

ACTIVITY PATTERNS OF MALE
AFRICAN BUFFALO

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Science

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I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

(Signature of candidate)

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ABSTRACT OF DISSERTATION

This study examined the daily activity patterns of adult African buffalo (*Syncerus caffer*) to address why males segregate from mixed groups during the mating season. Activity patterns were used to evaluate whether differences between adult males and females in time allocation would lead to activity asynchrony and thus sexual segregation. As male buffalo alternate between mixed and male groups during the reproductive period, termed alternating sexual segregation, changes in male behaviour in the presence and absence of females were also evaluated. Results of this study demonstrate that differences in activity budgets between males and females need not lead to activity asynchrony. Instead, segregation may result from time costs of reproductive activities. Male grazing time was depressed in mixed groups due to the occurrence of reproductive behaviours and elevated beyond nutritional expectations in male groups. Alternating sexual segregation may enable males to maintain their competitive ability throughout the extended mating season.

For my brother, Greg, who would have enjoyed my conclusions

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1. INTRODUCTION TO STUDY

1.1 Research Aim

To help understand why mature male buffalo leave mixed groups during the mating season.

1.2 Research Objectives

- A. To determine the differences in time allocation between mature male and female buffalo, and different age classes of males within mixed groups.
- B. To determine the differences in time allocation of mature male buffalo in mixed groups and male groups.
- C. a. To establish the degree of synchrony in activity bouts between male and female adult buffalo.
b. To determine if there are differences in the degree of synchrony between different age classes of males.
- D. To distinguish differences in feeding time between mature male buffalo in mixed groups and male groups.

1.3 Preview of Dissertation

Chapter 1 contains a literature review which through a discussion of previous segregation studies explains how I arrived at my objectives and hypotheses. It also presents my research methods as initially proposed and how

the methods changed and developed once data collection began in earnest.

Finally, this chapter explains the data analysis I conducted and discusses results that did not make it into my main chapter.

Chapter 2 is the main chapter, in preparation for publication, with co-authors Anna Jolles and Norman Owen-Smith.

Chapter 3 summarises the main results of the study, and discusses how effectively I achieved my aim and objectives. It also contains a discussion of how applicable the results of this study are to other buffalo populations and how this study contributes to park management and conservation.

1.4 Literature Review

Sexual segregation can be defined as periods when adult males and females live separately. Understanding the social organisation of ungulates therefore requires examination into the causes of sexual segregation. The occurrence of sexual segregation is linked to mating strategy: polygynous ungulates generally exhibit sexual segregation, while monogamous ungulates do not (Jarman 1974, 1983). The degree of body size dimorphism between male and female ungulates increases with increasing group size (increasing polygyny), from one to multiple females per breeding group (Loison et al. 1999). This may be due to sexual selection, wherein larger males are more likely to win access to females than smaller males in intermale competition, which results in selection for larger male body size (Darwin 1871). The differences in body size between males and females can have many physiological and behavioural effects, the study of which forms the basis of research on sexual segregation.

Three forms of sexual segregation have been identified: habitat segregation, spatial segregation and social segregation. Differentiating between these forms can be confusing, as they are not mutually exclusive. Habitat segregation occurs when males and females differ in the habitats they use, spatial segregation occurs when they utilise exclusive ranges, without necessarily utilising different habitats, and social segregation occurs when they separate for behaviourally mediated reasons, without necessarily utilising different areas or habitats. The overlap between the definitions of these forms can be misleading, for habitat segregation is an example of social and spatial segregation, and depending on the spatial scale studied, social segregation is an example of spatial segregation (and vice versa). Therefore, the use of these terms is often more a reflection of how the study was approached, rather than a meaningful description of the system.

Hypotheses on sexual segregation generally address habitat or social segregation. As spatial segregation is more a description of the distribution of animals in space, and not a functional or mechanistic description of segregation, there are no hypotheses that deal with this form in particular. The sexual segregation literature has been reviewed by Main et al. (1996) and Ruckstuhl and Neuhaus (2000). In discussion of the various hypotheses, I will use terminology from Ruckstuhl and Neuhaus (2000) with supplementation from other sources as necessary.

Hypotheses that would result in habitat segregation include the predation risk hypothesis, the forage selection hypothesis, the scramble competition hypothesis and the weather sensitivity hypothesis. The predation risk hypothesis

states that males are less vulnerable to predation than females and their young (Ruckstuhl & Neuhaus 2000). Therefore, males can select habitats with high quality or abundant food, while females are forced to choose habitats which provide safety from predators over high quality forage. This is due to a difference in reproductive strategies; male reproductive success is based on size and strength, and female reproductive success is based on offspring survival (Main et al. 1996). Examples of this pattern have been observed in mule deer, where males selected better quality food, and females selected areas with low predator numbers, proximity to water and palatable food (Main & Coblentz 1996). In caribou, females with young prefer the more open tundra and males prefer river valleys (Jakimchuk et al. 1987) and in giraffe, females with young use open habitats which force females to feed below the optimum height, and non-lactating females and males utilise denser woodlands with more appropriate feeding heights (Young & Isbell 1991).

The forage selection hypothesis, conversely, states that females must select higher quality forage than males. This hypothesis requires that the males must be larger than females, which results in different energy requirements and thus different constraints on food selection. Larger males have a larger rumen with slower passage rates of food than smaller females (Van Soest 1994), and thus are more efficient at extracting energy from fibre (Demment 1982). Smaller females would then need to increase their foraging efficiency by selecting higher quality forage (Gross et al. 1996). This hypothesis is controversial, however, for few studies have found that females select higher quality forage (Ruckstuhl and Neuhaus 2000). One example was observed in white-tailed deer, where females

consumed higher quality forage than males (Beier 1987) but only when there was snow cover (Beier 1988). Potential reasons for the inadequacy of this hypothesis include the possibility that females masticate their food more, which provides a larger surface area for digestion, and when lactating, females can substantially increase both intake and retention time (Gross et al. 1996). It is also not clear why males would select poorer-quality forage simply because they can digest it more efficiently than females.

The scramble competition hypothesis builds on the logic for the forage selection hypothesis, and suggests that larger males are out-competed for mutually preferred swards by smaller females and thus select poorer-quality, high-biomass forage (Illius & Gordon 1987). For this hypothesis to apply, high quality forage must be scarce. When sward heights are low, larger males would be less competitive than smaller females, for males have a smaller incisor arcade width and bite size in relation to body size (Illius & Gordon 1987). Therefore, due to the allometric relationships of bite size and metabolic requirements to body size, smaller females would be able to more efficiently exploit low-biomass, high-quality forage than larger males (Clutton-Brock et al. 1987, Illius & Gordon 1987). Clutton-Brock et al. (1987) suggest that as segregation was most pronounced on short grasslands, red deer stags may be excluded by indirect competition with hinds. However, experimental testing of this hypothesis indicates that scramble competition could not explain the observed segregation in red deer (Conradt et al. 1999). Du Toit (1995) also found that intersexual competition could not be causing segregation in kudu, for during the dry season

when high quality forage was scarce, kudu males and females were the least segregated.

Finally, Conradt et al. (2000) recently proposed the weather sensitivity hypothesis to account for habitat segregation in red deer. They argue that a higher absolute heat loss relative to intake rate for larger males would cause a greater sensitivity to cold weather than for smaller females. They tested this hypothesis empirically on red deer and determined that adult males responded more strongly to cold weather and foraged in more protected sites in windy weather than adult females. This hypothesis has a limited ability to generally explain sexual segregation, as it would only apply to species in temperate and sub-arctic regions.

For hypotheses on social segregation the terminology can be confusing, as the hypotheses are similarly named. Three main hypotheses for social segregation were clarified by Bon et al. (2001): the social factors hypothesis (Main et al. 1996), the social affinity hypothesis (Bon et al. 2001; also called the social factor hypothesis, Pérez-Barbería & Gordon 1998; and the social preference hypothesis, Ruckstuhl and Neuhaus 2000) and the activity budget hypothesis (Ruckstuhl and Neuhaus 2000).

The social factors hypothesis relates to the mating success of males, where males would segregate to develop fighting skills and establish a dominance hierarchy (McCullough 1979, Geist 1982, Verme 1988). This hypothesis has not yet received empirical support (Main et al. 1996).

The social affinity hypothesis states that behavioural compatibility between individuals with similar social motivation contributes to the cohesion of

groups, and behavioural incompatibilities between individuals would lead to segregation (Bon et al. 2001). An example they provide for a behavioural incompatibility is that of playing and pseudosexual behaviour by younger males. Females may avoid the play of young males, and younger males may be limited in their interactions with older males due to differences in body and horn size. