



## Behavioural patterns among female African savannah elephants: the role of age, lactational status, and sex of the nursing calf

Maggie Wisniewska<sup>a,\*</sup>, Elizabeth W. Freeman<sup>b</sup> and Bruce A. Schulte<sup>a</sup>

<sup>a</sup> Department of Biology, Western Kentucky University, Bowling Green, KY 42101, USA

<sup>b</sup> New Century College, George Mason University, Fairfax, VA 22030, USA

\* Corresponding author's e-mail address: maggie.wisniewska@gmail.com

Accepted 29 May 2015; published online 1 July 2015

---

### Abstract

For social mammals, phenotypic factors, such as age and reproductive state, and environmental factors, such as competition and requirements for offspring, shape individual resource needs and cause animals to display behavioural patterns most useful in resource acquisition. Female mammals trade off investment in growth and survival against complex and resource-intensive reproductive challenges; thus, they alter behaviours according to changing priorities. To maximize net gain females increase resource intake or limit its expenditure. Behaviours that involve resource acquisition, such as foraging, are potentially rewarding, yet lead to competition, especially in group-living species; whereas behaviours that do not provide resources, such as resting or grooming, encourage sharing and buffer competition. In cooperative species with linear dominance hierarchies such as female African elephants (*Loxodonta africana africana*), rank is often determined by age and size, which are highly correlated. When compared with younger, competitively disadvantaged individuals, higher ranked animals attain greater access to resources, but other phenotypic and environmental factors may influence their needs. Hence, we examined how lactational status and sex of the nursing offspring influenced time spent on resource acquisition, and we assessed how these factors affect rates of aggression related to age. We conducted the study at Addo Elephant National Park in South Africa from June to December 2010, using 20 min focal animal sampling on reproductively mature females ( $N = 109$ ). Adult females ( $N = 64$ ) exhibited aggression more frequently and socialized in a non-aggressive manner less frequently than subadult females ( $N = 45$ ). Lactating females ( $N = 75$ ) spent more time foraging, displayed aggression more frequently, socialized in a non-aggressive manner less frequently, and exhibited chemosensory behaviours less frequently than non-lactating conspecifics ( $N = 34$ ). Mothers of female calves ( $N = 39$ ) spent more time foraging than mothers of male calves ( $N = 36$ ). The latter spent more time nursing and resting. We show how behavioural patterns, permitted or limited by age (correlated with size and rank) and reproductive condition, pertain to resource needs in female elephants, in contexts not directly

related to survival or starvation avoidance. We discuss our findings in the context of female social relationships, for a long-lived, cooperative species.

**Keywords**

behavioural patterns, age, lactation, dominance, sex of offspring.

**1. Introduction**

Linear dominance hierarchies, characterized by individual social rank established along a discernible gradient (e.g., size), may be advantageous because they trigger synchronous behaviours (Conradt & Roper, 2003; Fischhoff et al., 2007), ameliorate competition (Berger, 1977; de Vries et al., 2006), and facilitate resource acquisition and sharing (Archie et al., 2006a). However, animals living within such hierarchies have to trade-off between maintaining social cohesion and competing for resources (Sterck et al., 1997) because individual resource needs cause divergence in behavioural patterns (Clutton-Brock & Lukas, 2011) and prompt competition (Bednekoff, 1996). Thus, an animal's decision about when and how to acquire resources depends upon the social cost and benefit of the behaviour (Zuberbuhler et al., 1997) and its effectiveness in resource acquisition (Beauchamp, 1999). Behavioural patterns that increase individual resource intake are rewarding but often lead to competition (Bednekoff, 1996), whereas behavioural patterns that do not provide resources limit energy expenditure and may avert competition (Harcourt, 1989; Link et al., 2006). Because resource needs are important determinants of behavioural patterns (Fischhoff et al., 2007; Hamel & Côté, 2008), animals should behave in ways that maximize their energy budgets through a combination of increased intake (Gittleman & Thompson, 1988) and limited expenditure (Illius et al., 2002), especially when comparing individuals with higher versus lower needs (Kacelnik & Bateson, 1996; Link et al., 2006; Luttbeg & Sih, 2010).

Resource needs of reproductively mature female mammals result from a confluence of phenotypic factors, such as age (Shannon et al., 2008), size (Pelletier & Festa-Bianchet, 2004) and lactational status (Clutton-Brock et al., 1989; Ruckstuhl & Festa-Bianchet, 1998; Kaighoadi & Stevens, 2013). With regard to age, larger, older females may have greater absolute requirements, but as Shannon et al. (2008) noted, smaller and younger individuals have lower digestive efficiency and higher mass-specific metabolic needs. Besides, younger females may have greater resource demands to support

their own rapid growth, as well as the development of their offspring during gestation or lactation (Vance, 1992). When considering individuals of similar age, size, and health status, lactating females are under up to 180% greater resource stress (Prentice & Prentice, 1988; Bartošová et al., 2011) and heightened mortality risk (White & Berger, 2001) than non-lactating females (even when the latter are pregnant).

For females living in groups their resource needs are further impacted by various environmental factors, such as competition (Thouless, 1990), individual social rank relative to that of other group members (Pelletier & Festa-Bianchet, 2004), resource availability (Valiex et al., 2007) and offspring sex (Landete-Castillejos et al., 2005). Through growth and maturation, they gain experience and become more dominant group members (Fawcett & Johnstone, 2010). Dominance enhances competitive ability and allows for priority access to resources (Pelletier & Festa-Banche, 2004), especially at spatially or temporarily limited resources, such as a waterhole (Atkinson & Shorrocks, 1981; Pérez-Barbería & Nores, 1994). Depending upon the sex of their offspring, lactating females incur different fitness and resource costs (Trivers & Willard, 1973; Lee & Moss, 1986). In a few mammalian species, lactating females allocate more resources to female offspring (Kojola & Helle, 1994; Koskela et al., 2009). However, in the majority of sexually dimorphic, herd-living mammals (particularly large-bodied herbivores), male offspring are more costly (Reinhardt & Reinhardt, 1981), because they grow faster and require more milk than do females (Lee & Moss, 1995; Sheldon & West, 2004).

Evidently resource needs that group-living females operate within are determined via the trade-off between investment in their age- and size-specific growth and competitive ability (Shannon et al., 2008; Neuhaus & Ruckstuhl, 2002) and their present or future reproductive success (Gittleman & Thompson, 1988; Hamel & Côté, 2008). Although these compromises may not have direct bearing on female survival, they should influence behavioural patterns apparent in activity patterns, evident through such behaviours as foraging, nursing, and resting (Caraco, 1981), in social behaviours such as aggression, and in investigation of the environment, such as chemosensory behaviours (Ferrari et al., 2009).

As with many mammals, age and reproductive condition also influence the behavioural patterns of female African savannah elephants (*Loxodonta*

*a. africana*; Lee & Moss, 1986; Archie et al., 2006a), but the interactive effects of these factors on their behavioural patterns are not well understood. Female African savannah elephants have a multilevel social organization, where the basic unit of fission and fusion is the matrilineal family (Douglas-Hamilton, 1972). Families are comprised of closely related females, their offspring, and the matriarch, typically the eldest, dominant female (Douglas-Hamilton, 1972; Moss & Pool, 1983), while fusion of related family units forms a kinship group (Moss & Pool, 1983). Elephant sociality is based on a stable dominance hierarchy, where older, larger females dominate over their younger, smaller conspecifics (Archie et al., 2006a); overt aggression is rare (Archie et al., 2006a), and group decision-making is common (Conradt & Roper, 2003). Older females, possessing more ecological knowledge and social experience, secure resources more efficiently than their younger, competitively disadvantaged conspecifics, which often wait for or share resources (McComb et al., 2001, 2011). Regardless of age, dominance rank, or experience, reproductively mature elephants are either pregnant, lactating, or in both states simultaneously throughout their lives (Wittemyer & Getz, 2007). As females approach ovulation, their rates of aggression towards conspecifics increase in captive Asian elephants (*Elephas maximus*) (Slade-Cain et al., 2008). Gestation (lasting approximately 22 months; Fayrer-Hosken et al., 2001) and lactation (lasting up to four years), especially when nursing larger and bolder male calves (Lee, 1987; Lee & Moss, 1986), must impose important resource stress. However, we know little about behavioural patterns used for resource acquisition by elephants of different age and reproductive conditions.

