

ACTIVITY BUDGETS AND SEXUAL SEGREGATION IN AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*)

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The activity budget hypothesis is 1 of 4 main hypotheses proposed to explain sexual segregation by large herbivores. Because of their smaller body size, females are predicted to have higher mass-specific energy requirements and lower digestive efficiency than males. As a result, females are expected to forage longer to satisfy their nutritional demands. Maintaining the cohesion of a mixed-sex group with differing activity budgets and asynchronous behavioral patterns is increasingly difficult, ultimately leading to spatial segregation of males and females. We tested this hypothesis using data (2002–2005) from 3 distinct populations of African elephants (*Loxodonta africana*), a species that exhibits marked sexual segregation. Group and individual behaviors were assessed at discrete points in time throughout the day, with a minimum of 10 min between consecutive records. Focal samples of individual male and female elephants also were recorded, with behavioral data logged every minute for 15 min. Data were grouped into 5 behavioral categories: drinking, resting, walking, feeding, and other. Neither activity rhythms nor feeding time varied significantly between the sexes and behavioral patterns were very similar. We propose that social and environmental factors influence behavioral rhythms to a greater extent than does body size, whereas increasing feeding time is only 1 method by which elephants can improve nutritional return. This is especially pertinent when considering their generalist foraging approach, substantial energy demands, and hindgut fermentation. We conclude that the activity budget hypothesis is unlikely to be the causal mechanism in the sexual segregation of African elephants, a finding that concurs with recent experimental and field research on a range of sexually dimorphic herbivores.

Key words: allometry, behavioral synchrony, body size, foraging, large herbivore

Sexual dimorphism is commonly observed in ungulates and is believed to have evolved because of competition for females in polygynous breeding systems (Clutton-Brock and Harvey 1978; Loison et al. 1999; Weckerley 1998). Larger males are conferred an advantage and therefore achieve greater reproductive success (McElligott et al. 2001; Pérez-Barbería and Gordon 1998). Females on the other hand are not exposed to the same selection pressure and direct energy into reproduction rather than growth (Le Blanc et al. 2001).

Ungulate species that are sexually dimorphic generally segregate into male and female groups outside of the breeding season (Ruckstuhl and Neuhaus 2002). Sexual segregation is further classified into social segregation (the formation of separate social groups on the basis of sex), habitat segregation (differential habitat use by the sexes), diet segregation (differ-

ential dietary preferences of the sexes), and spatial segregation (differential space use by the sexes—Conradt 1998; Mysterud 2000).

It is important to make a distinction between ecological (both habitat and diet segregation) and social segregation, because it is possible for groups to be socially segregated yet exhibit no habitat or dietary segregation (Conradt 1999, 2005). It is also likely that the causes and consequences differ significantly between social and ecological segregation, a subject much debated over the past decade (Bowyer and Kie 2004; Conradt 1999; Loe et al. 2006; Main 1996; Mysterud 2000). Furthermore, the extent of spatial segregation is species-specific and closely related to the scale of observation. For example, using the incorrect temporal scale may result in the occurrence of sexual segregation being underestimated or missed altogether (Bowyer 2004). Greater understanding of the mechanisms driving sexual segregation is important for the effective management of sexually dimorphic species (Bowyer 2004) and in furthering knowledge regarding the evolution of sociality (Pérez-Barbería et al. 2005).

Four broad hypotheses have been proposed to explain sexual segregation (Main et al. 1996; Ruckstuhl and Neuhaus 2000,

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2002). The reproductive strategy hypothesis proposes that females invest heavily in the survival of their offspring and will primarily select habitats that provide protection and safety (e.g., from predators) even if this requires a trade-off in nutritional return (Conradt 2005; Main et al. 1996). Males on the other hand are less sensitive to risk and will select habitats on the basis of forage availability, maximizing both their fitness and body size, which are directly related to reproductive success (Corti and Shackleton 2002). The forage selection hypothesis proposes that diet and habitat selection are predicted to vary between the 2 sexes as a result of the relationship between allometry, energy requirements, and foraging efficiency (Ruckstuhl and Neuhaus 2000; Stokke and du Toit 2000). The social factors hypothesis proposes that groups of the same sex are formed on the basis of shared behavior and social affinity (Bon and Campan 1996; Pérez-Barbería et al. 2005). For example, young males often group together and practice sparring; this behavior establishes dominance hierarchies that will be important when they compete for females in later life (Le Pendu et al. 2000; Ruckstuhl and Neuhaus 2000). The activity budget hypothesis proposes that allometric relationships predict smaller-bodied females will have higher relative energy requirements and lower digestive efficiency compared with adult males (Demment and Van Soest 1985; Stokke and du Toit 2000). As a result, females will need to forage longer to satisfy their nutritional demands, leading to divergent activity patterns between the sexes (Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000). Synchronizing behavior is likely to be an energetically expensive strategy when taking into account differing activity budgets. Therefore, mixed groups are expected to be less stable and more liable to segregate, whereas single-sex groups maintain their cohesion (Conradt 1998; Ruckstuhl 1999; Ruckstuhl and Kokko 2002; Ruckstuhl and Neuhaus 2001).

The 4 hypotheses are not mutually exclusive and sexual segregation may result from a combination of factors, especially when considering that ecological segregation will ultimately lead to social segregation (Conradt 2005; Neuhaus and Ruckstuhl 2004a). Moreover, the basic premise of all 4 hypotheses is based on differences in body size and reproductive strategies between the sexes.

The activity budget hypothesis is the most recently proposed hypothesis attempting to explain social segregation (Neuhaus and Ruckstuhl 2004b; Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000). However, it has garnered limited support (Conradt and Roper 2000; Mooring et al. 2003; Ruckstuhl and Neuhaus 2002; Yearsley and Pérez-Barbería 2005). The majority of studies have concentrated on temperate ruminants, including bighorn sheep (*Ovis canadensis*—Le Blanc et al. 2001; Mooring et al. 2003; Ruckstuhl 1998, 1999), ibex (*Capra ibex*—Ruckstuhl and Neuhaus 2001), mule deer (*Odocoileus hemionus*—Bowyer and Kie 2004), red deer (*Cervus elaphus*—Conradt 1998, 1999; Loe et al. 2006), and merino sheep (*Ovis aries*—Michelena et al. 2004). In this study, we investigate the influence of sexual dimorphism on both the activity budgets and behavioral rhythms of African elephants (*Loxodonta africana*). Elephants provide an interesting study

animal because they are large hindgut fermenters that exhibit pronounced body-size dimorphism (adult males weigh in excess of 6 metric tons, twice the weight of an adult female—Owen-Smith 1992) and divergent reproductive strategies. Previous research has shown that these sex differences play a significant role in the distinct foraging behavior of male and female elephants (Shannon et al. 2006a; Stokke and du Toit 2000).

