state was lactating (N = 16) or nonlactating (N = 19). Sex of nursing calf was female (N = 6), male or none (N = 5). For analysis of drinking and mudding only observations near water were considered. For analysis of nursing only lactating females were considered.

State Behavior	Variables	W	p
Drink	RState	132	0.5
Drink	Calf Sex	46.5	0.12
Eat	RState	220.5	0.02*
Eat	Calf Sex	51	0.03*
Mud	RState	191.5	0.17
Mud	Calf Sex	45.5	0.13
Nurse	Calf Sex	33.5	0.87
Stand	RState	116.5	0.23
Stand	Calf Sex	14	0.07
Walk	RState	132	0.5
Walk	Calf Sex	28	0.75

\*  $p \leq 0.05$

**Table 2.12.** Regression analysis testing the effects of age on subadult female elephants' activity budgets expressed as total state behaviors. Reproductive state was lactating (N = 16) or non-lactating (N = 19). Sex of nursing calf was female (N = 6), male or none (N = 5). For analysis of drinking and mudding only observations near water were considered. For analysis of nursing only lactating females (nursing female or male calves) were considered.

Variables	$\alpha + \beta \text{Age}$	$R^2$	p	F(df)
Age~%DR	0.37-0.02	0.06	0.09	(1,33)=3.1
Age~%E	0.24-0.07	-0.02	0.6	(1,33)=0.32
Age~%M	-0.02+0.003	-0.02	0.5	(1,33)=0.5
Age~%NR	0.01-0.001	-0.03	0.8	(1,33)=0.5
Age~%ST	0.02+0.02	0.02	0.2	(1,33)=1.5
Age~%W	0.17+0.0006	-0.03	0.95	(1,33)=0.05

\*  $p \leq 0.05$

**Table 2.13.** Wilcoxon-signed rank test testing the effects of age class (correlate of age), reproductive state and sex of nursing offspring on female elephants' rates of event behaviors ( $N_{\text{global}} = 109$ ,  $N_{\text{parous}} = 73$ ). Age class was adult or subadult. Reproductive state was lactating or non-lactating. Sex of nursing calf was female or male.

Event Behavior	Variables	W	p
Aggressive Sent	AClass	1878.5	0.005*
Aggressive Sent	RState	1775	0.0006*
Aggressive Sent	Calf Sex	614.5	0.57
Aggressive Received	AClass	1419.5	0.9
Aggressive Received	RState	1266	0.95
Aggressive Received	Calf Sex	818.5	0.09
Chemosensory	AClass	1147.5	0.07
Chemosensory	RState	841	0.005*
Chemosensory	Calf Sex	574	0.32
Social Sent	AClass	896.5	0.0004*
Social Sent	RState	746	0.0002*
Social Sent	Calf Sex	635	0.72
Social Received	AClass	1161	0.02*
Social Received	RState	1128	0.19
Social Received	Calf Sex	713.5	0.43

\*  $p \leq 0.05$ .

**Table 2.14.** Regression analysis testing the effects of age on female elephants' rates of event behaviors ( $N_{\text{global}} = 109$ ,  $N_{\text{parous}} = 73$ ).

Variables	$\alpha + \beta \text{Age}$	$R^2$	p	F(df)	$R_s$	$p_{R_s}$
Age~% Aggressive Sent	0.2+0.0008	0.02	0.07	(1,107)=3.3	0.27	0.005*
Age~% Aggressive Received	0.2-0.0008	-0.007	0.6	(1,107)=0.2	0.02	0.9
Age~% Chemosensory	1.3-0.0007	-0.0004	0.3	(1,107)=0.9	-0.16	0.11
Age~% Social Sent	0.03-0.0004	0.05	0.0004 *	(1,107)=0.01	-0.4	0.0001*
Age~% Social Received	$6.8^{e-03} - 1.2^{e-04}$	0.11	0.145	(1,107)=2.15	-0.15	0.12

\*  $p \leq 0.05$ .

**Table 2.15.** Wilcoxon-signed rank test testing the effects of reproductive state and sex of nursing offspring on subadult female elephants' rates of event behaviors. Reproductive state was lactating (N = 16) or nonlactating (N = 19). Sex of nursing calf was female (N = 6) or male (N = 5).