To determine how age and reproductive condition affect behavioural patterns, we examined the effects of age, lactational status, and sex of nursing calf on the expression of activity patterns (drink, dust, forage, mud, nurse, other, rest and walk), social behaviours (aggressive and non-aggressive interactions), and chemosensory investigation of their environment by female elephants. Behaviours that enable resource acquisition, such as foraging or drinking, may lead to competitive interactions, expressed as aggressive behaviours (Thouless, 1990; Hoogland, 1995; Bebié & McElligott, 2006). Conversely, behaviours that do not provide resources, such as resting, minimize energy expenditure (Link et al., 2006; Murray et al., 2012). Moreover, chemosensory assessment of the environment, walking away from a contest, and comfort behaviours such as mudding in a social context may help avoid

conflict, build social networks, and encourage resource sharing (Altmann, 1986; Rasmussen et al., 2002).

We made four assumptions based upon the literature: (1) absolute metabolic needs increase with age (Hennemann, 1983); (2) age correlates with size, dominance and experience (Archie et al., 2006a); (3) lactation is metabolically the most challenging reproductive condition (Mellish et al., 2000); and (4) the elephant population at our study site is below the carrying capacity and not under risk of starvation (Gough & Kerley, 2006).

We expected females with different resource demands to have divergent behavioural patterns. We hypothesized that elephants that were adults, lactating, or nursing a male calf would spend more time drinking and foraging than individuals that were subadults, non-lactating, or nursing a female calf. We also hypothesized that mothers of male calves would spend more time nursing than mothers of female calves. In addition, we hypothesized that adult, lactating, or elephants nursing a male calf would exhibit higher rates of aggressive behaviours and lower rates of chemosensory and non-aggressive behaviours than subadult, non-lactating, or elephants nursing a female calf. We predicted that when mixed with the demands of reproduction, the advantages of age and experience prompt behavioural patterns that grant priority access to resources but also trigger competition, expressed as aggressive behaviours (Bednekoff, 1996). Furthermore, the lack of experience, regardless of reproductive condition, would elicit behavioural patterns that are conducive to limited expenditure of energy, resource sharing (Link et al., 2006), and the avoidance of competition (Gobush et al., 2008).

## **2. Materials and methods**

### *2.1. Study site*

Addo Elephant National Park (AENP) is located ca. 70 km north of the city of Port Elizabeth, 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; Freeman et al., 2013). The park was established and fenced in 1931 to support a nearly extirpated population of 11 elephants in the area (Whitehouse & Hall-Martin, 2000). Since this time, the park has undergone several expansions (Gough & Kerley, 2006). At the time of this study, the park consisted of a fenced area of ca. 38 000 ha (J. Adendorff, conservation manager, pers.

comm.). We collected data from the main tourist section of the park readily accessible by a field vehicle (~25 000 ha; focal animal samples:  $N = 267$ ) because the elephant population in this area has been previously observed and catalogued.

## 2.2. *Population*

Longitudinal data have allowed scientists to reliably define two clans, six matriline and 37 family associations within AENP (Whitehouse & Hall-Martin, 2000; Gough & Kerley, 2006; Loizi et al., 2009; Merte et al., 2010). The matriline are more distantly related than would be expected from an extreme bottleneck event (Whitehouse, 2001). Over the past decade, almost the entire adult population has been identified based on physical characteristics and photographically catalogued (428 individuals within families; 196 males within bounded groups and solitary); the pedigrees of all 37 families have been updated annually and meticulously maintained throughout the year. Therefore, we were able to determine age and dominance rank of all females 10 years of age or older.

Importantly, at the age of 10 African savannah elephants begin displaying marked sexual dimorphism; moreover, females become sexually mature between the ages of 10 and 15 (Lee & Moss, 1995; Wittemyer et al., 2005). We collected data from 109 out of 132 presumably reproductively mature females of known ages (range 10–59 years). The majority of females younger than 19 years of age were either nulliparous or had at most two offspring; moreover, there were no matriarchs (oldest and most dominant elephant, leading individuals of at least one family unit) within this age class. On the contrary, the majority of females older than 19 years of age had at least two offspring, and 46% of females in this age class were matriarchs (the youngest matriarch was 22 years old; the oldest one was 59 years old). Because of this contrast, we considered females between 10 and 19 years of age as subadults ( $N = 45$ ) and females of 20 years of age or older as adults ( $N = 64$ ). We determined female lactational status via direct observation of nursing ( $N = 75$ ), and non-lactational status as reproductively mature females that we never observed nursing ( $N = 34$ ). We acknowledge that comfort suckling occurs and may yield no milk; however, in our study, all calves suckled continually and on multiple occasions, from females whose mammary glands were notably enlarged. We determined sex of nursing offspring via direct observation (female calves:  $N = 39$ , male calves:  $N = 36$ ).

### 2.3. Data collection

We collected data between June and December of 2010, during the local hours of 08:00 to 18:00. To quantify the duration of activity patterns and the frequency of social and chemosensory behaviours, we observed individuals engaged in natural, diurnal activities at eight permanent reservoir-fed waterholes (90.1%,  $N = 242$ ) or when they were on tourist roads adjacent to the waterholes (9.4%,  $N = 25$ ). The elephants were habituated to tourist traffic, permitting data to be collected from a field vehicle. Upon encountering a group of at least two families, each from a different kinship group, we recorded each family's identification (ID) based on ID of its matriarch or oldest, present female. Additionally, we recorded ID of all reproductively mature females and nursing females (along with sex of their offspring), and weather conditions. We preferentially collected data from reproductively mature females for whom we had the least number or shortest duration of focal samples. On occasions when more than one focal animal sample was collected, in order to allow for previously observed behavioural dynamics to resolve, consecutive sampling periods were separated by an interval of at least 5 min. We recorded 267 focal animal samples with continuous recording on 109 different females ( $2.4 \pm 0.01$  obs/female; range 1–6 obs/female; Altmann, 1974). The duration of sampling periods varied with the length of visible period per focal female ( $14.9 \pm 0.39$  min; range 6–20 min). During each focal animal sample, we measured duration of activity patterns (state behaviours in seconds, lasting  $\geq 5$  s) and frequency of social and chemosensory behaviours (event behaviours as rate per hour, lasting  $< 5$  s; Table 1). For all interactions between the focal animal and a conspecific, we recorded the identification of the sender and the receiver.

**Table 1.**

Ethogram of state (lasting longer than 5 s) and event ( $< 5$  s) behaviours performed by potentially reproductively mature female elephants during continuous focal observations at AENP.

Type	Behaviour	Definition
State <sup>a</sup>		Behaviour best measured by duration $> 5$ s
	Chase	Pursue another elephant
	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

**Table 1.**

(Continued.)

