

# Alternating sexual segregation during the mating season by male African buffalo (*Syncerus caffer*)

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(Accepted 1 March 2005)

## Abstract

Patterns of association in many ungulate species vary throughout the year, with males periodically segregating from females. Sexual segregation can occur if males and females use different habitats (habitat segregation), occupy exclusive ranges (spatial segregation) or occur in separate social groups (social segregation). Previous studies on social segregation in ungulates have focused mostly on non-reproductive periods and species in temperate systems with short mating seasons. This study examined social segregation in African buffalo *Syncerus caffer* at Hluhluwe-iMfolozi Park, South Africa, during their 6-month mating season. During this period, mature male buffalo alternated between joining mixed-sex herds which comprise females and young, and small all-male groups. Activity patterns of male buffalo in both group types were examined to determine if differences in time allocation or activity asynchrony could explain the observed segregation. Mature males foraged for less time than both adult females and younger males when they were with mixed herds. Mature male buffalo differed in how their active time was apportioned to foraging and reproductive activities between the two group types. Females maintained group cohesion despite only low synchrony in activity, therefore segregation of male buffalo could not be explained by the activity budget hypothesis. For males in mixed-sex herds, reproductive activities were apparently at the expense of foraging time. The high time and energy costs of reproductive activities were probably responsible for the periodic separation of male buffalo from mixed herds during the extended mating period.

**Key words:** activity patterns, sexual segregation, social segregation, *Syncerus caffer*, time allocation

## INTRODUCTION

In many ungulates, patterns of association vary throughout the year, with adult males often separated from mixed-sex groups, a behaviour termed sexual segregation. Three variants of sexual segregation have been identified: habitat segregation, spatial segregation (Geist & Petocz, 1977), and social segregation (Bon & Campan, 1989). Habitat segregation occurs when males and females occupy different habitats. Spatial segregation occurs when males and females occupy distinct home ranges, without using different habitats. Social segregation occurs when males and females occur in separate groups, without using exclusive home ranges or different habitats. The sexual segregation literature has been reviewed extensively (Main & Coblentz, 1990; Main, Weckerly & Bleich, 1996;

Gross, 1998; Main, 1998; Ruckstuhl & Neuhaus, 2000). As Conradt (1999) and Bon *et al.* (2001) examined the relative importance of these three forms and found that social segregation is the most common form of sexual segregation, we chose to evaluate social segregation for this study.

To date, studies of social segregation in ungulates have generally considered the non-reproductive period, and have been restricted almost exclusively to ungulate species in temperate regions (*Alces alces*: Miquelle, Peek & Van Ballenberghe, 1992; *Capra ibex ibex*: Villaret & Bon, 1995; Bon *et al.*, 2001; *Ovibos moschatus*: Côté, Schaefer & Messier, 1997; *Cervus elaphus*: Conradt, 1998, 1999; Conradt & Roper, 2000; *Ovis gmelini*: Cransac *et al.*, 1998; *Ovis canadensis*: Ruckstuhl, 1998, 1999; *Ovis aries*: Conradt, 1999; *Procapra przewalskii*: Lei, Jiang & Liu, 2001; *Cervus elaphus roosevelti*: Weckerly, Ricca & Meyer, 2001; but see Prins, 1989). Outside the mating season there may be little motivation for males and females to remain together, and no obvious costs to segregation.

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Benefits related to group size, such as increased vigilance and a dilution of predation risk (Krebs & Davies, 1993), can be achieved by single-sex groups as well as mixed-sex groups (hereafter, 'mixed herds'). At these times, even small ecological differences between males and females can therefore be expected to lead to segregation of the sexes. A recent hypothesis addressing social segregation is the activity budget hypothesis (Ruckstuhl & Neuhaus, 2002). This hypothesis posits that differences between males and females in body size, duration of foraging bouts and movement rates make it costly for males to remain associated with female herds (Conradt, 1998; Ruckstuhl, 1998). During the breeding season, however, sexual segregation warrants further explanation, as males might incur fitness costs owing to lost mating opportunities. This peculiar behaviour has been attributed to the need for males to regain body condition (Prins, 1989; Komers, Messier & Gates, 1992), or to search for alternative mating opportunities (Dunbar, Buckland & Miller, 1990).

Ungulates living in temperate regions typically have brief mating seasons spanning just a few weeks (Owen-Smith, 1988). By contrast, some tropical species have reproductive periods extending over several weeks or months (Sinclair, Mduma & Arcese, 2000). Depending on the length of the reproductive period, there will be different selective pressures on affiliation behaviour of male groups in segregating species. With increasing duration of this period, the temporal concentration of oestrous females is reduced, diluting the benefits of being in a mixed group. Accordingly, males in some tropical ungulate species adopt a pattern of alternating sexual segregation through the extended breeding season. Male kudus *Tragelaphus strepsiceros* are with females on *c.* 75% of days during their 6-week mating period Owen-Smith (1984, 1993). Male African buffalo alternate periods in mixed herds with periods of separation in bachelor groups in Tanzania where births are spread through most of the year, a situation termed 're-entrant consecutive polygyny' (Prins, 1996). Notably, certain species in which males remain in mixed groups year-round show a lack of body size dimorphism, giving some support to the activity budget hypothesis (e.g. *Equus burchelli*: Neuhaus & Ruckstuhl, 2002; Ruckstuhl & Neuhaus, 2002; *Oryx gazella*: Ruckstuhl & Neuhaus, 2002).