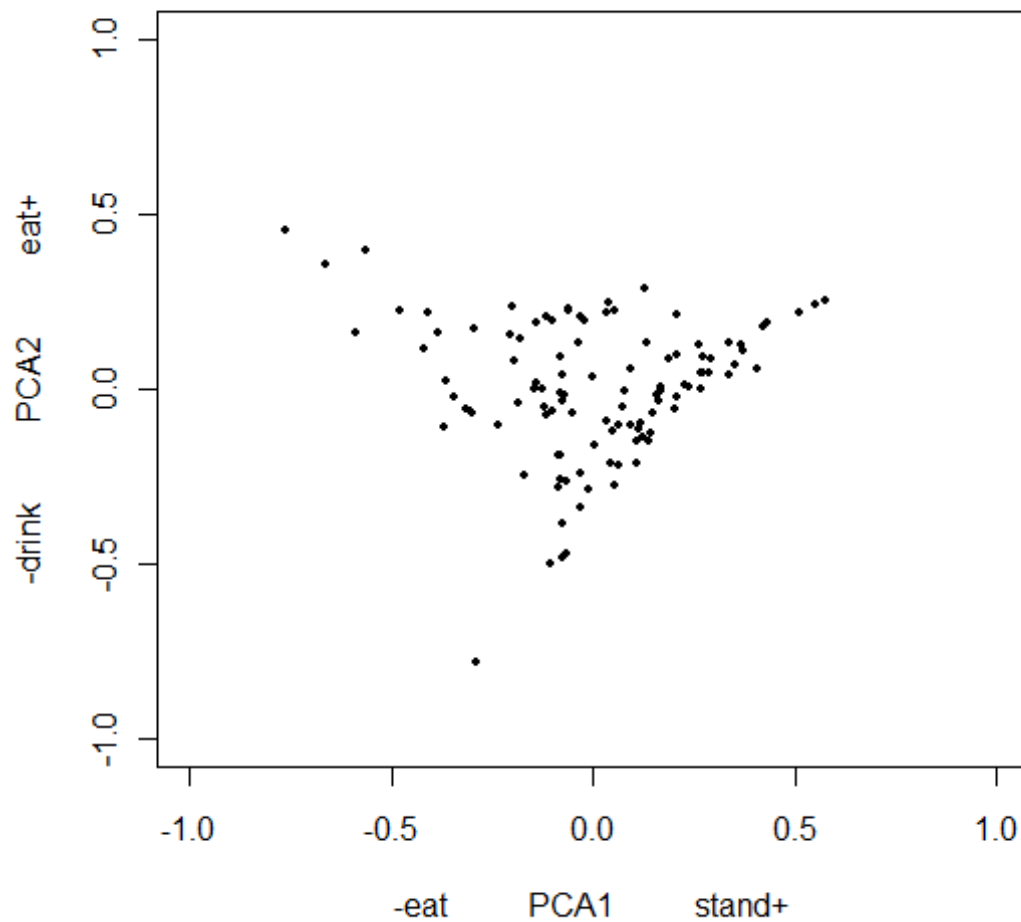
Event Behavior	Variables	W	p
Aggressive Sent	RState	172	0.5
Aggressive Sent	Calf Sex	21.5	0.3
Aggressive Received	RState	121.5	0.31
Aggressive Received	Calf Sex	42	0.29
Chemosensory	RState	93	0.05*
Chemosensory	Calf Sex	19	0..2
Social Sent	RState	47.5	0.0005*
Social Sent	Calf Sex	46	0.1
Social Received	RState	135.5	0.6
Social Received	Calf Sex	36	0.7

\*  $p \leq 0.05$ .

**Table 2.16.** Regression analysis testing the effects of age on subadult female elephants' rates of event behaviors (N = 35).

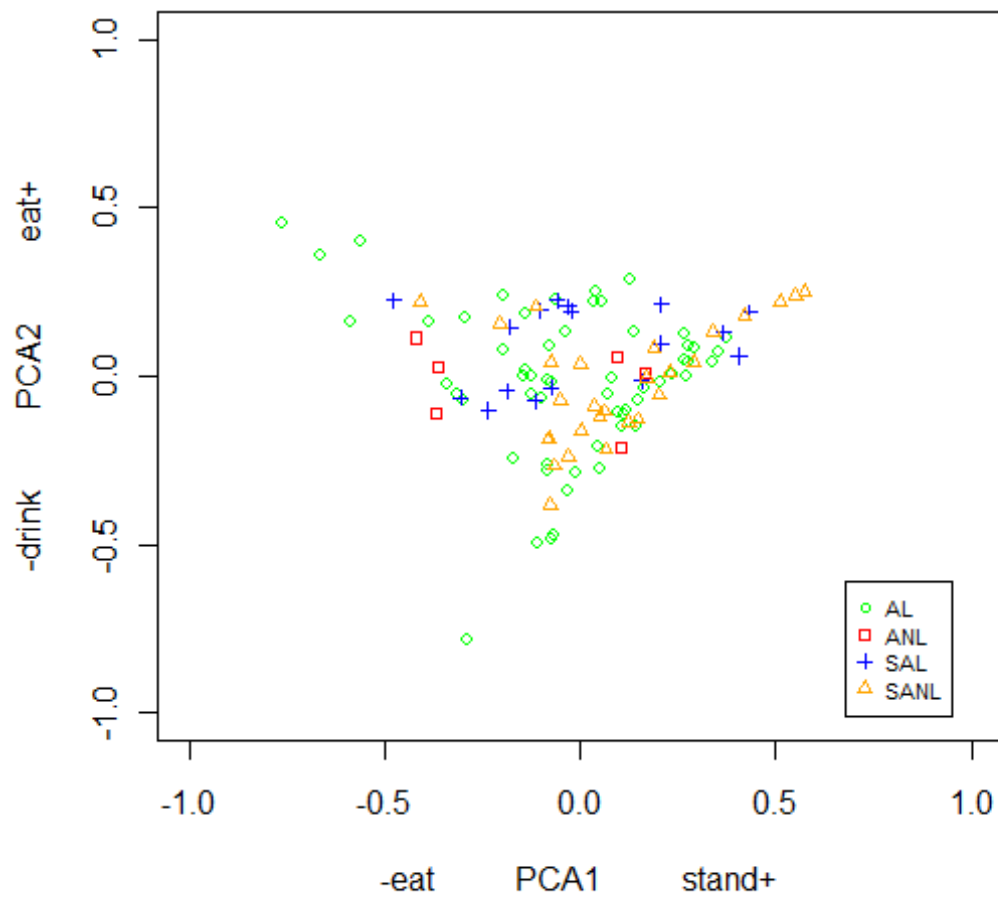
Variables	$\alpha + \beta \text{Age}$	$R^2$	p	F(df)
Age~% Aggressive Sent	-0.5+0.005	0.11	0.032*	(1,33)=5
Age~% Aggressive Received	-0.1+0.002	0.05	0.11	(1,33)=2.7
Age~% Chemosensory	0.97-0.01	-0.03	0.8	(1,33)=0.6
Age~% Social Sent	0.02-0.003	-0.03	0.8	(1,107)=0.04
Age~% Social Received	0.5-0.1	0.03	0.2	(1,107)=2

\*  $p \leq 0.05$ .