Social segregation is a well-documented aspect of elephant ecology, with females and their young living in permanent bond-groups, whereas males (>15 years old) range independently or in loosely associated bachelor groups (Charif et al. 2005; Laws et al. 1975; Moss and Poole 1983). Because of the comparatively long intercalving period (3–5 years—Moss 2001; Owen-Smith 1992), elephants do not exhibit a defined mating season. Instead, adult males (>30 years of age) annually enter a state known as “musth” during which time they experience elevated androgen levels and associate with females in order to reproduce (Poole 1987, 1989). The musth period is highly variable but lasts on average 2–3 months of the year (Poole 1987). Younger males (<30 years of age) only enter musth for short periods of time because there is an established hierarchy dominated by the older and larger individuals (Poole 1994).

The objectives of this study were to establish whether adult male and female elephants exhibit significantly different activity budgets; to determine whether the behavior of elephants is sexually asynchronous with regard to timing and duration; to determine if there was a seasonal influence on the activity budgets of male and female elephants; and to investigate whether patterns exist across 3 distinct populations of elephants.

MATERIALS AND METHODS

Study sites.—The Pongola Game Reserve (PGR) is 82 km² in extent and is situated in northern Zululand, South Africa (27°54′–27°35′S, 32°01′–31°86′E). The climate is hot and arid with an annual rainfall of 400–700 mm. The vegetation falls into 3 of Acocks' (1988) veld types: Zululand thornveld, lowveld, and arid lowveld. Seven vegetation or habitat types are recognized (Shannon et al. 2006b). The eastern boundary of the reserve is formed by the Jozini dam. In addition to the dam, there are a number of pumped water points throughout the western section of the reserve. As of October 2004, PGR had 3 distinct groups of elephants, a large herd of 38, a smaller herd of 7 individuals, and 3 fully grown adult males.

Pilanesberg National Park (PNP) is situated in North West Province of South Africa and is 500 km² in extent (25°8′–25°22′S, 26°57′–27°13′E). It occupies the crater of an extinct volcano and is roughly circular with hilly relief. The average yearly rainfall is 630 mm, mainly falling in summer (November–April—Slotow and van Dyk 2001). Acocks (1988) recognizes the vegetation as sour bushveld. Pumped water points are distributed throughout the reserve, with 1 large central dam. During 1979–1998, 58 male and 37 female elephants were introduced. Fourteen of the males were culled

and a further 15 elephants died (Slotow and van Dyk 2001). In 1998, 6 adult males were introduced from Kruger National Park. The total population in 2004 was 158, comprising 34 adult males and 124 females and juveniles in 16 family groups (mean group size 8 ± 3 SD).

Phinda Private Game Reserve (PPGR) is 180 km² in extent and is situated in northern KwaZulu-Natal, South Africa (27°92'–27°68'S, 32°44'–32°20'E). The reserve experiences hot, wet summers and dry, cooler winters with an average annual rainfall of 750 mm. PPGR has a diverse range of habitats from the endemic sand forest to the sweet lowveld bushveld, Natal low bushveld, and the coastal bushveld of the savanna biome (Low and Rebelo 1996). A river runs through the southern section of PPGR and there are 6 dams distributed throughout the reserve. These dams are fed with water from boreholes during the dry season. Twenty-four males and 34 females were introduced during 1992–1994. In 2003, 37 elephants were translocated and 3 adult males were introduced from Kruger National Park. The total population of elephants in 2004 was 75, comprising 18 adult males and 21 adult females in 5 family groups (mean group size 11 ± 3 SD).

The degree of sexual segregation and frequency of association with males.—To establish the extent of sexual segregation observed in the study populations, the proportion of sightings where males associated with groups of females was calculated. In PGR, the males were observed with females $34\% \pm 11\%$ (SD) of the time, in PPGR the proportion was $43\% \pm 11\%$, whereas in PNP the value was $25\% \pm 11\%$. These association values were similar to those found across a range of populations both fenced and open (G. Shannon, in litt.). When they were not associating with females, males from all 3 study sites ranged either in loosely associated groups of 2 or more (48% of the time) or independently (52% of the time).

Data collection.—The activity data were collected from 18 males (PGR = 4, PPGR = 7, and PNP = 7) and 9 family groups (PGR = 2, PPGR = 3, and PNP = 4) over a 3-year period (March 2002–June 2005) between 0600 and 1800 h. Nighttime data were logistically difficult to collect and the small amount available for analysis was therefore excluded. Two distinct seasons were defined using annual rainfall data with summer commencing 10 days after >15 mm of rain in September–October, and winter beginning when there had been no significant rainfall (<15 mm for a 2-week period) after March 15. Elephants were located using either traditional tracking methods or radiotelemetry. The size of the group was noted along with the number of adult males and females. Adult females were defined as individuals with at least 1 calf, and adult males were defined as being >15 years old and ranging independently of the bond groups of females. However, it must be noted that there is significant size difference between a fully grown male (>30 years old) and a young male recently independent of the herd (approximately 15 years old). Therefore, for the purpose of this study we only collected data for males > 25 years of age, which exhibited distinct body size dimorphism when compared to adult females (mean ages of males: PNP = 32 years, PGR = 36 years, and PPGR = 33 years).

Two methods were employed to collect behavioral data, which adhered to the guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). The 1st involved coding the dominant behavior of individuals and groups of elephants observed at discreet points in time. Using data collected from 430 observations of feeding bouts (from both males and females) recorded over a 2-year period in PGR, we established that 90% were <10 min in duration. Therefore, because feeding is the primary behavior of elephants (Owen-Smith 1992), we concluded that 10 min was a suitable minimum interval for obtaining independent behavioral observations.