Type	Behaviour	Definition
Event <sup>b</sup>	Forage	Take nutrients into the mouth via the trunk
	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
	Other	Behaviour not defined in the ethogram
	Play	Maintain contact with another elephant in an equivalent manner (e.g., rub or climb on another)
	Rest	Remain in the same location for at least two seconds with none of the following trunk behaviours observed
	Spar	Hold trunk down (not intertwined) and head in contact with another elephant; if tusks present they will be interlocked and pushing against one another
	Trunk Wrestle	Push against another individual while trunks are intertwined
	Walk	Leave location while all four legs are moving in a steady pace
	Aggressive <sup>c</sup>	Behaviour best measured as frequency (<5 s in duration) Any intentional social behaviour or bodily disposition intended to establish dominance hierarchy that may range from a settle threat to an overt attack (with or without contact between the sender and the receiver). Individual behaviours included: Back Away, Back Into, Displace, Ears Flat, Ears Wave, Head Butt, Kick, Present, Supplant, Tail Into, Threat, Trunk Hit, Tusk
	Chemosensory <sup>d</sup>	Any intentional trunk behaviour intended to process olfactory and tactile stimuli, either volatile or found on a substrate (with or without contact between the sender and the substrate). Individual behaviours included: Check, Dig, Flehmen, Flick, Horizontal Sniff, Place, Sniff, Object Play, Periscope Sniff, Trunk Wiggle
	Non-aggressive	Any intentional social behaviour or bodily disposition intended to express social affiliation or introduce environmental enrichment (with contact between the sender and the receiver). Individual behaviours included: Body Rub, Head Into, Lean, Mount, Trunk over Back, Trunk to Body, Trunk to Feet, Trunk to Genitals, Trunk on Head, Trunk to Head, Trunk to Mouth, Trunk to Tail, Trunk to Temporal Gland, Trunk to Trunk, Trunk Wrap

<sup>a</sup> State behaviour definitions derived from Loizi et al. (2009).<sup>b</sup> Event behaviours included recording identity of sender and receiver.<sup>c</sup> Refer to Wisniewska (2011) for definitions of aggressive and non-aggressive behaviours.<sup>d</sup> Chemosensory definitions were derived from Schulte & Rasmussen (1999).



## 2.4. Data analysis

For all statistical analyses, we used R (R Core Development Team, 2009). Data with Shapiro–Wilk test statistics less than 0.9 were analysed non-parametrically. All statistical tests used  $\alpha = 0.05$ .

First, the effects of age, lactational status, and sex of nursing calf on the time that elephants spent in respective state behaviours (chase, drink, dust, forage, mud, nurse, other, play, rest, spar, and walk) were analysed with PCA. We chose PCA analysis because it is a robust method for analysing repeated measures data where the proportions of time spent in each of the state behaviours are not independent (Hamel & Côté, 2008). The total duration of each state behaviour for all the focal samples per each focal female was determined separately, and the total proportion of time spent in each of the state behaviours was calculated by dividing total state duration by total visible focal time per each focal sample. Initially we tested the differences among the PCA scores with respect to age, lactational status, and sex of the nursing calf with factorial ANOVA. Using the Wilcoxon-signed rank test, we analysed only the state behaviours that occupied greater than 1% of total time (drink, forage, mud, nurse, rest and walk) of all the focal samples per each focal female. To estimate the states of drink and mud only data collected from female elephants observed near waterholes were considered. To estimate the state of nurse only data from lactating females were analysed.

Second, the effects of age, lactational status, and sex of nursing calf on the frequency elephants engaged in event behaviours were analysed using the Wilcoxon-signed rank test. All event behaviours were grouped into aggressive, chemosensory, or non-aggressive types of behaviours (Table 1) and further categorized by whether the focal female was the sender or receiver. The frequency of respective event behaviours for all the focal samples per each focal female was determined separately, and the mean rate was calculated by dividing the total frequency of each event behaviour by the total visible focal time per each focal female.

## 3. Results

In the PCA, the first three eigenvectors explained 89% of the variability in the female activity budget (Table 2); no multicollinearity or singularity was observed among behaviour measures that contributed to the PCA (Table 3). The first PCA axis (Table 2) contrasted time spent resting (+) to time spent

**Table 2.**

Eigenvectors derived from PCA of duration of state behaviours performed by reproductively mature female elephants ( $N = 109$ ).

State behaviour	Eigenvector 1 (0.49)	Eigenvector 2 (0.30)	Eigenvector 3 (0.10)
Mud	0.014	-0.040	0.090
Chase	0.001	-0.001	0.001
Drink	-0.100	-0.800*	-0.430*
Dust	0.002	0.010	0.020
Forage	-0.600*	0.500*	-0.300
Nurse	0.007	0.040	0.010
Other	0.000	-0.001	0.000
Play	-0.008	-0.020	0.050
Spar	-0.000	0.001	0.004
Rest	0.800*	0.300	-0.300
Walk	-0.400	-0.100	0.800*

Proportions represent the variation in activity budgets explained by each PCA axis. An asterisk denotes behaviours that contributed the most to the eigenvector (positively or negatively).

foraging (-). The second PCA axis differentiated time spent foraging (+) and time spent drinking (-). The third PCA axis weighed time spent walking (+) and time spent drinking (-). Although biplots of eigenvalues for the first three PCA axes did not reveal obvious grouping patterns, calf sex had a significant effect on PCA axis one ( $F_{1,107} = 6.22$ ,  $p = 0.014$ ). Specifically, there was a difference in the first PCA axis between elephants nursing female versus male calves ( $p = 0.006$ ) and between elephants nursing female calves versus individuals without calves ( $p = 0.007$ ). The first PCA had more negative values for mothers of female calves than for either mothers of males or females with no calves. There was no significant difference in the first PCA axis between elephants nursing male calves and individuals without calves ( $p > 0.05$ ). Calf sex did not have a significant effect on PCA axes two and three ( $p > 0.05$ ). Neither age category nor lactational status had a significant effect on PCA axes one, two or three ( $p > 0.05$ ). There was no significant difference in the age of male versus female calves age ( $W = 634.5$ ,  $p = 0.732$ ).

Adult and subadult females did not exhibit significantly different activity patterns as evinced by the analysis of state behaviours that occupied greater than 1% of total focal time ( $p > 0.05$ ; Table 4). Lactating elephants allotted a greater proportion of time to foraging than non-lactating conspecifics ( $W =$

**Table 3.**  
Maximum observed correlations of state behaviour measures that contributed to the PCA.

	Chase	Drink	Dust	Forage	Nurse	Mud	Other	Play	Spar	Rest	Walk
Chase	1	0.028	-0.021	-0.082	-0.040	-0.059	-0.012	-0.020	0.229	0.045	0.069
Drink	0.028	1	-0.120	-0.298	-0.193	-0.031	0.086	0.006	-0.052	-0.401	-0.031
Dust	-0.021	-0.120	1	-0.049	-0.050	-0.072	-0.017	-0.029	-0.031	-0.044	-0.113
Forage	-0.082	-0.298	-0.049	1	-0.008	-0.194	-0.074	-0.094	0.019	-0.543*	-0.150
Nurse	-0.040	-0.193	-0.050	-0.008	1	-0.039	-0.013	-0.082	-0.091	0.017	-0.124
Mud	-0.059	-0.031	-0.072	-0.194	-0.039	1	-0.007	0.165	-0.083	-0.067	-0.040
Other	-0.012	0.086	-0.017	-0.074	-0.013	-0.007	1	-0.016	-0.017	-0.016	0.056
Play	-0.020	0.006	-0.029	-0.094	-0.082	0.165	-0.016	1	-0.012	-0.137	-0.013
Spar	0.229	-0.052	-0.031	0.019	-0.091	-0.083	-0.017	-0.012	1	-0.006	0.143
Rest	0.045	-0.401	-0.044	-0.543*	0.017	-0.067	-0.016	-0.137	-0.006	1	-0.243
Walk	0.069	-0.031	-0.113	-0.150	-0.124	-0.040	0.056	-0.013	0.143	-0.243	1

\* Strong relationships ( $r > 0.5$ ).