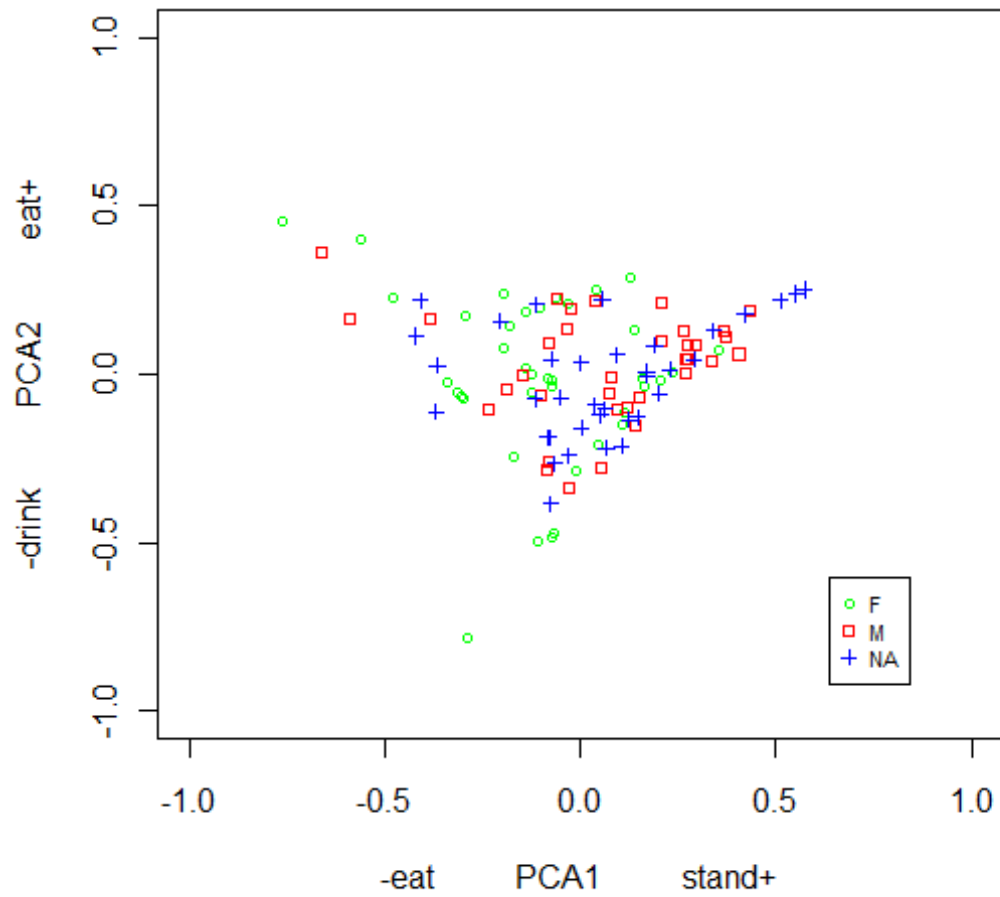


**Figure 2.1.** Biplot of eigenvalues of total state behaviors with respect to the first two principal components. First PCA axis opposed positive time standing to negative time eating. The second PCA axis opposed positive time eating to negative time drinking. For statistical analyses refer to Table 2.5.