The dominant behavior was determined as the activity in which $\geq 55\%$ of the group was engaged. Because of the strong social bonds between family members (Charif et al. 2005), behavioral rhythms were well synchronized with $84\% \pm 6\%$ (SD) of the sightings of family groups exhibiting a dominant behavior (i.e., $\geq 55\%$ of the individuals were engaged in the same activity). Behavioral codes were recorded instantaneously and elephants that subsequently moved out of sight did not invalidate the previous data point, because each sighting was independent of the next. Mixed-group data were not collected because adult males generally only associated with groups of females during their musth period and had a limited influence on the behavior of the family group as a whole (G. Shannon, in litt.). Therefore, to elucidate whether sexual segregation was driven by differing activity budgets, only data from independent males and bachelor groups were compared with those from females and their young. Continual scan sampling has commonly been used to assess the activity budgets of large herbivores (Michelenia et al. 2004; Ruckstuhl 1998); however, the limitations imposed by the mobility of elephants and dense vegetation of the savanna resulted in discrete data points being the most effective form of data collection for group activity by elephants.

Data were initially compared on the basis of sex and season. Behavioral codes of all sightings were filtered into one of six 2-h time intervals, from 0600 to 1800 h. The proportion of time spent engaged in each of the 4 main behaviors (feeding, resting, walking, and drinking) was calculated for each family group or individual male elephant by dividing the number of occurrences of a particular behavior by the total number of sightings within that time period. All remaining behaviors were grouped together under the category of other. These behavioral data were then compiled across all the reserves and averaged for each sex and season.

The 2nd method of data collection involved sampling the behavior of individual elephants using 15-min focal observations. The behavior of the focal elephant was recorded every minute using the same behavioral codes as in the previous method. Fifteen minutes provided an optimal time period in which to sample behavior before the elephant moved out of sight. If more than 5 of the scheduled observations occurred when the animal was out of sight, the data were discarded. Repeated sampling of known individuals allowed us to explore the activity budgets of male and female elephants with greater detail.

Statistical analysis.—Analysis of variance (ANOVA) was used to compare the proportion of time that males and females

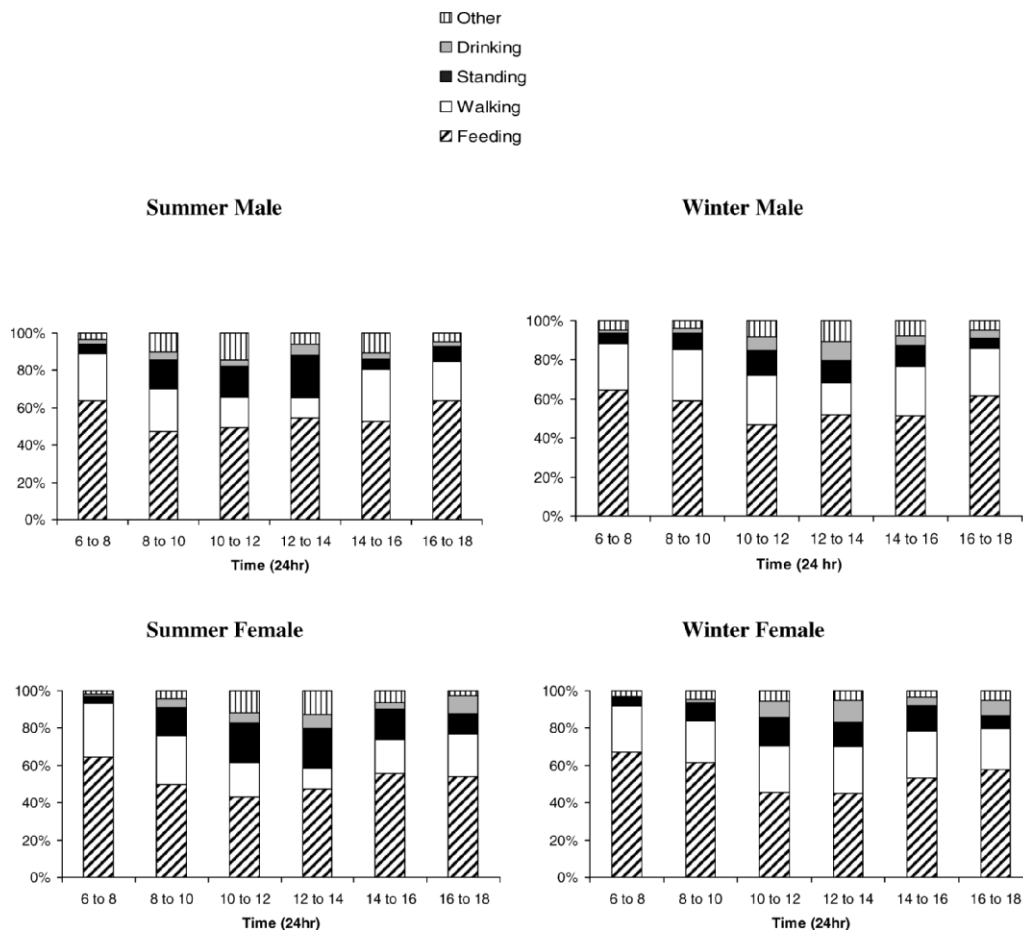


FIG. 1.—The seasonal activity budgets for male and female elephants (*Loxodonta africana*) from 0600 until 1800 h. Results are calculated by averaging the activity budgets for the 18 individual males and 9 groups of females across the 3 reserves.

dedicated to the 4 main behaviors during the 6 time categories (0600–0800 h, 0800–1000 h, etc.) with the data pooled for both seasons. The data were normalized using the arcsine square root transformation. Each of the 4 main behaviors was analyzed using ANOVA with the proportion of time for individual males or groups of females being used as a separate datum in the analysis. Additionally, reserve was included as a factor in the analysis to establish if behavioral differences occurred among the study sites. If this was the case, then the data from each reserve were analyzed separately; otherwise the data from the 3 reserves were pooled. The coefficient of variance also was calculated to account for intrasexual variation (especially pertinent for males because of the variability in body size) in each behavioral category.

The 15-min focal samples were used to examine the proportion of time that each sex devoted to feeding, in both the summer and winter seasons and across all 3 reserves. The initial analysis was done by calculating the proportion of feeding observations for all of the 15-min focal samples; this was completed for each sex, season, and reserve. The data could not be normalized, so a Kruskal–Wallis test was used to test the effects of reserve, season, and sex on the proportion of time spent feeding.

The final stage of the analysis involved using the mean proportion of time spent feeding for individual male and female

elephants. Because the mean proportion of time spent feeding was being examined, only elephants that had 3 or more 15-min observations were included in the analysis. Because of the small sample size of the PPGR data set ($n = 20$), only focal data from PGR and PNP were used. The average proportion of time spent feeding was calculated for each elephant using the results from their focal samples. These data were normalized using the arcsine square root transformation and an ANOVA was used to test for differences in the mean proportion of time spent feeding by male and female elephants. This method allowed differences to be accounted for on the basis of individual elephants rather than only distinguishing sex and season as in the previous analysis. An ANOVA of the coefficient of variance in foraging behavior also was carried out to determine the amount of variation within each sex.

RESULTS

Activity budgets.—The initial analysis of the activity budget data indicated that patterns were similar for both sexes throughout the year (Fig. 1), with reduced feeding and increased time spent resting toward the middle of the day. Seasonal differences were evident for both sexes with more time spent resting during the summer period, especially in the

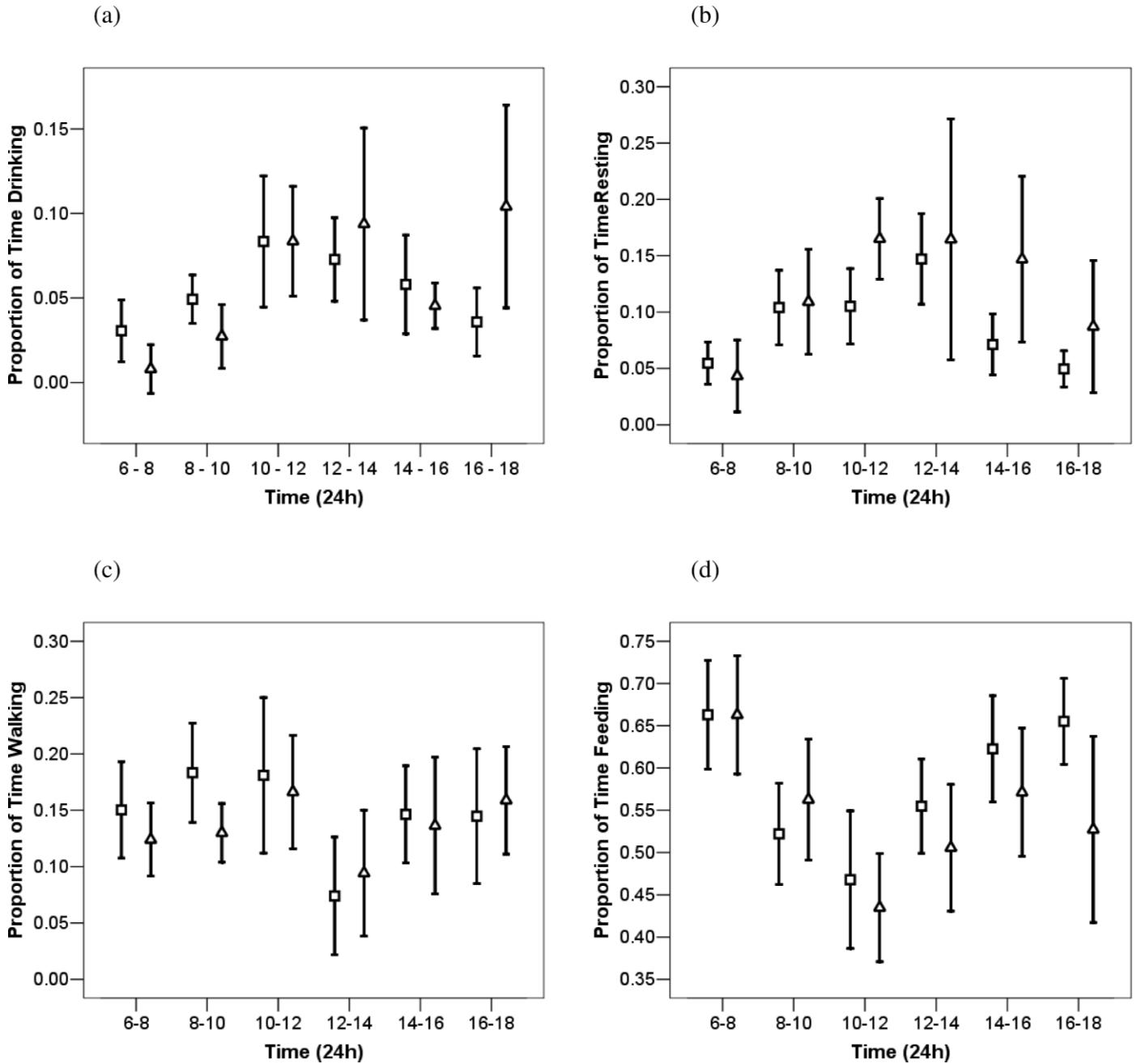


FIG. 2.—The proportion of time spent a) drinking, b) resting, c) walking, and d) feeding by both female (open triangles) and male (open squares) elephants (*Loxodonta africana*) between 0600 and 1800 h. Both sexes exhibited similar activity patterns throughout the day (data are mean \pm 95% confidence interval, $n = 18$ males and 9 females).

middle of the day ([mean \pm SD] 21% \pm 7% for females in summer and 23% \pm 8% for males in summer, compared with 13% \pm 3% for females in winter and 16% \pm 4% for males in winter). The proportion of time spent walking was relatively consistent throughout the day for males and females in winter (24% \pm 8% for females and 24% \pm 7% for males). In contrast, walking rates peaked in the early morning and late afternoon in summer. Midday periods in summer were associated with the highest incidence of other behavior, such as mud bathing.

Drinking.—Data for this analysis were pooled because there was no reserve effect ($F = 0.315$, $df. = 2, 120$, $P > 0.5$). There

was a significant difference in drinking times between the sexes ($F = 9.543$, $df. = 1, 120$, $P < 0.01$; Fig. 2a) and across time of day ($F = 5.692$, $df. = 5, 120$, $P < 0.001$), with males spending more time than females at water points (Fig. 2a). The sexes exhibited similar levels of variation in drinking behavior throughout the day, with an average coefficient of variance of 75% for males and 71% for females.

Resting.—No effect of reserve was noted ($F = 0.430$, $df. = 2, 126$, $P > 0.5$) and the data were pooled for analysis. There were no significant differences in resting patterns for male and female elephants ($F = 2.010$, $df. = 1, 126$, $P > 0.1$).