African buffalo are dimorphic in body size, with adult males *c.* 25% heavier than adult females (Owen-Smith, 1988). Adult females, sub-adults of both sexes and juveniles live in mixed herds throughout the year, while mature males are either attached to mixed herds or associate in all-male 'bachelor' groups (Sinclair, 1977; Mloszewski, 1983; Prins, 1996). In our study area, the mating season spans a 6-month period, with 80% of conceptions occurring from January to April (Jolles, 2004). During this prolonged mating season, adult male buffalo transfer between mixed herds and male groups at intervals of days to weeks.

In an earlier study of African buffalo, Prins (1989) attributed segregation during the mating season to changes in male body condition, presumably from reduced grazing.

Using time allocation data from Prins & Iason (1989) for buffalo in mixed herds, Ruckstuhl & Neuhaus (2002) attributed this segregation to activity asynchrony. Sexual segregation during mating periods may be affected by several factors, including competition among males for reproductive opportunities.

Our study compared the activity budgets of mixed herds and male groups, to determine whether differences in male time allocation could explain the alternating sexual segregation shown by African buffalo during the reproductive period. Female ungulates invariably forage for longer than males (Owen-Smith, 1988), and the feeding time of males should decrease with increasing age and body size, as growth imposes additional energy costs above maintenance (Bunnell & Gillingham, 1985). We studied the activity synchronization of females to evaluate whether asynchrony between the sexes could be driving segregation. It was expected that, while in male groups, mature males would be less active, forage more, and cover smaller distances than when attached to mixed herds. It was further expected that within mixed herds: (1) mature adult males would forage for less time than adult females; (2) activity bouts of mature males would be poorly synchronized with those of females; (3) sub-adult and young adult males similar in size to adult females would differ from mature males in their activity budgets.

## METHODS

### Study area and animals

The study was conducted between September 2001 and April 2002. The study area was the Nqumeni section of the Hluhluwe-iMfolozi Park (HiP; formerly known as Hluhluwe-Umfolozi Park) in KwaZulu-Natal, South Africa, located between 28°10' and 28°14'S, and 31°54' and 32°03'E. The mean annual rainfall for Nqumeni was 760.5 mm from 1934 to 2002. Rainfall is strongly seasonal with most rain falling between October and March. The monthly mean of daily maximum temperatures over the study period ranged from 26.6°C in October to 32.3°C in March. HiP vegetation comprises open fire-maintained grasslands, open savanna woodlands, bush-encroached woodlands, thickets and closed woodlands. Buffalo often used open hillsides, enabling observations from an opposite hillside without disturbing their activity. Observations were made using a spotting telescope from distances of 300–1500 m.

Mixed herds of buffalo in HiP ranged from 30 to 250 individuals, but separated into 2 to 3 smaller subgroups periodically. The groups of females plus young observed within our study area ranged from 30 to 150 individuals. All-male groups varied from 1 to 12 males, with most groups comprising 2–5 males.

Adult females were distinguished from males by the absence of horn bosses, and from younger females by body

size and coat condition. Three size classes of males over 5 years of age, and thus potentially reproductively active (Grimsdell, 1973), were distinguished through differences in body size and shape, horn wear and coat condition. Sub-adult males have hair between their bosses, unridged horns, sleek coats, the same shoulder height as adult females, and body shapes similar to those of adult females. Young adult males show very little hair between their bosses, wear on the distal side of their bosses, coats with small bald patches at the shoulder, size slightly larger than adult females, and signs of shape dimorphism, i.e. a dewlap and thickening neck and shoulders. Mature males have no hair between their bosses, bosses showing wear throughout, coats with substantial hair-loss, size conspicuously larger than adult females, large dewlaps and thick shoulders and necks. These size classes were related to age using mean incisor height, recorded while buffalo were immobilized for disease testing in HiP, as follows: adult females (6+ years), sub-adult males (5–6 years), young adult males (7–9 years), and mature adult males (10+ years).

#### Data collection and analyses

Daily activity patterns of buffalo were recorded using scan samples at 15-min intervals (after Altmann, 1974). The behaviours categorized as active included grazing, moving, courting (testing or tending females), sparring, scanning (for predators or mates) and other miscellaneous activities (scratching, grooming, nursing young, defecating and urinating). Inactive behaviours included ruminating, standing-motionless, and lying down.