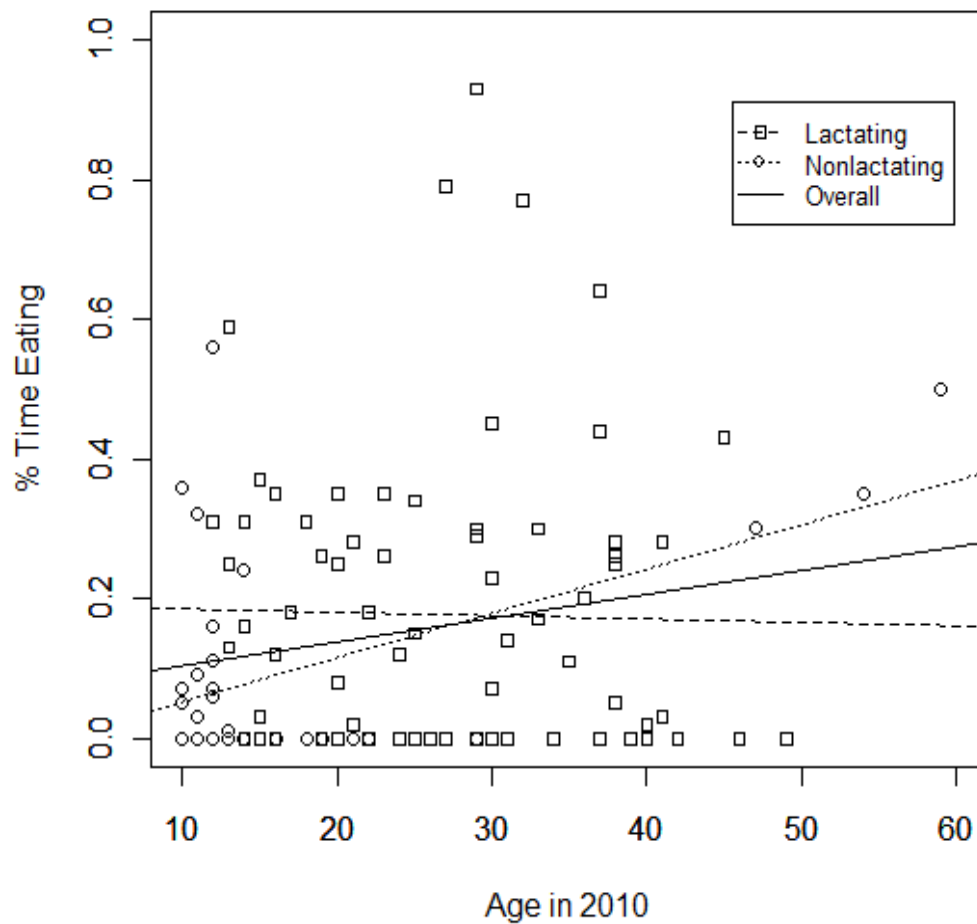




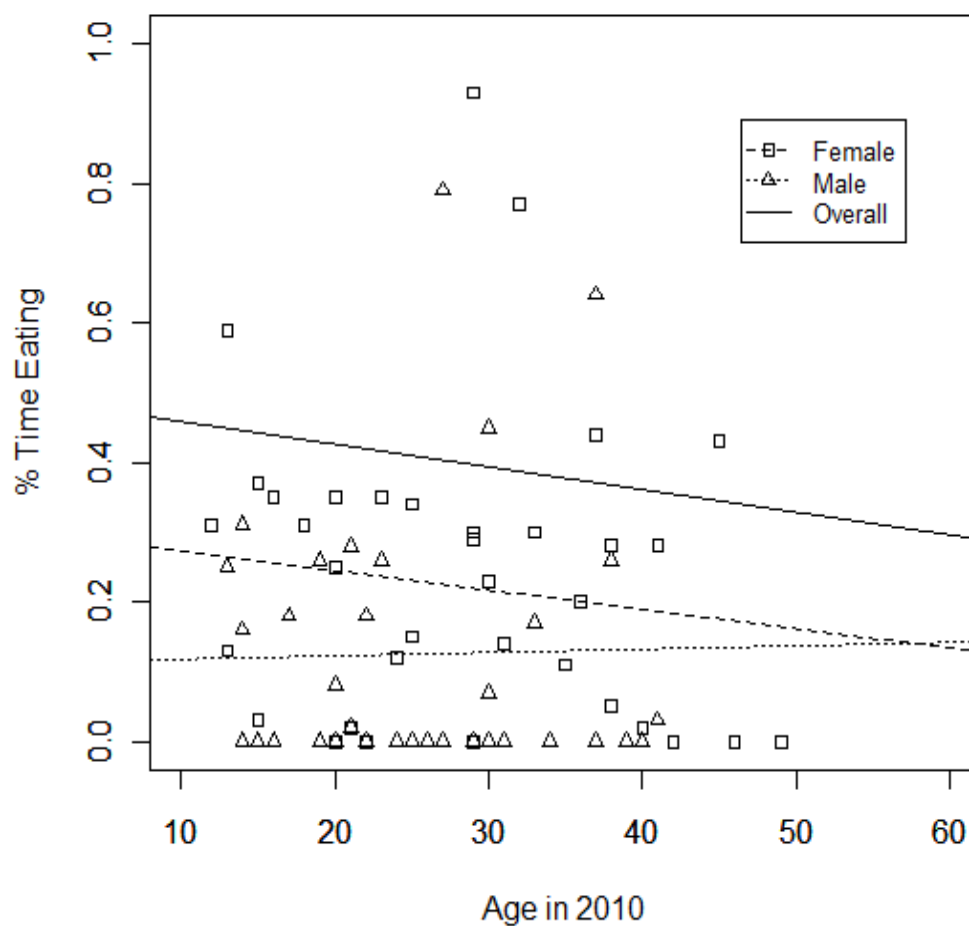
**Figure 2.2.** Biplot of eigenvalues of total state behaviors with respect to the first two principal components, differentiated between adult lactating (N = 58) adult nonlactating (N = 6) subadult lactating (N = 17) and subadult nonlactating (N = 28). See Tables 2.5 and 2.6 for statistical analyses.



**Figure 2.3.** Biplot of eigenvalues of total state behaviors with respect to the first two principal components, differentiated among mothers of female calves (N = 38), male calves (N = 35) and females without calves (N = 36). See Tables 2.5 and 2.6 for statistical analyses.



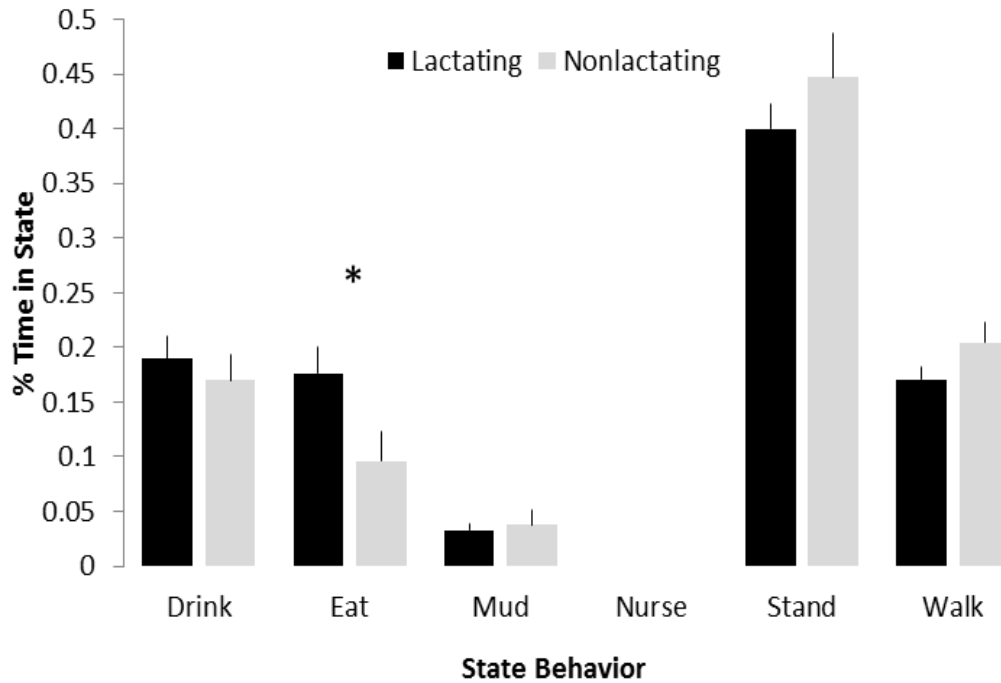
**Figure 2.4.** Linear regression of age on percentage of time spent eating with separate trendlines for lactating ( $N = 75$ ) and nonlactating ( $N = 34$ ) females. See Table 2.7 for statistical analyses.