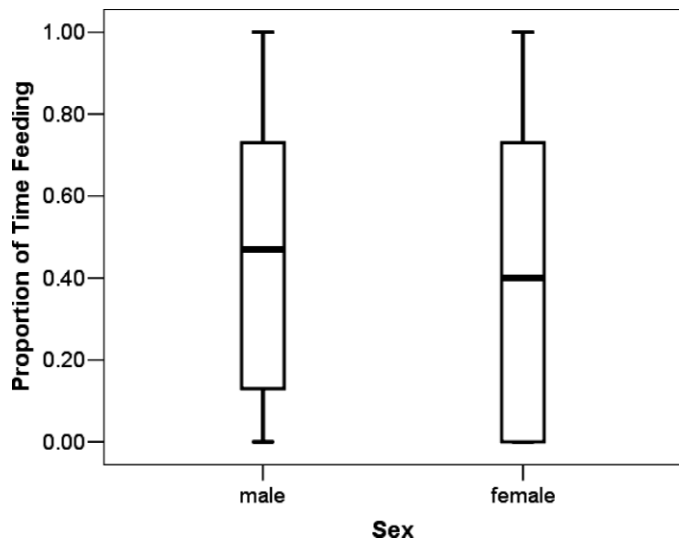


FIG. 3.—Proportion of time that male and female elephants (*Loxodonta africana*) spent feeding, based on analysis of all 15-min behavioral observations (data are presented as box and whisker plots, $n = 432$ observations of males and 256 observations of females).

The proportion of time spent resting increased until the middle of the day, after which levels dropped again (Fig. 2b). Levels of resting in the early morning and late afternoon were significantly lower than those at midday ($F = 6.202$, $d.f. = 5$, 126, $P < 0.001$). Males exhibited a relatively consistent level of variation throughout the day with an average coefficient of variance of 64%. Females exhibited very low variation during the 1000–1200 h time period, with a coefficient of variance of 28% compared to a daily average of 69%.

Walking.—The proportion of time spent walking was significantly different among reserves ($F = 9.999$, $d.f. = 2$, 126, $P < 0.001$) and walking data therefore were analyzed separately for each reserve. Both PNP ($F = 5.029$, $d.f. = 1$, 54, $P < 0.05$) and PPGR ($F = 6.118$, $d.f. = 1$, 54, $P < 0.05$) exhibited differences between the sexes, in contrast to PGR ($F = 0.476$, $d.f. = 1$, 18, $P > 0.25$). In PPGR, females tended to spend more time walking, whereas in PNP males spent more time walking. Females exhibited the least variation from one time period to the next with an average coefficient of variance of 47%, whereas males had an average of 54%. The combined data showed distinct patterns over the 12-h period (Fig. 2c).

Feeding.—Data on feeding were pooled across the 3 reserves because no effect of reserve was detected ($F = 1.580$, $d.f. = 1$, 126, $P > 0.2$). Males and females showed the greatest proportion of feeding per unit time between 0600 and 0800 h, followed by a reduction until early afternoon when the proportion of feeding increased once again (Fig. 2d). The relationship was matched for both sexes and there was no statistical difference across the 6 time periods ($F = 1.244$, $d.f. = 1$, 126, $P > 0.25$). There was a significant relationship between time of day and the proportion of time spent feeding ($F = 7.748$, $d.f. = 1$, 126, $P < 0.001$). Feeding had the lowest level of variation from one time period to the next out of all 4 of the

behaviors and for both sexes. Males had an average coefficient of variation of 22% compared to 18% for females.

Analysis of focal data.—There was no significant difference between the sexes in the proportion of time spent feeding (Kruskal–Wallis $\chi^2 = 2.014$, $d.f. = 1$, $P > 0.1$; Fig. 3), with means of 42% and 45% for females and males, respectively, when data on time budgets were pooled across the 3 reserves for all individuals. Data were analyzed per reserve to assess whether significant differences in the time spent feeding occurred within the 3 data sets. All of the reserves returned a nonsignificant result (PNP: $\chi^2 = 3.78$, $d.f. = 1$, $P = 0.052$; PPGR: $\chi^2 = 1.43$, $d.f. = 1$, $P > 0.7$; PGR: $\chi^2 = 1.03$, $d.f. = 1$, $P > 0.3$). The proportion of time spent feeding by males and females was not significantly different in either summer or winter (summer: $\chi^2 = 3.005$, $d.f. = 1$, $P > 0.05$; winter: $\chi^2 = 0.082$, $d.f. = 1$, $P > 0.5$).

Further analysis was carried out by calculating the feeding time budgets for individual male and female elephants in PNP and PGR (PPGR was excluded because of the limited sample size). Time budgets for feeding were significantly different between reserves ($F = 4.2$, $d.f. = 1$, 39, $P < 0.05$). However, the feeding time budgets were not significantly different between males and females in PGR ($F = 0.90$, $d.f. = 1$, 14, $P > 0.75$) or in PNP ($F = 3.78$, $d.f. = 1$, 32, $P > 0.05$; Fig. 4). The levels of variation in time spent feeding within the data sets also were compared. The coefficient of variation in feeding time of individuals was not different between reserves ($F = 0.80$, $d.f. = 1$, 39, $P > 0.35$), but there was a significant difference between the sexes ($F = 6.15$, $d.f. = 1$, 39, $P < 0.025$), with females having a greater coefficient of variation than males.

DISCUSSION

Although behavioral differences between male and female elephants did occur, our results indicated a broad similarity in the duration and patterns of behavior, which leads us to conclude that the activity budget hypothesis is not playing a significant role in the sexual segregation of elephants. This conclusion is all the more apparent when considering that the data come from 3 distinct populations of elephants.

Seasonal activity budgets.—Both sexes exhibited distinct peaks in feeding activity during the early morning and late afternoon, a pattern that was likely to be in response to atmospheric temperature, with the daily maximum (between midday and 1400 h) corresponding to the lowest activity period of the day. Similar activity patterns have been previously noted in elephants (Owen-Smith 1992) and a range of other African herbivores including white rhino (*Ceratotherium simum*—Owen-Smith 1992); giraffe, kudu, and impala (*Giraffa camelopardalis*, *Tragelaphus strepsiceros*, and *Aepyceros melampus*—du Toit and Yetman 2005; Owen-Smith 1998); and blesbok and wildebeest (*Damaliscus pygargus phillipsi* and *Connochaetes taurinus*—Twine 2002). The similarities in the seasonal activity budgets of male and female elephants suggest that thermoregulatory constraints outweigh the influence of body size and the associated physiological differ-

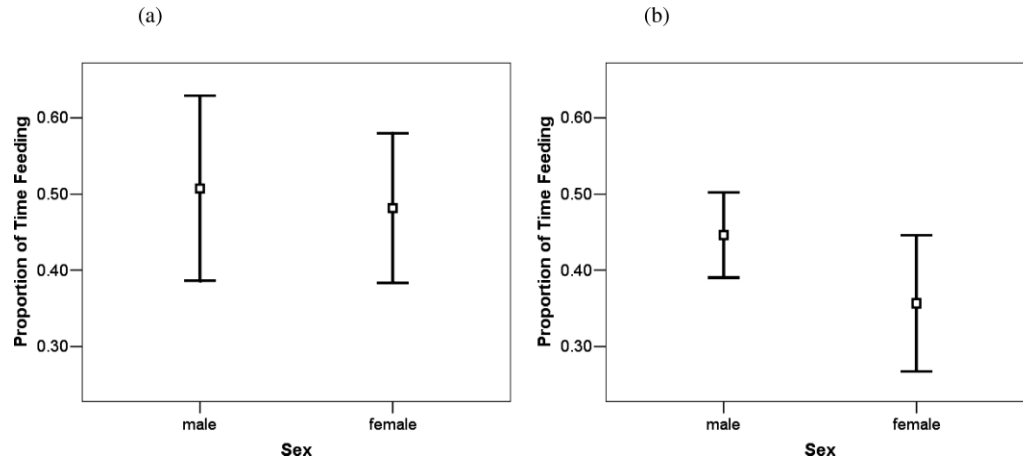


FIG. 4.—The proportion of time individual male and female elephants (*Loxodonta africana*) feed during the 15-min focal observations in a) Pongola Game Reserve (PGR) and b) Pilanesberg National Park (PNP) (data are mean \pm 95% confidence interval, $n = 4$ males and 12 females in PGR and 13 males and 12 females in PNP).

ences, particularly during the hot summer season (Jeschke and Tollrain 2005).

Feeding budgets.—There was no overall difference between sexes in the proportion of time spent feeding when the activity budget data were pooled, suggesting that foraging time is not playing a significant role in the social segregation of populations of elephants. However, the activity budgets of individual elephants in PNP did exhibit a trend for males to feed for longer times than females. Although the difference between sexes was not statistically significant, it is worth noting that previous research has shown that increasing body size of African herbivores is associated with an increase in the proportion of daily time spent feeding, because of physical differences in forage (e.g., spinescence) and increased handling time (Cooper and Owen-Smith 1986; du Toit and Yetman 2005; Mysterud 1998). The marked size disparity between male and female elephants may be significant enough for such an effect to be observed in PNP, which had the lowest status of the 3 reserves in terms of forage availability and quality (B. Page, University of KwaZulu-Natal, pers. comm.). In contrast, species of temperate herbivores exhibit reduced activity time with increasing body size (Mysterud 1998; Pelletier and Festa-Bianchet, 2004), further highlighting the role that environmental conditions and forage availability and quality play in dictating the length of daily foraging time (Owen-Smith 1998).

Behavioral rhythms.—The sexes exhibited similar patterns of behavior during the 12-h study periods and these appeared to be dictated by environmental conditions (e.g., atmospheric temperature) and the substantial energy demands that require both sexes to spend the majority of their time foraging (Owen-Smith 1992). The main differences were in the drinking patterns and the proportion of time spent walking by male and female elephants. The disparity in drinking behavior may occur because males do not experience the social constraints of living in family groups and are less sensitive to disturbance (e.g., tourism and predators) in areas around water points (G. Shannon, in litt.). Despite this, drinking only accounted for an average 6% of the 12-h study period, and therefore we suggest

that it is unlikely that a behavior of such short duration is driving sexual segregation. Walking behavior varied between the sexes within 2 of the reserves (PPGR and PNP). However, it is difficult to ascribe the variation to differences between sexes because in PPGR females spent a greater proportion of their time walking and in PNP the converse was true. Although this result may be an artifact of site-specific behavior, we suggest that greater attention is focused on movement rates because marked differences could ultimately lead to sexual segregation (Ruckstuhl 1998; Ruckstuhl and Kokko 2002), especially in open savanna systems where the ranging behavior of elephants is less restricted than in the comparatively small reserves of this study.

The activity budget hypothesis is based on the premise that the proportion of time spent feeding differs between the 2 sexes, leading to asynchronous behavioral patterns (Conradt 1998; Ruckstuhl 1999). The majority of research has been carried out on temperate grazers that concentrate on food sources similar in physical structure and nutritional return, including bighorn sheep (Ruckstuhl 1999), ibex (Ruckstuhl and Neuhaus 2001), red deer (Conradt and Roper 2000; Loe et al. 2006), and mule deer (Bowyer and Kie 2004). These species of herbivores are generally only able to increase their energy intake by faster bite rates, longer periods spent feeding, and, to a lesser extent, selection of higher-quality habitats (Shipley 1999). Therefore, sexually dimorphic ruminant grazers are predicted to segregate because males will rest and ruminate for longer periods, whereas females will continue to feed in order to satisfy their higher relative energy requirements. For example, male bighorn sheep fed for 39% of the time and females 53% of the time (Ruckstuhl 1998). Ultimately this is predicted to result in spatial and temporal segregation, even in homogeneous environments, because of differing activity budgets and asynchronous behavioral patterns (Conradt 1998; Conradt and Roper 2000; Ruckstuhl 1998; Ruckstuhl and Kokko 2002; Ruckstuhl and Neuhaus 2001).

Elephants, on the other hand, spend most of their time foraging and are not limited by the need to feed selectively or

remasticate ingesta like ruminants. Elephants also are faced with a much wider diversity of resources because of their catholic diets, generalist foraging approach (grazing and browsing), large size, and tolerance of fibrous plant parts (Laws et al. 1975; Owen-Smith 1992; Stokke 1999; Stokke and du Toit 2000). Therefore, increasing the time spent feeding is only 1 of several methods that can be employed by smaller-bodied females to increase their nutritional intake. Furthermore, foraging time is positively correlated with body size in African herbivores (du Toit and Yetman 2005; Mysterud 1998), which may negate differences in activity patterns that are based on allometric relationships. An alternative explanation suggests that elephants meet their different energetic demands using distinct foraging approaches (forage selection hypothesis), which ultimately leads to spatial segregation (Shannon et al. 2006a; Stokke and du Toit 2000).