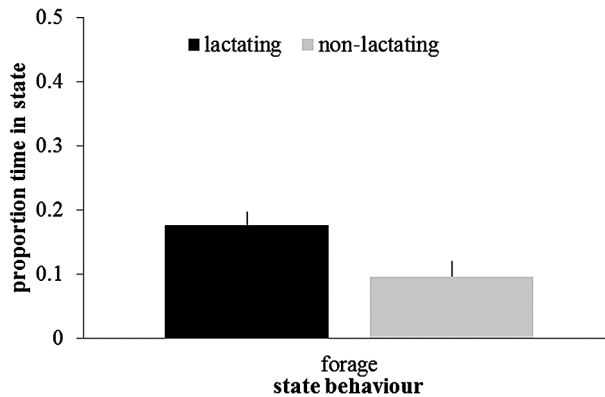
**Table 4.**

Wilcoxon-signed rank test ( $p > 0.05$ ) on the effects of age class ( $N = 109$ ), lactational status ( $N = 109$ ), and sex of nursing offspring ( $N = 75$ ) on proportion of time in state behaviours and frequency of event behaviours observed in female elephants.

Type	Behaviour	Variables	<i>W</i>	<i>p</i>
State	Drink	AClass	1636.0	0.170
		LStatus	1201.5	0.710
		Calf Sex	772.0	0.700
	Forage	AClass	1553.5	0.470
	Mud	AClass	1592.5	0.250
		LStatus	1412.5	0.300
		Calf Sex	669.5	0.800
	Nurse	AClass	405.0	0.250
	Rest	AClass	1174.0	0.100
		LStatus	1174.0	0.513
	Walk	AClass	1282.5	0.300
		LStatus	984.0	0.057
		Calf sex	740.5	1.000
Event	Aggressive sent	Calf sex	614.5	0.570
	Aggressive received	AClass	1419.5	0.900
		LStatus	1266.0	0.950
		Calf sex	818.5	0.090
	Chemosensory	AClass	1147.5	0.070
		Calf sex	574.0	0.320
	Non-aggressive sent	Calf sex	635.0	0.720
	Non-aggressive received	LStatus	1128.0	0.190
		Calf sex	713.5	0.430

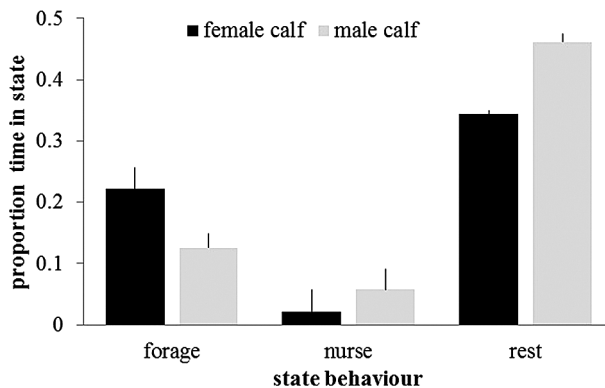
Age class (AClass) compared adults ( $\geq 20$  years) and subadults (10–19 years). Lactational status (LStatus) compared lactating and non-lactating elephants. Sex of nursing calf (Calf sex) compared mothers nursing female or male calves. For analysis of drinking and mudding only observations near water were considered. For statistically significant findings see results section.

1567.0,  $p = 0.048$ ; Figure 1). No other differences existed in the activity patterns between lactating and non-lactating elephants ( $p > 0.05$ ; Table 4). While mothers of female calves spent a significantly greater proportion of time foraging ( $W = 889.0$ ,  $p = 0.011$ ), mothers of male calves nursed ( $W = 449.5$ ,  $p = 0.014$ ) and rested ( $W = 463.5$ ,  $p = 0.005$ ; Figure 2) for a greater proportion of time. Proportion of time drinking, mudding, and walking did not vary with respect to sex of the calf ( $p > 0.05$ ; Table 4).

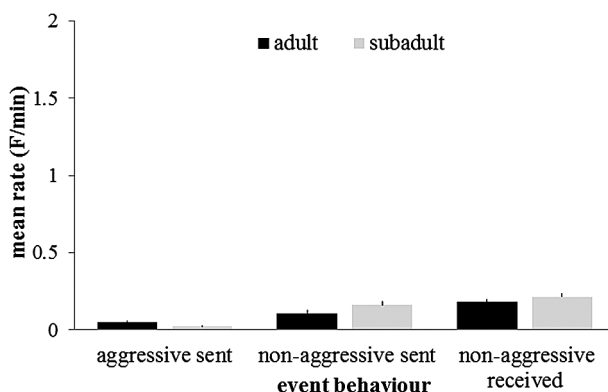


**Figure 1.** Proportion of time spent in forage state behaviour ( $\pm$  SEM) for lactating ( $N = 75$ ) and non-lactating ( $N = 34$ ) females. All  $p < 0.05$ . See Table 1 for description of specific state behaviours. See results section for statistical analyses.

Adult females displayed higher rates of sent aggressive behaviours than subadult females ( $W = 1878.5$ ,  $p = 0.005$ ). In contrast, subadult females sent ( $W = 896.5$ ,  $p = 0.000$ ) and received ( $W = 1161.0$ ,  $p = 0.018$ ; Figure 3) non-aggressive behaviours at higher rates than their adult conspecifics. Lactating elephants sent aggressive behaviours at higher rates than non-lactating individuals ( $W = 1775.0$ ,  $p = 0.001$ ). The latter exhibited higher



**Figure 2.** Proportion of time spent in each state behaviour ( $\pm$  SEM) for female elephants with female ( $N = 39$ ) or male ( $N = 36$ ) calves. For analysis of drinking only observations near water were considered, for mothers of females ( $N = 37$ ) and mothers of females ( $N = 35$ ). All  $p < 0.05$ . See Table 1 for description of specific state behaviours. See results section for statistical analyses.

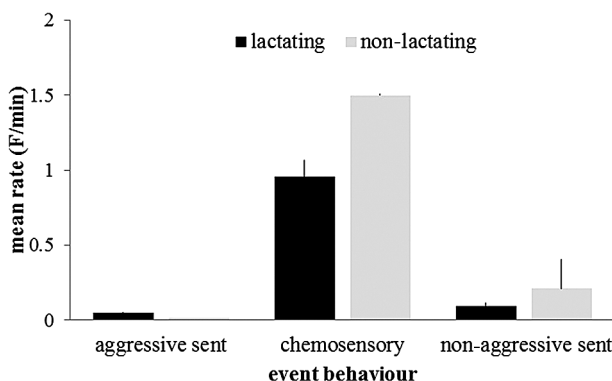


**Figure 3.** Mean ( $\pm$  SEM) rate (frequency/time visible) of pooled social event behaviours in adult ( $N = 64$ ) and subadult ( $N = 45$ ) females. All  $p < 0.05$ . See Table 1 for description of specific event behaviours. See results section for statistical analyses.

rates of chemosensory behaviours ( $W = 841.0$ ,  $p = 0.005$ ) and sent non-aggressive behaviours ( $W = 746.0$ ,  $p = 0.000$ ; Figure 4). Mothers of female and male calves did not exhibit significant differences in the rates of social and chemosensory behaviours ( $p > 0.05$ ; Table 4).