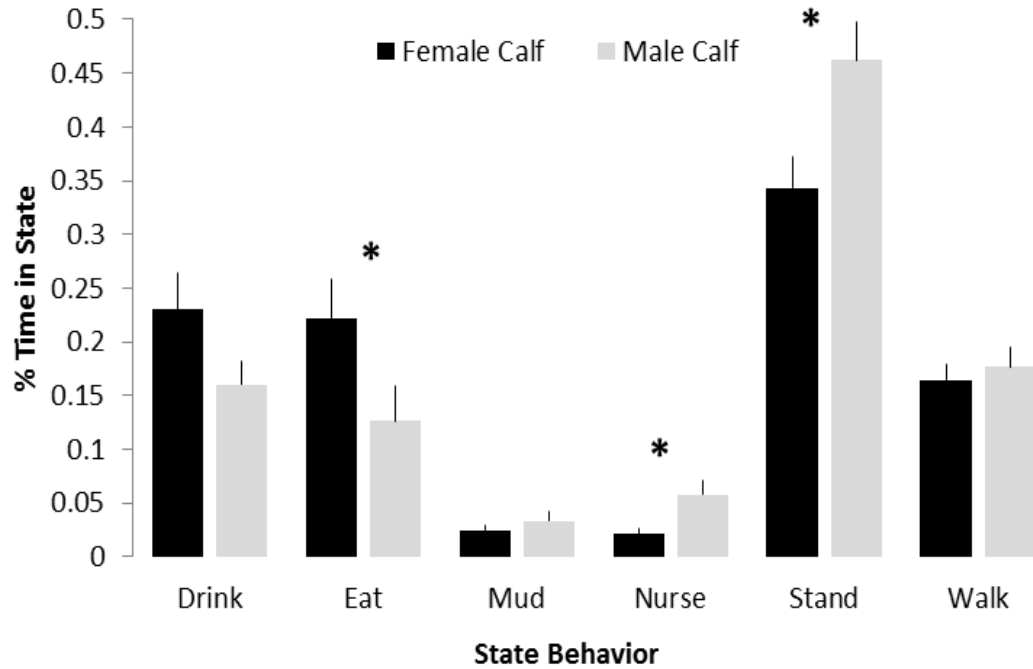
**Figure 2.5.** Linear regression of age on percentage of time spent eating with separate trendlines for mothers of female (N = 38) and male calves (N = 35). See Table 2.7 for statistical analyses.



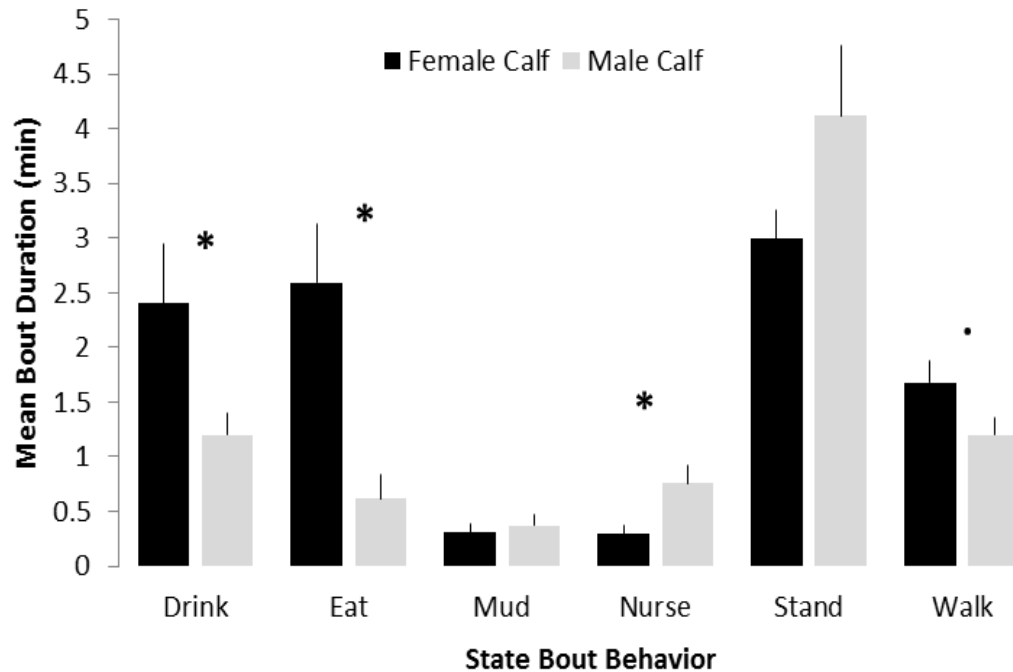
**Figure 2.6.** Percentage of time spent in each state behavior ( $\pm$  SE) for adult (N = 64) and subadult (N = 45) females. For analysis of drinking only observations near water were considered, for adult (N = 63) and subadult females (N = 45). For analysis of nursing only adult lactating (N = 58) and subadult lactating (N = 17) females were considered. \* indicates p-value  $\leq 0.05$ . See Tables 2.8 and 2.9 for statistical analyses.



**Figure 2.7.** Percentage of time spent in each state behavior ( $\pm$  SE) for lactating (N = 75) and nonlactating (N = 34) females. For analysis of drinking only observations near water were considered, for lactating (N = 74) and nonlactating females (N = 34). \* indicates  $\leq 0.05$ ; • indicates  $< 0.1$ . See Tables 2.8 and 2.9 for statistical analyses.

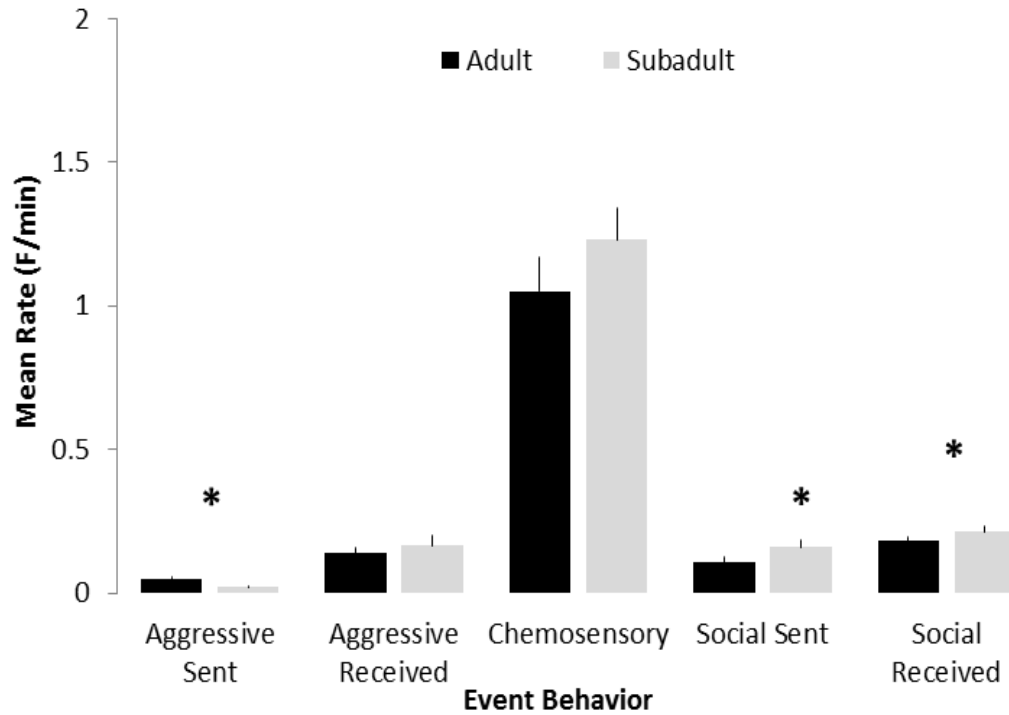


**Figure 2.8.** Percentage of time spent in each state behavior ( $\pm$  SE) for female elephants with female (N=38) or male (N=35) calves. For analysis of drinking only observations near water were considered, for mothers of females (N = 37) and mothers of females (N =35). \* indicates  $\leq 0.05$ . See Tables 2.8 and 2.9 for statistical analyses.

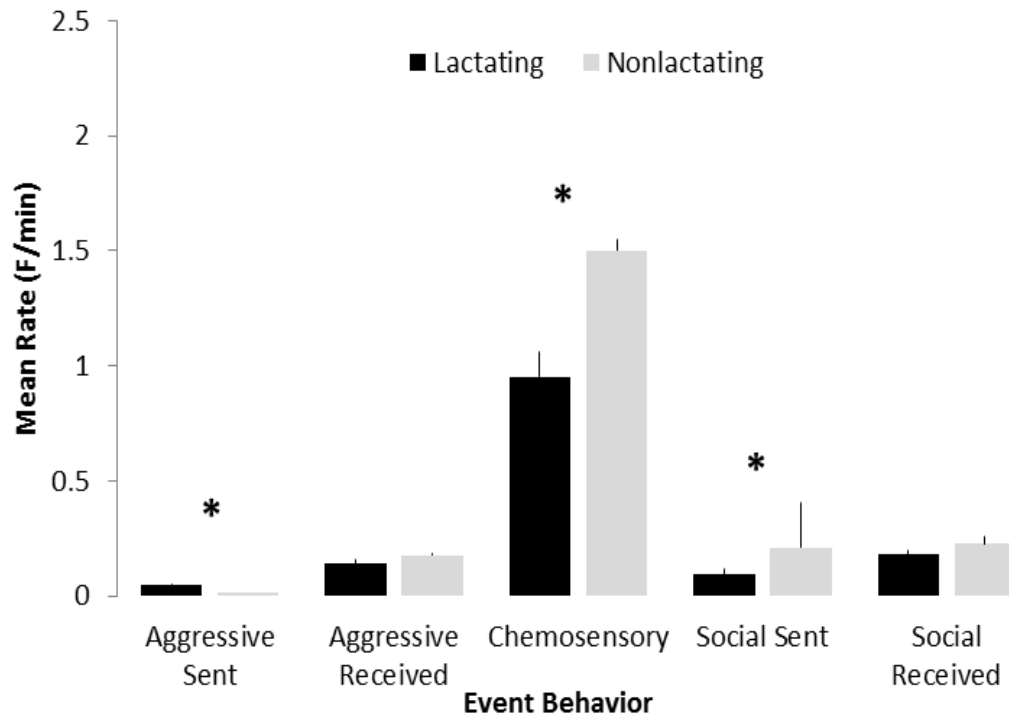


**Figure 2.9.** Percentage of time spent in each bout behavior ( $\pm$  SE) in relation to sex of nursing offspring. Calf sex was female (N=38) and male (N=34). For analysis of drinking only observations near water were considered, for mothers of females (N = 37) and mothers of females (N =34). \* indicates p-value  $\leq 0.05$ ; • indicates p-value  $< 0.1$ . See Table 2.10 for statistical analyses.