Buffalo were observed for as long as was possible during daylight hours. Observations were curtailed when buffalo moved into low-lying woodlands and ravines for shade or wallows at mid-day. To use part-day samples, the day was divided into morning (06:00–12:00) and afternoon (12:00–18:00) time segments. For these half-day segments, the mean proportion of time devoted to an activity for each age-sex class was calculated. Only observations spanning 3 h and longer were considered; 37 half-day observations on mixed herds, and 36 half-day observations on male groups, were analysed for differences in time spent active and grazing. The proportion of the full (10+h) day devoted to each activity type (mixed herds:  $n = 10$  days, male groups:  $n = 6$  days) is also presented for comparison with our half-day observations and with other studies.

Two-tailed comparisons were used when testing for differences in time spent active and 1-tailed comparisons were used when testing for differences in grazing time. Time spent grazing required a square root transformation to approximate a normal distribution. Comparisons of minor activities, including moving, sparring, scanning, and miscellaneous activities by males were performed using Wilcoxon rank-sum tests. Courting was not analysed statistically as this activity does not occur in male groups.

Observations comparing the active and grazing time of mature males in mixed herds vs male groups were conducted on different days, and so could be affected by variability in extraneous conditions between days. Differences were tested using an ANOVA, including as factors the maximum daily temperature, cloud cover (clear, partly cloudy and overcast), precipitation (none, light rain; observations were terminated during heavy rain), different stages of the wet season (early, mid, late), the presence of oestrous females, and time period (morning or afternoon). The presence of oestrous females was noted by observing male courtship behaviour (Sinclair, 1977). Maximum daily temperature data were obtained from a weather station of the Zululand Grassland Project located within our study area. Previous studies have found that activity levels of African ungulates decreased above 32 °C, including eland (Lewis, 1977), giraffe (Leuthold & Leuthold, 1978), impala and blesbok (Klein & Fairall, 1986). Therefore, daily maximum temperature was categorized as either 32 °C and above, or below 32 °C.

For activity levels of particular age-sex classes within mixed herds, observations were made on the same days, thus controlling for the effects of weather variation. Nevertheless, we initially tested whether the difference in activity levels between these classes was affected by exogenous variables using ANOVA. If a factor had a significant effect on activity differences, then separate paired *t*-tests were performed on activity levels within each category of the exogenous factor. A Bonferroni correction was used to avoid compounding type I error on all additional *t*-tests performed as a result of these exogenous factors. For the paired comparisons, females vs mature males, and the three male size classes were tested against each other. Significant differences were assessed using  $P < 0.05$ . In the results, means are reported with standard errors.

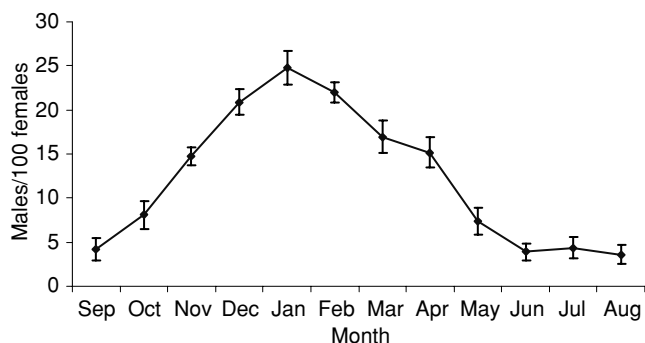
Distance travelled was determined by recording the GPS location at the beginning and end of each observation period and tracking the path of movement between the 2 locations on a topographical map. The rate of movement was compared for mixed herds and male groups by temperature category in Wilcoxon rank-sum tests. Samples < 4 h were excluded from analysis.

Large herd sizes and concealing vegetation prevented us from recording the activity bouts of individual animals to assess activity synchrony directly. To estimate synchrony in activity among females, all observations were divided into 1- to 2-h activity bouts based on the degree of group activity or inactivity. A mean proportion of females active or grazing was calculated for a total of 166 bouts.

To determine the degree of sexual segregation throughout the year in our study area, the monthly presence of mature males in mixed herds was evaluated. Between October 2000 and April 2002, up to 12 discrete mixed herds were located 1–3 times per week using radio-telemetry. The age-sex composition of the herds was recorded during observations. The mean ratio of adult males to females was then calculated for each herd per month and then these ratios averaged by month.

**Table 1.** Comparisons of time allocated to active and grazing activities of African buffalo *Syncerus caffer* for different age-sex classes within mixed groups. Comparisons were done for half-day observations, and were partitioned into temperature or time of day categories when these exogenous factors had significant effects on time allocation. X and Y, age-sex classes compared in each *t*-test. AF, adult female; MM, mature male; YAM, young adult male; SM, sub-adult male; T, maximum daily temperature. Means  $\pm$  SE