#### 4. Discussion

Individual resource needs are a composite function of phenotypic factors, such as age (Shannon et al., 2008) and lactational status (Clutton-Brock et



**Figure 4.** Mean ( $\pm$  SEM) rate (frequency/time visible) of pooled social event behaviours in lactating ( $N = 75$ ) and non-lactating ( $N = 34$ ) females. All  $p < 0.05$ . See Table 1 for description of specific event behaviours. See results section for statistical analyses.

al., 1989), and environmental factors such as competition (Thouless, 1990), social rank of an individual dependent upon rank of other group members (Pelletier & Festa-Bianchet, 2004), and offspring sex (Hamel & Côté, 2008). These factors shape behavioural patterns in group-living mammalian species (e.g., red deer (*Cervus elaphus*), Gittleman & Thompson, 1988). For the female African elephants at AENP, we first found that lactating females and mothers nursing female calves, regardless of their age, allocated significantly greater proportion of their time to foraging than non-lactating females and those nursing male calves. Lack of effect of age on time foraging in our study was similar to findings of Hamel & Côté (2008) in mountain goats (*Oreamnos americanus*), but it contrasted trends found by du Toit & Yetman (2005) in African ruminants of different size (and age). An increase in foraging time by lactating females at AENP confirmed the patterns observed in other systems where lactation correlated with increased food consumption (e.g., brown long-eared bat (*Plecotus auritus*), Gittleman & Thompson, 1988). In turn, compared with mothers of female calves, mothers of male calves in the AENP population allotted a significantly greater proportion of their time to nursing and resting, at the expense of foraging. This was a novel finding and diverged from results found in other sexually dimorphic, polygynous species where rearing of male offspring related to increased resource intake (Reinhardt & Reinhardt, 1981; Ruckstuhl & Festa-Bianchet, 1998). Secondly, as typically seen in other systems, whenever age (bighorn sheep (*Ovis canadensis*), Pelletier & Festa-Bianchet, 2004) or reproductive condition (human female (*Homo sapiens sapiens*), Hahn-Holbrook et al., 2011) is considered, aggressive displays at AENP were more frequently observed in adult and lactating females, regardless of calf sex which in some species increases aggression in mothers of male calves (red deer (*Cervus elaphus*), Clutton-Brock et al., 1989). On the other hand, non-aggressive or chemosensory behaviours, although similar in mothers of males and females, were more frequently observed in subadult and non-lactating individuals. Similar age- and resource need-specific preference for non-aggressive behaviours have been reported in species with high cost of aggressive behaviours (Agta hunter-gatherers (*Homo sapiens sapiens*), Goodman et al., 1985; crayfish (order Astacidea), Sato & Nagayama, 2011).

Whenever the costs of a behaviour exceed its benefits, an individual should choose an alternative approach that avails her resource needs (Gittleman & Thompson, 1988; Illius et al., 2002). Across mammalian taxa,

females of different ages use heterogeneous strategies to acquire resources (e.g., forage) or limit resource expenditure (e.g., rest), by altering their activity patterns (Dunbar & Dunbar, 1988; Bednekoff, 1996; Neuhaus & Ruckstuhl, 2002). In some group-living females with nonlinear dominance hierarchy (Vervaecke et al., 2007) and low degree of relatedness among group members, time spent foraging does not seem to be affected by age (Camargue horse (*Equus ferus caballus*), Duncan, 1980); however, in matrilineal species with linear dominance hierarchies, foraging time correlates positively with age-related resource needs (Japanese monkey (*Macaca fuscata yakui*), Watanuki & Nakayama 1993). In concurrence with this latter finding and as stated in our first hypothesis, we expected different activity patterns for adult and subadult female elephants at AENP. Regardless of their matrilineal sociality, adults and subadults did not allocate significantly different proportion of their time to any of the activities. Similarities in time allotment to activity patterns among female elephants may stem from synchronous activity (African savannah elephant (*Loxodonta a. africana*), Wittemyer & Getz, 2007; Shannon et al., 2008), common among socially advanced species that rely on widely distributed resources (chacma baboons (*Papio ursinus*), King & Cowlishaw, 2001; Masai giraffe (*Giraffa camelopardalis tippelskirchi*), Ginnett & Demment, 2007; African savannah elephant (*Loxodonta a. africana*), Wittemyer & Getz, 2007). Moreover, older animals (including elephants) often are more dominant (Archie et al., 2006a), forage uninterrupted more regularly, and satisfy their resource needs faster than younger, subordinate conspecifics (Thouless, 1990). Such freedom from the constraints of social rank (Pelletier & Festa-Bianchet, 2004) in older, dominant group members may create concurrence in their activity patterns with those of lower ranking, younger individuals.

Age-specific resource investment in growth and survival is traded off against reproductive output, especially in resource-stressed reproductively mature individuals (Gittleman & Thompson, 1988). As lactation imposes considerable energetic needs, mothers attempt to maximize their net resource gain by foraging more and more efficiently (Hamel & Côté, 2008) or resting more (Link et al., 2006) than their non-lactating conspecifics. In partial support of our first hypothesis about the divergence in activity patterns among elephants of different reproductive condition, we observed a significantly greater investment in foraging time among resource-stressed lactating



females, compared with non-lactating individuals. However, we cannot confirm that time spent foraging equated to the amount of forage consumed. In addition, previous research has shown that to achieve greater reproductive success, lactating mothers should invest more in their male offspring (Trivers & Willard, 1973; Clutton-Brock et al., 1989) than female offspring (Campagne et al., 1991; Koskela et al., 2009), particularly in species where males are the dispersing sex and their potential reproductive success, compared with that of female offspring, depends more heavily on the quality of nursing received as calves (Zebu cattle (*Bos indicus*), Reinhardt & Reinhardt, 1981; red deer (*Cervus elaphus*), Kruuk et al., 1999). The amount and quality of milk needed for successful weaning of males creates a resource challenge (Cassinello, 1996; Savalli & Fox, 1999; Hollister-Smith et al., 2007), and, unlike mothers of females, mother of males often compensate for that challenge with increased foraging time (Sheldon & West, 2004). Informed by these findings, in our first prediction we expected mothers of males to forage and nurse for longer time than mother of females. As predicted, mothers of males spent significantly more time nursing, but instead of compensating for it with foraging, they dedicated significantly more time to resting than mothers of females. We do not know if this equated to more milk for calves because we could not determine true intake success and rates of comfort suckling incidences (which may yield no milk). Surprisingly, even though Lee & Moss (1986) reported that male calves nurse for a longer duration and more often than female calves, mothers of female calves in our study spent significantly more time foraging than mothers of male calves. Because mothers of males may have compensated for resources lost during nursing only through rest and not increased foraging or drinking, their resource needs may not have been much greater compared to those of mothers nursing female calves. However, we do not know if year-round access to quality vegetation and water in AENP, unlike in other well studied habitats with prolonged dry seasons, such as Amboseli National Park, Kenya (Altmann et al., 2004; Western, 2007), has contributed to this interesting finding.

In group living animals, changes in activity patterns, such as the allocation of time to foraging or resting, by females of different ages and reproductive conditions can influence their social dynamics (Bednekoff, 1996; Sterck et al., 1997). In some species individuals with the greatest resource needs are most inclined to aggressively compete over a given resource (black-tailed prairie dog (*Cynomys ludovicianus*), Hoogland, 1995); whereas, in other

species resource-stressed individuals avoid aggressive competition, submit to their conspecifics, and wait for shared resources (owl monkeys (*Aotus* spp.), Wolovich et al., 2008). This type of impact was the basis for our second hypothesis on the divergence in rates of social or chemosensory behaviours among females with different resource needs. The majority of aggressive behaviours recorded were of the subtle, non-contact form (e.g., displace or supplant); while overt, contact forms of aggression (e.g., kick) were rare. In partial support of this hypothesis, we found that older and lactating females at AENP were significantly more likely to behave aggressively and less likely to exhibit non-aggressive and chemosensory behaviours than younger and non-lactating individual. Contrary to our expectation, mothers nursing male and female calves did not differ in their propensity to display social or chemosensory behaviours. Although the differences in social and chemosensory behaviours among females of different age and lactational status in AENP were statistically significant, their biological meaning would not be substantive without considering the species' sociality and its ecological habitat. Female elephants have well-resolved linear dominance hierarchies, where older, larger individuals are dominant and more socially experienced than smaller or younger conspecifics (Robbins et al., 2005; Archie et al., 2006a). Therefore, instead of being solely driven by resource needs, their social and chemosensory behaviours may have, in part, resulted from their competitive abilities (Archie et al., 2006a; McComb et al., 2011). However, an increased propensity for aggression among lactating females (regardless of whether they had male or female calves) may still have been driven by elevated resource needs (Koskela et al., 2009). In addition, given the fission-fusion nature of elephant society, socially disadvantaged individuals, subject to frequent, overt aggression, are free to leave the family and search for resources independently. Yet, elephant families rely on all group members for cooperative defence, finding resources (McComb et al., 2011), and rearing of calves (Lee, 1987), so overt aggression by dominant individuals would not be an evolutionarily stable strategy. Instead, competitively disadvantaged subordinate females remain within a family and buffer the effects of aggression by affiliative interactions, which favour resource sharing (McComb et al., 2001).