The activity budget hypothesis has received only limited support in explaining the social segregation of temperate ruminants. For example, mule deer (Bowyer and Kie 2004), merino sheep (Michelena et al. 2004), and desert bighorn sheep (Mooring et al. 2003) demonstrated no significant differences between sexes in either their activity budgets or behavioral synchronization. In red deer, the activity budget hypothesis was found to play only a contributing role in sexual segregation (Loe et al. 2006). Yearsley and Pérez-Barbería (2005) also concluded from their model of 144 species of ungulates that the activity budget hypothesis is unlikely to be the main factor driving segregation. If similar-sized ruminants are not conforming to the same ecological theory, then the sexual segregation of elephants (large, hindgut fermenters) also may be driven by factors other than foraging time.

We acknowledge that further research is required to conclusively reject the role of the activity budget hypothesis in the sexual segregation of elephants. For example, the discrepancy in drinking behavior between male and female elephants appears relatively small and inconsequential in our study, but it may have greater implications in open savanna systems with limited water availability, particularly because females and their young experience higher water turnover rates than do males (Stokke and du Toit 2002). Furthermore, Shannon et al. (2006c) noted an absence of habitat segregation between male and female elephants (using data from the same reserves used in this study) and postulated that forage availability may be less of a determining factor in the habitat use of elephants than the availability of water, a point also highlighted by Stokke and du Toit (2002). Therefore, activity budgets may change as a function of elephants selecting ranges on the basis of water availability as opposed to nutritional return.

Finally, social and reproductive strategies may play a role, because sexual segregation may be driven in part by the need to maximize breeding opportunities and avoid unnecessary conflict (Main et al. 1996; Wolf et al. 2005). The social hypothesis has largely been ignored with regard to elephants and requires greater consideration in order to explain the causal factor(s) in sexual segregation. The distinct life histories of male and female elephants may lead to the formation of same-sex or age-class groups, or both, on the basis of social affinity

and shared learning, for example, sparring between males or the nursing of young by females (Bon and Campan 1996; Pérez-Barbería et al. 2005).

In conclusion, the activity rhythms of elephants were consistent for females and males throughout the 3 study sites and across seasons. The reduction in activity (feeding and walking) during the middle of the day (1200–1400 h) suggests that environmental factors may play a greater role in dictating the diurnal activity patterns of elephants than body size and its associated physiological differences. The proportion of time spent feeding was not significantly different between males and females and there was no indication that activity budgets would vary significantly enough to be a driving factor in the sexual segregation of elephants. Instead, it seems that the activity budgets of male and female elephants may differ primarily as a result of segregation, a finding that concurs with research on a range of sexually dimorphic ungulates (Bowyer and Kie 2004; Conradt and Roper 2000; Mooring et al. 2003; Yearsley and Pérez-Barbería 2005), further outlining the need to distinguish between proximal and ultimate causes of sexual segregation.

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LITERATURE CITED

- ACOCKS, J. P. H. 1988. Veld types of South Africa. 3rd ed. Botanical Research Institute, Pretoria, South Africa.
- BON, R., AND R. CAMPAN. 1996. Unexplained sexual segregation in polygamous ungulates: a defense of an ontogenetic approach. *Behavioural Processes* 38:131–154.
- BOWYER, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses and implications for conservation and management. *Journal of Mammalogy* 85:1039–1052.
- BOWYER, R. T., AND J. G. KIE. 2004. Effects of foraging activity on sexual segregation in mule deer. *Journal of Mammalogy* 85:498–504.
- CHARIF, R. A., R. R. RAMEY, W. R. LANGBAUER, K. B. PAYNE, R. B. MARTIN, AND L. M. BROWN. 2005. Spatial relationships and matrilineal kinship in African savanna elephant (*Loxodonta africana*) clans. *Behavioral Ecology and Sociobiology* 57:327–338.
- CLUTTON-BROCK, T. H., AND P. H. HARVEY. 1978. Mammals, resources and reproductive strategies. *Nature* 273:191–195.
- CONRADT, L. 1998. Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proceedings of the Royal Society of London, B. Biological Sciences* 265:1359–1363.
- CONRADT, L. 1999. Social segregation is not a consequence of habitat segregation in red deer and feral soay sheep. *Animal Behaviour* 57:1151–1157.
- CONRADT, L. 2005. Definitions, hypotheses, models and the measures in the study of animal segregation. Pp. 11–34 in *Sexual segregation*