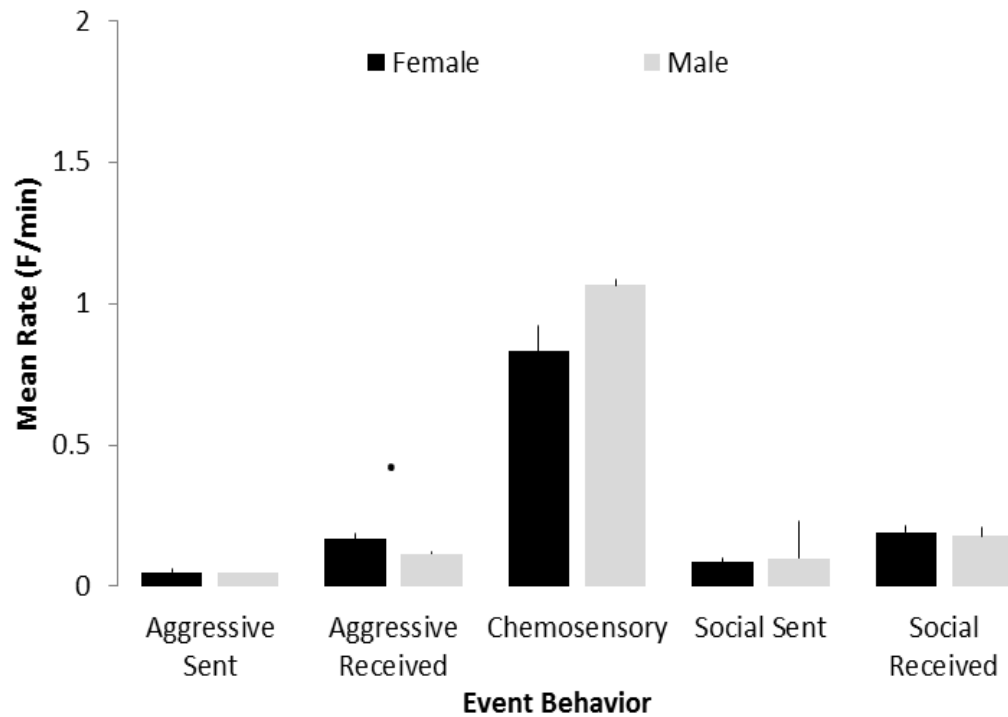




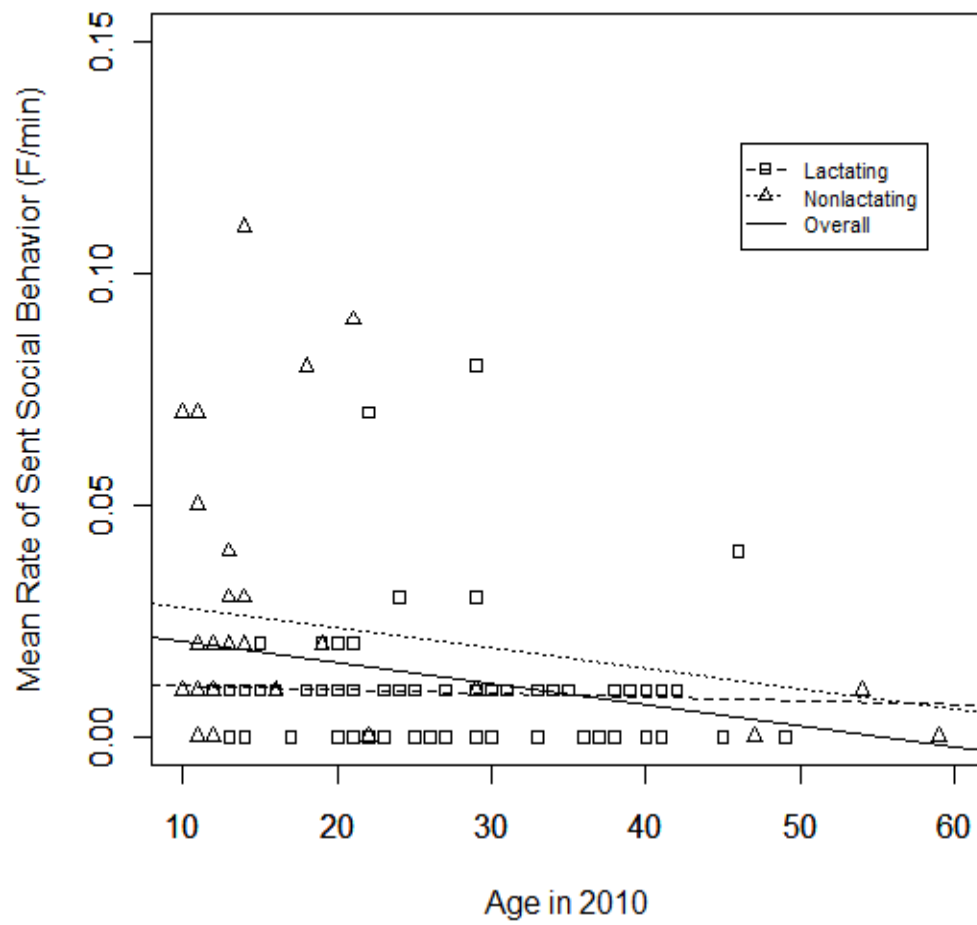
**Figure 2.10.** Mean ( $\pm$  SE) rate (frequency/time visible) of pooled event behaviors in adult (N = 64) and subadult (N = 45) females. \* indicates  $\leq 0.05$ . See Table 2.3 for description of specific event behaviors. See Table 2.13 for statistical analyses.