Whenever social interactions take place within aggregations of multiple kinship groups, even within a population of genetic kin (Whitehouse, 2001), the frequency of aggressive interactions may increase (Archie et al., 2006b);

therefore, some aggressive interactions we recorded may have been triggered by the presence of other kinship groups (Esposito, 2008). Moreover, the fact that most of our data were collected at waterholes, which are points of shared resource (where elephant compete not for access to water but for access to cleanest water; Valiex et al., 2007), may have resulted in minimally elevated rates of costly aggression.

African savannah elephant life history and cognitive advancement shape a dynamic where the costs of injury during a challenge generally outweigh its benefits (Douglas-Hamilton, 1972; Povinelli, 1989; Wittemyer et al., 2007; Byrne et al., 2008). Therefore, the outward displays of aggression should be less apparent among female elephants than they are in species with despotic or nepotistic dominance relationships (Mooring et al., 2006; Wolf et al., 2007). Instead, due to social structure of elephant families, individual fitness of older (experienced) and more dominant females, regardless of their reproductive condition, indirectly benefits the fitness of all closely related females, lactating or otherwise (Douglas-Hamilton, 1972; Archie et al., 2006b). Therefore, it is more difficult to determine to what extent specific phenotypic and environmental factors influence individual behavioural patterns. According to the classical life-history model, age-dependent reproductive investment is common in species with predictable lifespans (Stearns, 1992; Cotter et al., 2010). This model predicts that individuals should exhibit increased investment in reproduction until shortly before death (Lindeque, 1988). As a long-lived species with few predators and rather predictable lifespans, ageing female elephants exhibit this pattern of increased reproductive investment until relatively late in life (Ward et al., 2009) when they become reproductively senescent and switch to kin-directed helping behaviours, such as allomothering (Packer et al., 1998; Freeman et al., 2013). In turn, this schedule of reproduction (by investing either in direct or indirect fitness) is known as state-dependent reproductive investment (Cotter et al., 2010). Therefore, the variance in behavioural patterns observed in female elephants at AENP may have been affected by the advantages and constraints of both their age and reproductive condition. Lastly, due to their life-long cooperative interactions, sharing of ecological knowledge, and allocare (frequently provisioned by juvenile or subadult female offspring), elephant mothers may be the odd herbivore by investing differently but equivalently in male and female calves (Lee, 1987). Unlike many studies that examine behavioural patterns in contexts directly related to survival or starvation

avoidance, we show how these patterns differed with the resource demands of age or reproductive condition in a highly social mammal, living in an environment where available resources were not limiting. An interesting future research avenue, and one that may help further tease apart the relative importance of reproductive condition in a species with age-determined dominance hierarchy, is to investigate if behavioural patterns considered in our study will vary in similarly aged females with known behavioural tendencies (Dall et al., 2004; Luttbeg & Sih, 2010; Lee & Moss, 2012).

### **Acknowledgements**

We are grateful for financial support from Western Kentucky University's Graduate Studies and Ogden College of Science and Engineering, from George Mason University and from the NSF BREAD program (Award 0965445 to Drs. Michael Stokes and B.A. Schulte). Many people contributed their constructive comments from the initial to the final moments of writing this manuscript. Particularly we acknowledge the members of Maggie Wisniewska's Masters Graduate Advisory Committee, Drs. Cheryl D. Davis, M. Stokes, Jarrett R. Johnson and Michael Collyer. We thank Margaret R. Hook and Jordana M. Meyer for their contribution to data collection, and past graduate students of B.A. Schulte who have worked with the AENP elephants and helped to maintain the family trees. We also appreciate the collaboration on the study of elephants of AENP with Dr. Graham Kerley, at Nelson Mandela Metropolitan University, and past researchers at this institution, Drs Anna Whitehouse and Katie Gough. We are especially appreciative of the assistance by John Adendorff at AENP. This research had been approved by Western Kentucky University's Institutional Animal Care and Use Committee (Welfare Assurance No. A3558-01A) and by South African National Parks (SANParks permit No. SCHBA669).

### **References**

- Altmann, J. (1974). Observational study of behaviour: sampling methods. — *Behaviour* 94: 227-267.
- Altmann, J. (1986). Parent-offspring interactions in the Anthropoid primates: an evolutionary perspective. — In: *Evolution of behavior: paleontological and field approaches* (Nitecki, M.H. & Kitchell, J.A., eds). Oxford University Press, Oxford.
- Altmann, J., Alberts, S.C., Altmann, S.A. & Roy, S.B. (2004). Dramatic changes in local climate patterns in the Amboseli basin, Kenya. — *Afr. J. Ecol.* 40: 248-251.

- Archie, E.A., Morrison, T.A., Foley, C.A.H., Moss, C.J. & Alberts, S.C. (2006a). Dominance rank relationships among wild female African elephants, *Loxodonta africana*. — Anim. Behav. 71: 117-127.
- Archie, E.A., Moss, C.J. & Alberts, S.C. (2006b). The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. — Proc. Roy. Soc. Lond. B: Biol. Sci. 273: 513-522.
- Atkinson, W.D. & Shorrocks, B. (1981). Competition on a divided and ephemeral resource: simulated model. — J. Anim. Ecol. 50: 461-471.
- Bartošová, J., Komárková, M., Dubcová, J., Bartoš, L. & Pluháček, J. (2011). Concurrent lactation and pregnancy: pregnant domestic horse mares do not increase mother–offspring conflict during intensive lactation. — PLoS ONE 6: e22068.
- Beauchamp, G. (1999). The evolution of communal roosting in birds: origin and secondary losses. — Behav. Ecol. 10: 675-687.
- Bebié, N. & McElligott, A.G. (2006). Female aggression in red deer: does it indicate competition for mates? — Mammal. Biol. 71: 347-355.
- Bednekoff, P.A. (1996). Risk-sensitive foraging, fitness, and life histories: where does reproduction fit into the big picture? — Am. Zool. 36: 471-483.
- Berger, J. (1977). Organizational systems and dominance in feral horses in the Grand Canyon. — Behav. Ecol. Sociobiol. 2: 131-146.
- Byrnes, R., Lee, P.C., Njiraini, N., Poole, J.H., Sayialel, K., Sayialel, S., Moss, C.J. & Byrnes, R.W. (2008). Do elephants show empathy? — J. Consciousness Stud. 15: 204-225.
- Campagne, C., Le Boeuf, B.J., Lewis, M. & Bisioli, C. (1991). Equal investment in male and female offspring in southern elephant seals. — J. Zool. Soc. Lond. 226: 551-561.
- Caraco, T. (1981). Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). — Behav. Ecol. Sociobiol. 8: 213-217.
- Cassinello, J. (1996). High-ranking females bias their investment in favour of male calves in captive *Ammotragus lervia*. — Behav. Ecol. Sociobiol. 38: 417-424.
- Clutton-Brock, T.H. & Lukas, D. (2011). The evolution of social philopatry and dispersal in female mammals. — Mol. Ecol. 21: 472-492.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1989). Fitness costs of gestation and lactation in wild mammals. — Nature 337: 260-262.
- Conradt, L. & Roper, T.J. (2003). Group decision-making in animals. — Nature 421: 155-157.
- Cotter, S.C., Ward, R.J.S. & Kilner, M.R. (2010). Age-specific reproductive investment in female burying beetles: independent effects of state and risk of death. — Funct. Ecol. 25: 652-660.
- Dall, S.R.X., Houston, A.I. & McNamara, J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. — Ecol. Lett. 7: 734-739.
- de Vries, H., Stevens, J.M.G. & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. — Anim. Behav. 71: 589-592.
- Douglas-Hamilton, I. (1972). On the ecology and behaviour of the African elephant. — PhD thesis, University of Oxford, Oxford.