| Activity | Comparison |                | Category      | Time allocation (%) |                | Paired <i>t</i> -test           |                |
|----------|------------|----------------|---------------|---------------------|----------------|---------------------------------|----------------|
|          | X          | Y              |               | X                   | Y              | <i>t</i> statistic ( <i>n</i> ) | <i>P</i> value |
| Active   | AF         | MM             | T $\geq$ 32°C | 44.4 $\pm$ 4.4      | 36.0 $\pm$ 4.4 | 4.4 (13)                        | < 0.001        |
|          |            |                | T < 32°C      | 43.6 $\pm$ 4.0      | 43.5 $\pm$ 4.5 | 0.01 (22)                       | > 0.5          |
|          | MM         | YAM            | –             | 40.7 $\pm$ 3.3      | 41.3 $\pm$ 2.8 | 0.4 (35)                        | > 0.5          |
|          |            |                | SM            | morning             | 44.3 $\pm$ 3.7 | 43.1 $\pm$ 4.1                  | 0.6 (20)       |
|          | afternoon  | 31.4 $\pm$ 3.8 |               | 37.2 $\pm$ 4.4      | 3.5 (14)       | 0.016                           |                |
| Grazing  | YAM        | SM             | –             | 39.6 $\pm$ 2.7      | 41.0 $\pm$ 3.0 | 1.0 (36)                        | 0.318          |
|          | AF         | MM             | T $\geq$ 32°C | 29.2 $\pm$ 2.0      | 15.5 $\pm$ 2.1 | 4.9 (13)                        | < 0.001        |
|          |            |                | T < 32°C      | 29.3 $\pm$ 3.4      | 22.3 $\pm$ 3.0 | 3.6 (22)                        | 0.002          |
|          | MM         | YAM            | –             | 19.8 $\pm$ 2.1      | 23.6 $\pm$ 2.1 | 2.6 (35)                        | 0.007          |
|          | MM         | SM             | –             | 18.8 $\pm$ 2.0      | 26.6 $\pm$ 2.7 | 4.1 (34)                        | < 0.001        |
|          | YAM        | SM             | –             | 22.9 $\pm$ 2.1      | 26.6 $\pm$ 2.6 | 2.7 (36)                        | 0.005          |



**Fig. 1.** The monthly presence of mature male African buffalo *Syncerus caffer* in mixed herds throughout the year. Means are reported with SE.

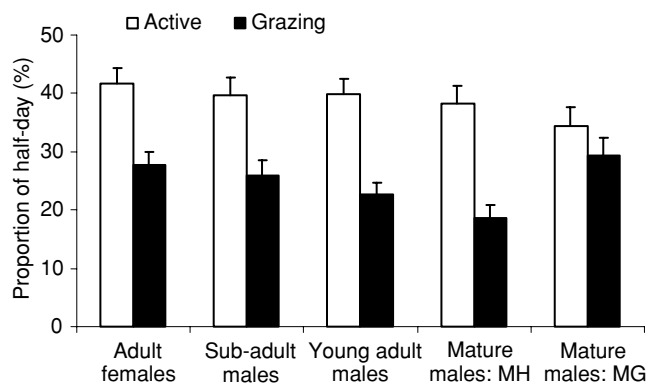
## RESULTS

### Male segregation

During non-reproductive periods there were fewer than five mature males per 100 adult females in mixed herds (Fig. 1). The adult male to female ratio in mixed herds is highest during the mating season, reaching about one male per four females.

### Active time

Whether in mixed herds or male groups, mature males showed no significant difference in the proportion of time spent active (mixed herds: 34.5  $\pm$  3.2%, male groups: 39.6  $\pm$  3.4%,  $F = 2.1$ ,  $d.f. = 1$ ,  $P = 0.155$ ). Mature males in both groups were more active in the morning than in the afternoon (morning: 40.8  $\pm$  3.0%, afternoon: 30.8  $\pm$  3.0%,  $F = 5.6$ ,  $d.f. = 1$ ,  $P = 0.021$ ). Within mixed herds, mature males spent significantly less time active than adult females only at temperatures above 32°C (Table 1). No significant differences were found in the time spent active



**Fig. 2.** Time allocation to active and grazing activities of African buffalo *Syncerus caffer* during half-day observations, combining morning and afternoon samples. The mean time spent active or grazing is presented for age-sex classes in mixed herds (MH) and male groups (MG). Mixed herds:  $n = 37$ , male groups:  $n = 36$ . Means are reported with SE.

between mature males and young adult males, or young adult males and sub-adult males (Fig. 2). Sub-adult males spent more time active than mature males in mixed herds during afternoon segments, but not during morning segments (Table 1).

Of the exogenous factors tested, only temperature and period of the day had significant effects on active times of buffalo. Cloud cover, precipitation, different stages of the wet season, and the presence of oestrous females had no significant effect on activity. During morning segments activity levels were generally higher than those over the whole daylight period for all age-sex classes, but differences between these classes remained fairly consistent (Table 2).