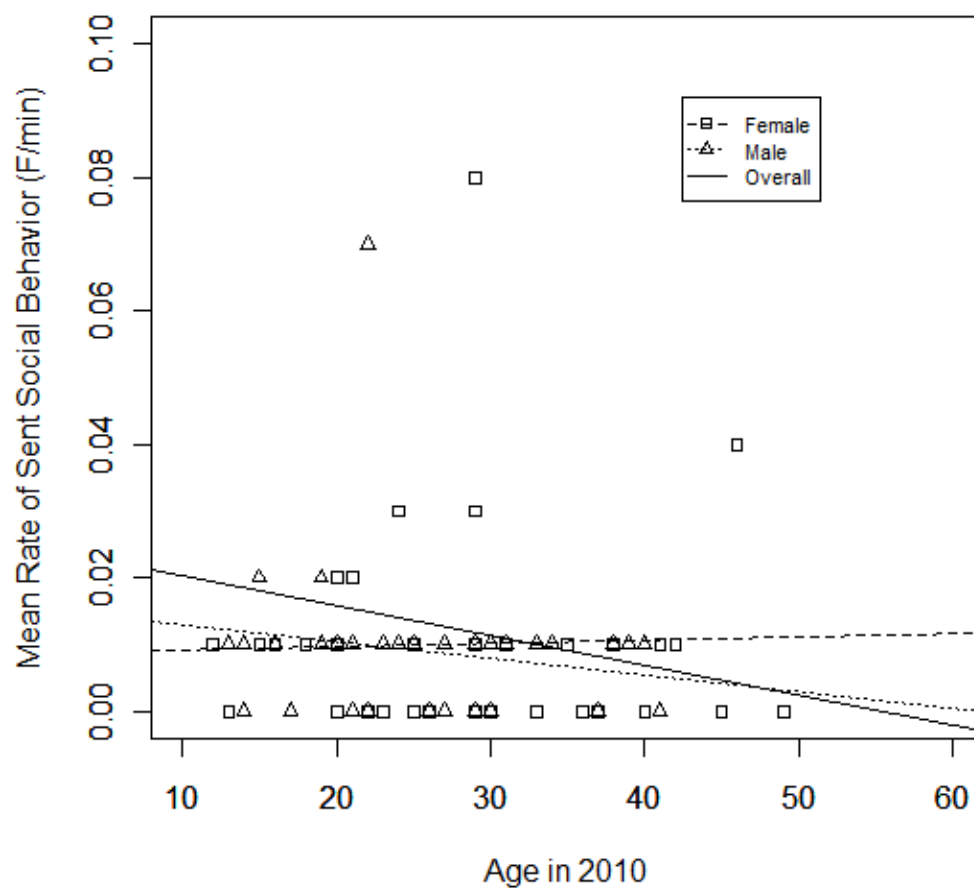
**Figure 2.11.** Mean ( $\pm$  SE) rate (frequency/time visible) of pooled event behaviors in lactating (N = 75) and nonlactating (N = 34) females. \* indicates  $\leq 0.05$ . See Table 2.3 for description of specific event behaviors. See Table 2.13 for statistical analyses.



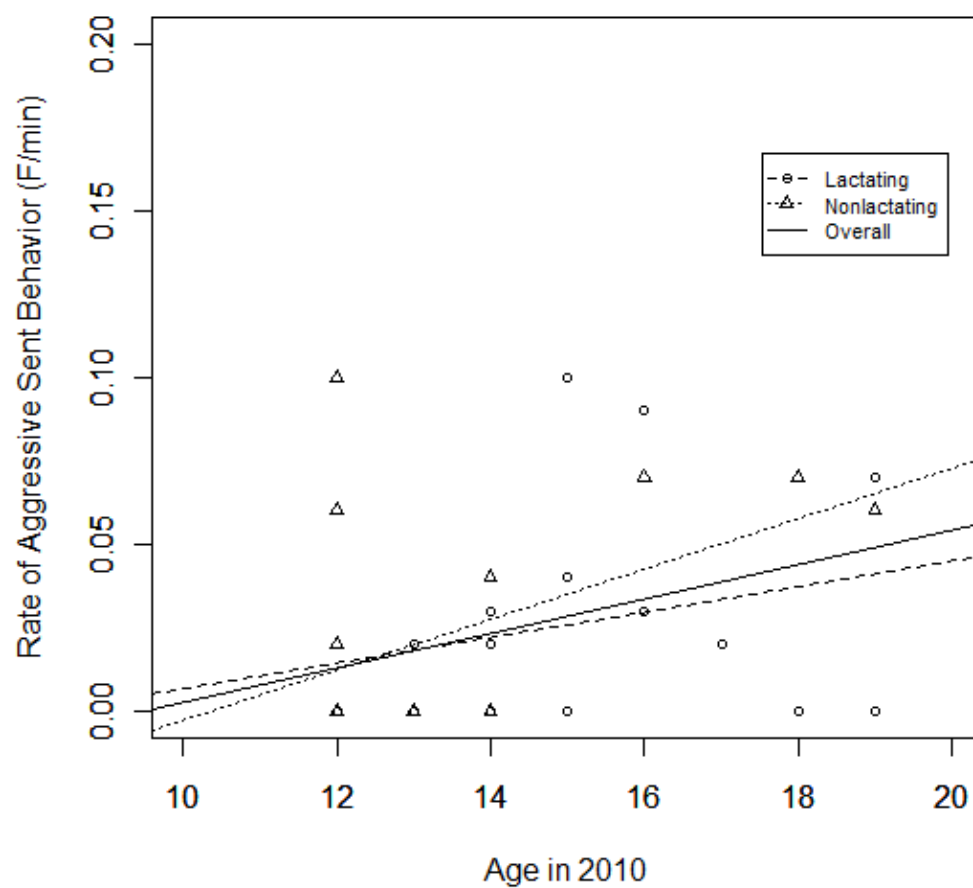
**Figure 2.12.** Mean ( $\pm$  SE) rate (frequency/visible focal min) of pooled event behaviors in mothers of female calves (N =38) and male calves (N = 35) females. • indicates < 0.1. See Table 2.3 for description of specific event behaviors. See Table 2.13 for statistical analyses.



**Figure 2.13.** Linear regression of age on the rate of sent social interactions with separate trendlines for lactating (N = 75) and nonlactating (N = 34) females. See Table 2.14 for statistical analyses.



**Figure 2.14.** Linear regression of age on the rate of sent social interactions with separate trendlines for mothers of female (N = 38) and male calves (N = 35). See Table 2.14 for statistical analyses.



**Figure 2.15.** Linear regression of age on the rate of sent social interactions with separate trendlines for lactating (N = 16) and nonlactating (N = 19) subadult females. See Table 2.16 for statistical analyses.

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