- du Toit, J.T. & Yetman, C.A. (2005). Effects of body size on the diurnal activity budgets of African browsing ruminants. — *Oecologia* 143: 317-325.
- Dunbar, R.I. & Dunbar, P. (1988). Maternal time budgets of gelada baboons. — *Anim. Behav.* 36: 970-980.
- Duncan, P. (1980). Time-budgets of Camargue horses II. Time budgets of adult horses and weaned sub-adults. — *Behaviour* 72: 26-49.
- Esposito, R.M.M. (2008). The effect of matriarchs on group interactions, kinship fitness, and differences in chemosensory behavior of African elephants (*Loxodonta africana*). — Electronic theses and dissertations, paper 716, MSc thesis, Georgia Southern University, Statesboro, GA.
- Fawcett, T.W. & Johnstone, R.A. (2010). Learning your own strength: winner and loser effects should change with age and experience. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 277: 1427-1434.
- Fayrer-Hosken, R.A., Grobler, D., van Altena, J.J., Bertschinger, H.J. & Kirkpatrick, J.F. (2001). African elephants and contraception. — *Nature* 411: 766.
- Ferrari, M.C.O., Sih, A. & Chivers, D.P. (2009). The paradox of risk allocation: a review and prospectus. — *Anim. Behav.* 78: 579-585.
- Fischhoff, I.R., Sundaresan, S.R., Cordingle, J., Larkin, H.M., Sellier, J.J. & Rubenstein, D.I. (2007). Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus bruchellii*. — *Anim. Behav.* 73: 825-831.
- Freeman, E.W., Meyer, J.M., Putman, S., Schulte, B.A. & Brown, J.L. (2013). Ovarian cycle activity varies with respect to age and social status in free-ranging elephants in Addo Elephant National Park, South Africa. — *Conserv. Physiol.* 1: DOI:10.1093/conphys/cot025.
- Ginnett, T.F. & Demment, M.W. (1997). Sex differences in giraffe foraging behavior at two spatial scales. — *Oecologia* 110: 291-300.
- Gittleman, J.I. & Thompson, S.D. (1988). Energy allocation in mammalian reproduction. — *Am. Zool.* 28: 863-875.
- Gobush, K.S., Mutayoba, B.M. & Wasser, S.K. (2008). Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female African elephants. — *Conserv. Biol.* 22: 1590-1599.
- Goodman, M.J., Griffin, P.B., Estioko-Griffin, A.A. & Grove, J.S. (1985). The compatibility of hunting and mothering among the Agta hunter-gatherers of the Philippines. — *Sex Roles* 12: 1199-1209.
- Gough, K.F. & Kerley, G.I.H. (2006). Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: is there evidence of density dependent regulation? — *Oryx* 40: 434-441.
- Hahn-Holbrook, J., Holt-Lunstad, J., Holbrook, C., Coyne, S.M. & Lawson, E.E. (2011). Maternal defense: breast feeding increases aggression by reducing stress. — *Psychol. Sci.* 22: 1288-1295.
- Hamel, S. & Côté, S. (2008). Trade-offs in activity budget in an alpine ungulate: contrasting lactating and non-lactating females. — *Anim. Behav.* 75: 217-227.
- Harcourt, A.H. (1989). Environment, competition, and reproductive performance of female monkeys. — *Trends Ecol. Evol.* 4: 101-105.

- Hennemann, W.W. (1983). Relationship among body mass, metabolic rate and intrinsic rate of natural increase in mammals. — *Oecologia* 56: 104–108.
- Hollister-Smith, J.A., Poole, J.H., Archie, E.A., Vance, E.A., Georgiadis, N.J., Moss, C.J. & Alberts, S.C. (2007). Age, musth and paternity success in wild male African elephants, *Loxodonta africana*. — *Anim. Behav.* 74: 287–296.
- Hoogland, J.L. (1995). The black-tailed prairie dog: social life of a burrowing mammal. — University of Chicago Press, Chicago, IL.
- Illius, A.W., Tolkamp, B.J. & Yearsley, J. (2002). The evolution of the control of food intake. — *Proc. Nutr. Soc.* 61: 465–472.
- Kacelnik, A. & Bateson, M. (1996). Risky theories — the effects of variance on foraging decisions. — *Am. Zool.* 36: 402–434.
- Kaighoadi, F. & Stevens, J.R. (2013). Does fertility status influence impulsivity and risk taking in human females? Adaptive influences on intertemporal choice and risky decision making. — *Evol. Psychol.* 11: 700–717.
- King, A.J. & Cowlishaw, G. (2001). All together now: behavioural synchrony in baboons. — *Anim. Behav.* 79: 1381–1387.
- Kojola, I. & Helle, T. (1994). Offspring sex ratio adjustment in reindeer, *Rangifer tarandus*. — *Ann. Zool. Fenn.* 31: 405–410.
- Koskela, E., Mappes, T., Niskanen, T. & Rutkowska, J. (2009). Maternal investment in relation to sex ratio and offspring number in a small mammal—a case for Trivers and Willard theory? — *J. Anim. Ecol.* 78: 1007–1014.
- Kruuk, L.E.B., Clutton-Brock, T.H., Rose, K.E. & Guinness, F.E. (1999). Early determinants of lifetime reproductive success differ between the sexes in red deer. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 266: 1655–1661.
- Landete-Castillejos, T., García, A.J., López-Serrano, F.R. & Gallego, L. (2005). Maternal quality and differences in milk production and composition for male and female Iberian red deer calves (*Cervus elaphus hispanicus*). — *Behav. Ecol. Sociobiol.* 57: 267–274.
- Lee, P.C. (1987). Allomothering among African elephants. — *Anim. Behav.* 35: 278–291.
- Lee, P.C. & Moss, C.J. (1986). Early maternal investment in male and female African elephant calves. — *Behav. Ecol. Sociobiol.* 18: 353–361.
- Lee, P.C. & Moss, C.J. (1995). Statural growth in known-age African elephants (*Loxodonta africana*). — *J. Zool.* 236: 29–41.
- Lee, P.C. & Moss, C.J. (2012). Wild female African elephants (*Loxodonta africana*) exhibit personality traits of leadership and social integration. — *J. Comp. Psychol.* 126: 224–232.
- Lindeque, M. (1988). Population dynamics of elephants in Etosha National Park, S.W.A./Namibia. — PhD thesis, University of Stellenbosch.
- Link, A., Palma, A.C., Velez, A. & de Luna, A.G. (2006). Cost of twins in free-ranging white-bellied spider monkeys (*Ateles belzebuth belzebuth*) at Tinigua National Park, Colombia. — *Primates* 47: 131–139.
- Loizi, H., Goodwin, T., Rasmussen, L.E.L., Whitehouse, A.M. & Schulte, B.A. (2009). Sexual dimorphism in the performance of chemosensory investigatory behaviours by African elephants (*Loxodonta africana*). — *Behaviour* 146: 373–392.

- Luttbeg, B. & Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. — *Phil. Trans. R. Soc. B.* 365: 3977-3990.
- McComb, K., Moss, C., Durant, S.M., Baker, L. & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. — *Science* 292: 491-494.
- McComb, K., Shannon, G., Durant, S.M., Sayialel, K., Slotow, R., Poole, J. & Moss, C. (2011). Leadership in elephants: the adaptive value of age. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 278: 3270-3276.
- Mellish, J.E., Iverson, S.J. & Bowen, S.W. (2000). Metabolic compensation during high energy output in fasting, lactating grey seals (*Halichoerus grypus*): metabolic ceilings revisited. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 267: 1245-1251.
- Merte, C.E. (2006). Age effects on social and investigative behaviors in a closed population of African elephants. — *Electronic theses & dissertations*, paper 709, MSc thesis, Georgia Southern University, Statesboro, GA.
- Merte, C.E., Goodwin, T.E. & Schulte, B.A. (2010). Male and female developmental differences in chemosensory investigations by African elephants (*Loxodonta africana*) approaching waterholes. — *Behav. Ecol. Sociobiol.* 64: 401-408.
- Mooring, M.S., Patton, M., Lance, V.A., Hall, B.M., Schaad, E.W., Fetter, G.A., Fortin, S.S. & McPeak, K.M. (2006). Glucocorticoids of bison bulls in relation to social status. — *Horm. Behav.* 49: 369-375.
- Moss, C.J. & Poole, J.H. (1983). Relationships and social structure of African elephants. — In: *Primate social relationships: an integrated approach* (Hinde, R.A., ed.). Blackwell Scientific, Oxford, p. 315-325.
- Murray, C.M., Lonsdorf, E.V., Eberly, L.E. & Pusey, A. (2012). The energetics of lactation and the return to fecundity in wild chimpanzees. — *Behav. Ecol.* 6: 1234-1241.
- Neuhaus, P. & Ruckstuhl, K.E. (2002). Foraging behaviour in Alpine ibex (*Capra ibex*): consequences of reproductive status, body size, age and sex. — *Ethol. Ecol. Evol.* 14: 373-381.
- Packer, C., Tatar, M. & Collins, A. (1998). Reproductive cessation in female mammals. — *Nature* 392: 807-811.
- Pelletier, F. & Festa-Bianchet, M. (2004). Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis canadensis*. — *Behav. Ecol. Sociobiol.* 56: 546-551.
- Pérez-Barbería, F.J. & Nores, C. (1994). Seasonal variation in group size of Cantabrian chamois in relation to escape terrain and food. — *Acta Theriol.* 39: 295-305.
- Povinelli, D.J. (1989). Failure to find self-recognition in Asian elephants in contrast to their use of mirror cues to discover hidden food. — *J. Comp. Psychol.* 103: 122-131.
- Prentice, A.M. & Prentice, A. (1988). Energy cost of lactation. — *Annu. Rev. Nutr.* 8: 63-79.
- Rasmussen, L.E.L., Riddle, H.S. & Krishnamurthy, V. (2002). Mellifluous matures to malodorous in musth. — *Nature* 415: 975-976.
- Reinhardt, V. & Reinhardt, A. (1981). Natural suckling performance and age of weaning in Zebu cattle (*Bos indicus*). — *J. Agr. Sci.* 96: 309-312.



- Robbins, M.M., Robbins, A.M., Gerald-Steklis, N. & Steklis, H.D. (2005). Long-term dominance relationships in female mountain gorillas: strength, stability and determinants of rank. — Behaviour 142: 779-809.
- Ruckstuhl, K.E. & Festa-Bianchet, M. (1998). Do reproductive status and lamb gender affect the foraging behavior of bighorn ewes? — Ethology 104: 941-954.
- Sato, D. & Nagayama, R. (2011). Development of agonistic encounters in dominance hierarchy formation in juvenile crayfish. — J. Exp. Biol. 215: 1210-1217.
- Savalli, U.M. & Fox, C.W. (1999). The effect of male size, age, and mating behaviour on sexual selection in the seed beetle *Callosobruchus maculatus*. — Ethol. Ecol. Evol. 11: 49-60.
- Schulte, B.A. & Rasmussen, L.E.L. (1999). Signal–receiver interplay in the communication of male condition by Asian elephants. — Anim. Behav. 57: 1265-1274.
- Shannon, G., Page, B.R., Mackey, R.L., Duffy, K.J. & Slotow, R. (2008). Activity budgets and sexual segregation in African elephants (*Loxodonta africana*). — J. Mammal. 89: 467-476.
- Sheldon, B.C. & West, S.A. (2004). Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. — Am. Nat. 163: 40-54.
- Slade-Cain, B.E., Schulte, B.A. & Rasmussen, L.E.L. (2008). Estrous state influences on investigative, aggressive and tail flicking behavior in captive female Asian elephants. — Zoo Biol. 27: 167-180.
- Stearns, S.C. (1992). The evolution of life histories. — Oxford University Press, Oxford.
- Sterck, E.H.M., Watts, D.P. & van Schaik, C.P. (1997). The evolution of female social relationships in nonhuman primates. — Behav. Ecol. Sociobiol. 41: 291-309.
- Thouless, C.R. (1990). Feeding competition between grazing red deer hinds. — Anim. Behav. 40: 105-111.
- Trivers, R.L. & Willard, D.E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. — Science 179: 90-92.
- Valiex, M., Chaille-Jamme, S. & Fritz, H. (2007). Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. — Oecologia 153: 739-748.
- Vance, R.R. (1992). Optimal somatic growth and reproduction in a limited, constant environment: the general case. — J. Theor. Biol. 157: 51-70.
- Vervaecke, H., Stevens, J.M.G., Vandemoortele, H., Sigurjónsdóttir, H. & de Vries, H. (2007). Aggression and dominance in matched groups of subadult Icelandic horses (*Equus caballus*). — J. Ethol. 25: 239-248.
- Ward, E.J., Parsons, K., Holmes, E.E., Balcomb, K.C. & Ford, J.K.B. (2009). The role of menopause and reproductive senescence in a long-lived social mammals. — Front. Zool. 6: 4.
- Watanuki, Y. & Nakayama, Y. (1993). Age difference in activity pattern of Japanese monkeys: effects of temperature, snow, and diet. — Primates 34: 419-430.
- Western, D. (2007). A half of a century of habitat change in Amboseli National Park, Kenya. — Afr. J. Ecol. 45: 302-310.

- White, K.S. & Berger, J. (2001). Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity. — *Can. J. Zool.* 79: 2055-2062.
- Whitehouse, A.M. (2001). The Addo elephants: conservation biology of a small closed population. — PhD thesis, University of Port Elizabeth, Port Elizabeth.
- Whitehouse, A.M. & Hall-Martin, A.J. (2000). Elephants in Addo Elephant National Park, South Africa: reconstruction of the population's history. — *Oryx* 34: 46-55.
- Wisniewska, M. (2011). Factors influencing travel order as proxy for leadership & trade-offs in activity budgets in lactating & non-lactating African savanna elephants. — MSc thesis, Western Kentucky University, Bowling Green, OH, available online at <http://digitalcommons.wku.edu/theses/1121>.
- Wittemyer, G. & Getz, W.M. (2007). Hierarchical dominance structure and social organization in African elephants. — *Horm. Behav.* 51: 346-354.
- Wittemyer, G., Daballen, D., Rasmussen, H., Kahindi, O. & Douglas-Hamilton, I. (2005). Demographic status of elephants in the Samburu and Buffalo Springs National Reserves, Kenya. — *Afr. J. Ecol.* 43: 44-47.
- Wittemyer, G., Getz, W.M., Vollrath, F. & Douglas-Hamilton, I. (2007). Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. — *Behav. Ecol. Sociobiol.* 61: 1919-1931.
- Wolf, M., von Doorn, G.S., Leimar, O. & Weissing, F.J. (2007). Life-history trade-offs favour the evolution of animal personalities. — *Nature* 447: 581-585.
- Wolovich, K.C., Evans, S. & French, J.A. (2008). Dads do not pay for sex but do buy the milk: food sharing and reproduction in owl monkeys (*Aotus* spp.). — *Anim. Behav.* 75: 1155-1163.
- Zuberbuhler, K., Noe, R. & Seyfarth, R.M. (1997). Diana monkey long distance calls: messages for conspecifics and predators. — *Anim. Behav.* 53: 589-604.