### Grazing time

While in mixed herds, mature males grazed for significantly less time than adult females, young adult

**Table 2.** Proportion of active time allocated to particular activities by buffalo in mixed herds and male groups, including all-day and morning observations, taking into account the daily temperature maximum. Values are reported with mean  $\pm$  SE

| Temperature             | Herd type | Age-sex class      | Observation period | <i>n</i> | Grazing        | Moving         | Courting      | Sparring      | Scanning      | Other         | Inactive       |                |
|-------------------------|-----------|--------------------|--------------------|----------|----------------|----------------|---------------|---------------|---------------|---------------|----------------|----------------|
| $\geq 32^\circ\text{C}$ | Mixed     | Adult females      | Day                | 5        | 28.1 $\pm$ 2.4 | 4.1 $\pm$ 1.4  | 0             | 0             | 0.6 $\pm$ 0.1 | 1.3 $\pm$ 0.4 | 65.9 $\pm$ 3.2 |                |
|                         |           |                    | Morning            | 9        | 32.3 $\pm$ 2.5 | 11.6 $\pm$ 3.9 | 0             | 0             | 1.5 $\pm$ 0.4 | 2.1 $\pm$ 0.7 | 52.4 $\pm$ 4.8 |                |
|                         |           | Sub-adult males    | Day                | 5        | 23.5 $\pm$ 4.9 | 4.0 $\pm$ 1.2  | 0             | 0.5 $\pm$ 0.2 | 0.5 $\pm$ 0.4 | 2.2 $\pm$ 0.9 | 69.4 $\pm$ 6.0 |                |
|                         |           |                    | Morning            | 9        | 26.8 $\pm$ 5.0 | 11.4 $\pm$ 4.5 | 0.5 $\pm$ 0.3 | 0.5 $\pm$ 0.3 | 2.2 $\pm$ 1.0 | 2.6 $\pm$ 0.9 | 56.0 $\pm$ 7.8 |                |
|                         |           | Young adult males  | Day                | 5        | 19.4 $\pm$ 3.5 | 4.9 $\pm$ 1.4  | 0.9 $\pm$ 0.4 | 0.5 $\pm$ 0.3 | 0.8 $\pm$ 0.2 | 1.3 $\pm$ 0.5 | 72.1 $\pm$ 5.3 |                |
|                         |           |                    | Morning            | 9        | 21.8 $\pm$ 4.2 | 13.0 $\pm$ 3.1 | 0.9 $\pm$ 0.5 | 0.8 $\pm$ 0.4 | 1.5 $\pm$ 0.5 | 1.8 $\pm$ 0.4 | 60.2 $\pm$ 5.6 |                |
|                         |           | Mature adult males | Day                | 4        | 14.2 $\pm$ 3.2 | 7.4 $\pm$ 1.0  | 1.9 $\pm$ 0.8 | 0.6 $\pm$ 0.4 | 1.1 $\pm$ 0.5 | 1.1 $\pm$ 0.7 | 73.7 $\pm$ 4.6 |                |
|                         |           |                    | Morning            | 8        | 14.9 $\pm$ 3.2 | 13.5 $\pm$ 4.1 | 1.1 $\pm$ 1.0 | 0.6 $\pm$ 0.5 | 3.0 $\pm$ 1.2 | 0.9 $\pm$ 0.5 | 64.9 $\pm$ 6.4 |                |
|                         |           | All-Male           | Mature adult males | Day      | 1              | 26.2           | 3.3           | 0             | 0             | 0.4           | 0              | 70.1           |
|                         |           |                    |                    | Morning  | 8              | 26.5 $\pm$ 6.4 | 3.4 $\pm$ 1.2 | 0             | 0             | 0.3 $\pm$ 0.2 | 2.3 $\pm$ 0.8  | 67.4 $\pm$ 7.1 |
| $< 32^\circ\text{C}$    | Mixed     | Adult females      | Day                | 5        | 21.3 $\pm$ 4.7 | 7.5 $\pm$ 1.2  | 0             | 0.1 $\pm$ 0.1 | 3.2 $\pm$ 1.0 | 2.2 $\pm$ 0.5 | 65.7 $\pm$ 4.4 |                |
|                         |           |                    | Morning            | 13       | 33.7 $\pm$ 4.3 | 12.4 $\pm$ 2.4 | 0             | 0.2 $\pm$ 0.1 | 2.4 $\pm$ 0.5 | 2.0 $\pm$ 0.4 | 49.4 $\pm$ 5.0 |                |
|                         |           | Sub-adult males    | Day                | 5        | 19.0 $\pm$ 6.2 | 6.3 $\pm$ 1.6  | 0.4 $\pm$ 0.3 | 1.9 $\pm$ 0.4 | 3.0 $\pm$ 1.3 | 1.3 $\pm$ 0.6 | 68.1 $\pm$ 5.7 |                |
|                         |           |                    | Morning            | 12       | 27.3 $\pm$ 4.4 | 9.0 $\pm$ 1.9  | 0.6 $\pm$ 0.3 | 2.1 $\pm$ 0.7 | 1.8 $\pm$ 0.5 | 0.7 $\pm$ 0.4 | 58.5 $\pm$ 4.8 |                |
|                         |           | Young adult males  | Day                | 5        | 20.6 $\pm$ 4.1 | 7.2 $\pm$ 1.5  | 2.0 $\pm$ 0.7 | 1.6 $\pm$ 0.5 | 2.8 $\pm$ 1.0 | 1.6 $\pm$ 0.6 | 64.3 $\pm$ 4.0 |                |
|                         |           |                    | Morning            | 13       | 28.1 $\pm$ 3.5 | 12.2 $\pm$ 2.4 | 1.6 $\pm$ 0.5 | 2.4 $\pm$ 0.8 | 1.8 $\pm$ 0.6 | 1.2 $\pm$ 0.3 | 52.6 $\pm$ 5.1 |                |
|                         |           | Mature adult males | Day                | 5        | 18.4 $\pm$ 5.8 | 7.9 $\pm$ 1.8  | 3.0 $\pm$ 0.7 | 0             | 1.8 $\pm$ 0.7 | 1.7 $\pm$ 0.5 | 67.2 $\pm$ 4.6 |                |
|                         |           |                    | Morning            | 13       | 24.9 $\pm$ 3.5 | 16.8 $\pm$ 3.7 | 2.9 $\pm$ 0.9 | 0.7 $\pm$ 0.5 | 2.0 $\pm$ 0.7 | 1.7 $\pm$ 0.7 | 50.7 $\pm$ 6.3 |                |
|                         |           | All-Male           | Mature adult males | Day      | 5              | 28.6 $\pm$ 4.8 | 0.5 $\pm$ 0.3 | 0             | 0.4 $\pm$ 0.2 | 0.2 $\pm$ 0.1 | 0.9 $\pm$ 0.5  | 69.5 $\pm$ 5.6 |
|                         |           |                    |                    | Morning  | 19             | 32.2 $\pm$ 4.0 | 1.7 $\pm$ 0.6 | 0             | 0             | 0.8 $\pm$ 0.3 | 2.1 $\pm$ 0.7  | 63.3 $\pm$ 4.8 |