- in vertebrates: ecology of the two sexes (K. E. Ruckstuhl and P. Neuhaus, eds.). Cambridge University Press, Cambridge, United Kingdom.
- CONRADT, L., AND T. J. ROPER. 2000. Activity synchrony and social cohesion: a fission–fusion model. *Proceedings of the Royal Society of London, B, Biological Sciences* 267:2213–2218.
- COOPER, S. M., AND N. OWEN-SMITH. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68:446–455.
- CORTI, P., AND D. M. SHACKLETON. 2002. Relationship between predation-risk factors and sexual segregation in Dall's sheep (*Ovis dalli dalli*). *Canadian Journal of Zoology* 80:2108–2117.
- DEMMENT, M. W., AND P. J. VAN SOEST. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125:641–672.
- DU TOIT, J. T., AND C. A. YETMAN. 2005. Effects of body size on the diurnal activity budgets of African browsing ruminants. *Oecologia* 143:317–325.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- JESCHKE, J. M., AND R. TOLLRAIN. 2005. Predicting herbivore feeding times. *Ethology* 111:187–206.
- LAWS, R. M., I. S. C. PARKER, AND R. C. B. JOHNSTONE. 1975. Elephants and their habitats. The ecology of elephants in North Bunyoro, Uganda. Clarendon Press, Oxford, United Kingdom.
- LE BLANC, M., M. FESTA-BIANCHET, AND J. T. JORGENSEN. 2001. Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. *Canadian Journal of Zoology* 79:1661–1670.
- LE PENDU, Y., C. GUILHEM, L. BRIEDERMANN, M. MAUBLANC, AND J. GERARD. 2000. Interactions and associations between age and sex classes in mouflon sheep (*Ovis gmelini*). *Behavioural Processes* 52:97–107.
- LOE, L. E., ET AL. 2006. Testing five hypotheses of sexual segregation in an arctic ungulate. *Journal of Animal Ecology* 75:485–496.
- LOISON, A., J. GAILLARD, C. PELABON, AND N. G. YOCOZ. 1999. What factors shape sexual size dimorphism in ungulates? *Evolutionary Ecology Research* 1:611–633.
- LOW, A. B., AND A. G. REBELO (EDS.). 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, South Africa.
- MAIN, M. B., F. W. WECKERLY, AND V. C. BLEICH. 1996. Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* 77:449–461.
- MC ELLIGOTT, A. G., ET AL. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behavioral Ecology and Sociobiology* 49:266–272.
- MICHELENA, P., ET AL. 2004. An experimental test of hypotheses explaining social segregation in dimorphic ungulates. *Animal Behaviour* 68:1371–1380.
- MOORING, M. S., ET AL. 2003. Sexual segregation in desert bighorn sheep (*Ovis canadensis mexicana*). *Behaviour* 140:183–207.
- MOSS, C. J. 2001. The population demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology (London)* 255:145–156.
- MOSS, C. J., AND J. H. POOLE. 1983. Relationships and social structure of African elephants. Pp. 315–325 in *Primate social relations* (R. A. Hinde, ed.). Blackwell Scientific Publications, Oxford, United Kingdom.
- MYSTERUD, A. 1998. The relative roles of body size and feeding type on activity time of temperate ruminants. *Oecologia* 113:442–446.
- MYSTERUD, A. 2000. The relationship between ecological segregation and sexual body size dimorphism in large herbivores. *Oecologia* 124:40–54.
- NEUHAUS, P., AND K. E. RUCKSTUHL. 2004a. Can the activity budget hypothesis explain sexual segregation in desert bighorn sheep? *Behaviour* 141:513–520.
- NEUHAUS, P., AND K. E. RUCKSTUHL. 2004b. Reply to Mooring and Rominger. *Behaviour* 141:531–532.
- OWEN-SMITH, R. N. 1992. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge, United Kingdom.
- OWEN-SMITH, R. N. 1998. How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). *Journal of Zoology (London)* 246:183–192.
- PELLETIER, F., AND M. FESTA-BIANCHET. 2004. Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis canadensis*. *Behavioral Ecology and Sociobiology* 56:546–551.
- PÉREZ-BARBERÍA, F. J., AND I. J. GORDON. 1998. The influence of sexual dimorphism in body size and mouth morphology on diet selection and sexual segregation in cervids. *Acta Veterinaria Hungarica* 46:357–367.
- PÉREZ-BARBERÍA, F. J., E. ROBERTSON, AND I. J. GORDON. 2005. Are social factors sufficient to explain sexual segregation in ungulates? *Animal Behaviour* 69:827–834.
- POOLE, J. H. 1987. Rutting behaviour in African elephants: the phenomenon of musth. *Behaviour* 102:283–316.
- POOLE, J. H. 1989. Announcing intent: the aggressive state of musth in African elephants. *Animal Behaviour* 37:140–152.
- POOLE, J. H. 1994. Sex differences in the behaviour of African elephants. Pp. 331–346 in *The difference between the sexes* (R. V. Short and E. Balaban, eds.). Cambridge University Press, Cambridge, United Kingdom.
- RUCKSTUHL, K. E. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour* 55:99–106.
- RUCKSTUHL, K. E. 1999. To synchronise or not to synchronise: a dilemma for young bighorn males? *Behaviour* 136:805–818.
- RUCKSTUHL, K. E., AND H. KOKKO. 2002. Modelling sexual segregation in ungulates: effects of group size, activity budgets and synchrony. *Animal Behaviour* 64:909–914.
- RUCKSTUHL, K. E., AND P. NEUHAUS. 2000. Sexual segregation in ungulates: a new approach. *Behaviour* 137:361–377.
- RUCKSTUHL, K. E., AND P. NEUHAUS. 2001. Behavioural synchrony in ibex groups: effects of age, sex and habitat. *Behaviour* 138:1033–1046.
- RUCKSTUHL, K. E., AND P. NEUHAUS. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews* 77:77–96.
- SHANNON, G., B. P. PAGE, K. J. DUFFY, AND R. SLOTOW. 2006a. The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia* 150:344–354.
- SHANNON, G., B. P. PAGE, K. J. DUFFY, AND R. SLOTOW. 2006b. African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology* 41:37–44.
- SHANNON, G., B. P. PAGE, K. J. DUFFY, AND R. SLOTOW. 2006c. The consequences of body size dimorphism: are African elephants sexually segregated at the habitat scale? *Behaviour* 143:1145–1168.
- SHIPLEY, L. A. 1999. Grazers and browsers: how digestive morphology affects diet selection. Pp. 20–27 in *Grazing behavior of livestock and wildlife* (K. L. Launchbaugh, J. C. Mosley, and K. D. Sanders, eds.). Idaho Forest, Wildlife and Range Experiment Station Bulletin 70. University of Idaho, Moscow.

- SLOTOW, R., AND G. VAN DYK. 2001. Role of delinquent young "orphan" male elephants in high mortality of white rhinoceros in Pilansberg National Park, South Africa. *Koedoe* 44:85–94.
- STOKKE, S. 1999. Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. *Canadian Journal of Zoology* 77:1723–1732.
- STOKKE, S., AND J. DU TOIT. 2000. Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* 23:70–80.
- STOKKE, S., AND J. DU TOIT. 2002. Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology* 40:360–371.
- TWINE, W. 2002. Feeding time budgets of selected African ruminant and non-ruminant grazers. *African Journal of Ecology* 40:410–412.
- YEARSLEY, J. M., AND F. J. PÉREZ-BARBERÍA. 2005. Does the activity budget hypothesis explain sexual segregation in ungulates? *Animal Behaviour* 69:257–267.
- WECKERLY, F. W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* 79:33–52.
- WOLF, J. B. W., G. KAUERMANN, AND F. TRILLMICH. 2005. Males in the shade: habitat use and sexual segregation in the Galapagos sea lion (*Zalophus californianus wollebaeki*). *Behavioral Ecology and Sociobiology* 59:293–302.

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