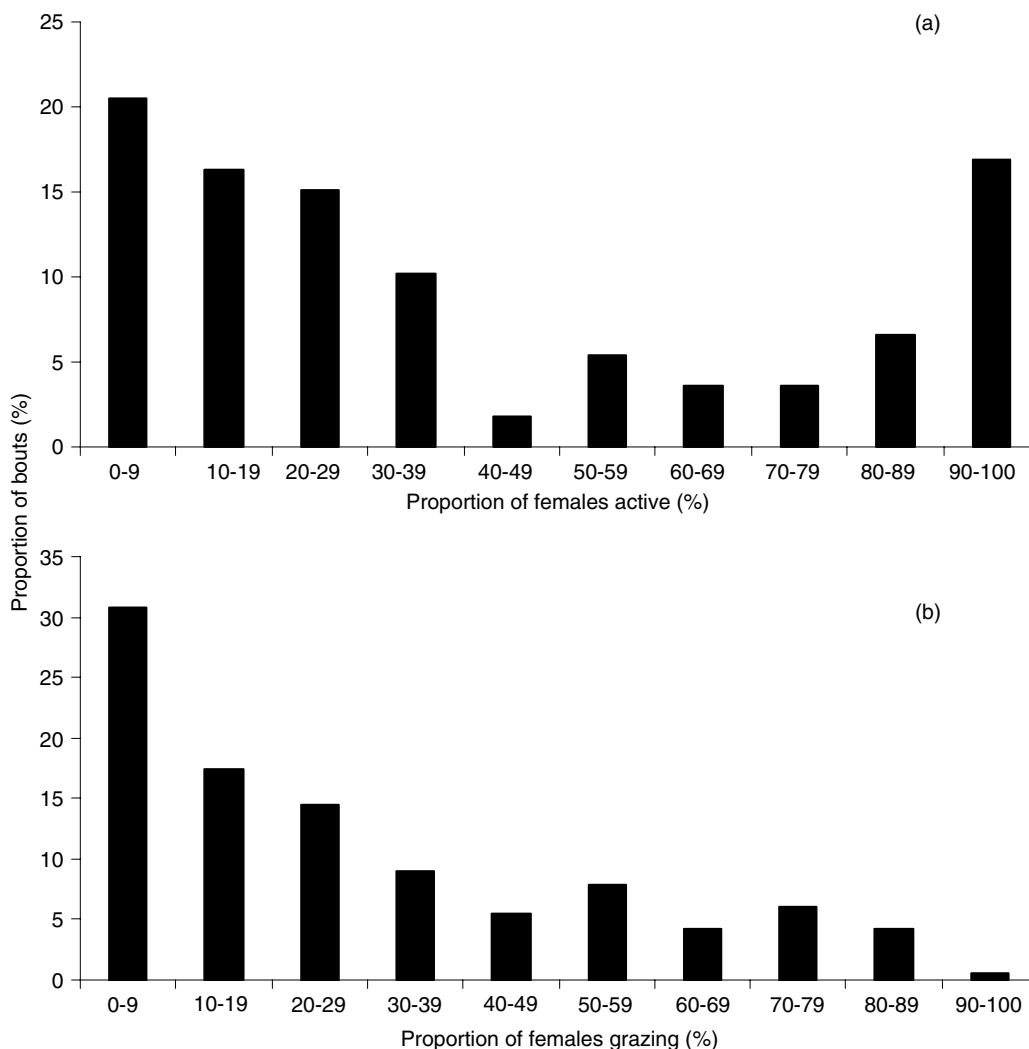


Fig. 3. The proportion of female African buffalo *Syncerus caffer* active (a) or grazing (b) during 1–2 h activity bouts. Bouts:  $n = 166$ .

males and sub-adult males (Table 1). Young adult males within mixed herds also spent significantly less time grazing than sub-adult males (Table 1). Mature males grazed for significantly less time while in mixed herds than when in male groups (mixed herds:  $19.8 \pm 2.1\%$ , male groups:  $29.1 \pm 2.8\%$ ,  $F = 8.4$ ,  $d.f. = 1$ ,  $P = 0.003$ , Fig. 2). Maximum daily temperature affected the magnitude of the difference in grazing time between mature males and adult females (Table 1), but no other exogenous factors affected grazing times.

### Other activities

Because mature males did not differ significantly in their time spent active between group types, but devoted significantly more time to grazing while in male groups, we analysed how the remainder of active time was spent. Mature males in mixed herds allocated significantly more of their active time to moving ( $Z = 4.8$ ,  $n = 71$ ,  $P < 0.0001$ ), scanning ( $Z = 2.6$ ,  $n = 71$ ,  $P = 0.0086$ ) and courting than when in male groups. Mature males in

these groups did not differ significantly in the proportion of active time allocated to sparring ( $Z = 1.6$ ,  $n = 71$ ,  $P = 0.116$ ) or miscellaneous activities ( $Z = 0.2$ ,  $n = 71$ ,  $P = 0.840$ ). The proportion of active time allocated to these activities is presented in Table 2.

Mixed herds travelled farther per observation time than male groups when the maximum daily temperature was below  $32^\circ\text{C}$  ( $157 \pm 29.1$  m/h vs  $41.1 \pm 9.1$  m/h,  $Z = 3.9$ ,  $n = 29$ ,  $P < 0.001$ ), but not at temperatures above  $32^\circ\text{C}$  ( $135 \pm 36.1$  m/h vs  $98.2 \pm 15.0$  m/h,  $W = 50$ ,  $n = 14$ ,  $P = 0.8$ ).

### Activity synchrony

Adult females were only loosely synchronized in their individual activities (Fig. 3). The bowl-shaped distribution of Fig. 3a indicates that there was some synchrony in the timing of active and inactive periods by females. However, there was little synchronization in the timing of grazing periods (Fig. 3b). Only a small proportion (10.8%) of activity bouts had a high proportion ( $>70\%$ ) of females

grazing. Since a low degree of synchrony among females was found, the extent of the synchrony between males and females was not of much relevance.

## DISCUSSION

### Male segregation

The strong female bias in the sex ratio of adult buffalo in mixed herds indicates that mature males segregated from mixed herds throughout the year, spending the majority of their time outside mixed herds even during the mating season. The adult sex ratio in the buffalo population at HiP seems to be between 1:1 and 1.5:1 in favour of females. The sex ratio was even for sub-adult buffalo (Jolles, 2004), but mortality rates for adult males are likely to be slightly higher than for females (Sinclair, 1977; Prins, 1996).

### Activity patterns

Ruckstuhl & Neuhaus (2002) proposed that sexual segregation was most generally explained by activity asynchrony arising from differences in activity bout durations, accentuated by size dimorphism between adult males and females. For the buffalo herds that we studied, however, females maintained group cohesion despite being only loosely synchronized in their activities, so that activity asynchrony is likely to be inconsequential for the males associated with these herds. The extended mating season falls within the late wet season when high-quality forage is abundantly available, so that herds often move little, allowing some animals to rest while others continue feeding without becoming separated. Although differences in body size can lead to activity asynchrony, individuals with equal body size are not necessarily synchronous in their activity patterns. If individuals with the same body size are not synchronous in activity, differences in body size between the sexes cannot explain sexual segregation.

Nevertheless, substantial differences were found in the proportion of time spent grazing between mature males and females in mixed herds, and for mature males between times when they were attached to mixed herds vs periods spent in all-male groups. There were also large differences in movement rate between mixed herds and male groups. Mature males grazed for less time than females when in mixed herds, but for a similar time to females in mixed herds while these males were in male groups. The overall activity level of males seemed to be influenced more by daily temperature conditions than by group type. As larger animals have a lower surface to volume ratio, mature male buffalo may be less efficient at dissipating body heat than smaller-bodied classes. The difference in grazing time for males in the two group types was associated largely with differences in the time devoted to moving, courting and scanning, rather than differences in overall active time.

Previous studies examining activity patterns of buffalo in mixed herds show similar levels of activity to those reported in this study, with mixed herds grazing between 18% and 38% of the daytime depending on the study area (Stark, 1986; Prins & Iason, 1989; Winterbach & Bothma, 1998). Comparable data do not seem to be available on the daily foraging time of buffalo in all-male groups. Females have higher energy demands than males owing to the energetic requirements of lactation and gestation (Robbins, 1983), and thus are expected to have longer grazing times. Studies on other African ungulates generally show differences of up to 10% in the daily foraging time of adult males and females (Owen-Smith, 1988). The sex difference in daily feeding time for buffalo was within this range when the daily maximum temperature was below 32 °C, but adult males responded more negatively to high ambient temperatures than did females, resulting in differences in grazing time between the sexes of nearly 15%.

Our study did not examine night activity patterns, and males in mixed herds could have compensated for deficits in their time budget for daytime grazing by increased foraging at night. Greater activity at night than during the day is commonly seen in buffalo (Grimsdell & Field, 1976; Sinclair, 1977; Prins & Iason, 1989; Winterbach & Bothma, 1998). In Lake Manyara National Park, however, males grazed on average 12.6% less than adult females at night (Prins & Iason, 1989). Since daytime matings are rarely witnessed, most reproduction must occur at night (Prins, 1996; pers. obs.). Heightened reproductive activities make it unlikely that males compensated after dark for reduced daytime grazing.

### Time costs

We suggest that buffalo males segregated owing to the compounded time and energy costs of reproductive activities incurred when in mixed herds. Besides courting activity, additional time is diverted from feeding to scanning, possibly associated with searching for potential mates or competitors, and greater movement distances are energetically more costly.

Prins (1989) found that mature male buffalo lost condition in mixed herds and gained condition while in male groups, perhaps owing to grazing time differences between males and females. Komers *et al.* (1992) showed that male wood bison *Bos bison athabasca* left mixed herds temporarily during the 6-week mating season for a recovery period. In HiP, condition changes in male buffalo were not visually apparent, probably because movement between group types often took place at intervals of only a few days. Nevertheless, the increased grazing time that these males showed while in male groups may have provided recovery periods, which enabled males to maintain their body condition and consequently their competitive ability.

The alternating sexual segregation may have enabled buffalo males to sustain reproductive activities throughout the 6-month mating period. Males of species with brief

rutting periods lasting only 2–3 weeks almost cease feeding during the peak conception period and show fierce competition for females (e.g. *Cervus elaphus*: Clutton-Brock, Guinness & Albon, 1982). The extended mating season in buffalo may make these extremes in behaviour untenable; adult males reduce their feeding when with females, but not drastically, and while males are clearly equipped for aggressive competition with other males, fights amongst them are rare (Sinclair, 1977; Prins, 1989). For greater kudu *Tragelaphus strepsiceros*, with a peak mating period extending over 6 weeks, adult males reduce their daily foraging time by only about 7% during periods when they are associated with females, while increasing the time they spend moving, vigilant and courting (Owen-Smith, 1984). In contrast to buffalo males, this is at the expense of inactive time. The mating period of kudu occurs during autumn, however, when temperature levels are milder than during mid-summer, which is the peak conception period for buffalo.

Males incur various costs in time, energy, and risk from competition for mating opportunities (Owen-Smith, 1977). The risks associated with direct male combat may be reduced through dominance relationships established in space (i.e. territoriality) or by rank relationships. Male groups provide a context in which dominance relationships can be established, often subtly by seemingly playful sparring (Owen-Smith, 1993). This function of male groups may provide a more general explanation of sexual segregation, encompassing even species with little size dimorphism (e.g. wildebeest *Connochaetes* spp., topi *Damaliscus lunatus* and hartebeest *Alcelaphus* spp.; Estes, 1991).

Associations between mature males and females among ungulates can vary in duration from tending bonds of a few days before mating (e.g. white-tailed deer *Odocoileus virginianus*; Hirth, 1977) to year-round affiliations (e.g. plains zebra *Equus burchelli*; Klingel, 1969). During the mating season reproductive opportunities become available, and activities associated with courtship can take up much time, often at the expense of foraging. When the mating period extends over more than a few weeks, males may not be able to maintain their body condition, and hence dominance status, if they associate continuously with female groups. This may explain the pattern of alternating association and segregation over the course of the mating season shown not only by African buffalo, but also by greater kudu (Owen-Smith, 1993) and, in a modified form, by African elephants (Poole & Moss, 1981). Patterns of association between male and female ungulates are best viewed as the outcome of a complex interplay of costs and benefits at different times of the year, rather than as being the result of any single factor.

### Acknowledgements

We thank Ezemvelo KwaZulu-Natal Wildlife for permission to carry out this research, and the management of HiP including Peter Hartley, Yoliswa Ndlovu, and Dave Robertson for their support. Dave Balfour and Owen and

Ruth Howison at Hluhluwe Research Centre did much to facilitate the running of this project. We appreciate Nobuhle Zodwa Mnyandu's assistance with data collection. This manuscript benefited from discussions with the Lytle laboratory at Oregon State University and the Community and Conservation Ecology Group at University of Groningen, and comments from Allison Bidlack, Paul Cross, Marco Festa-Bianchet, Verinne Fuld, Wayne Getz, Sadie Ryan, and George Wittemyer. This work was supported by grants to AEJ from the National Geographic Society, the Wildlife Conservation Society, the Heinz Foundation, the Explorer's Club and SigmaXi; and NSF DEB-0090323 to Wayne Getz. This research was done in accordance with animal use and care guidelines from Princeton University.

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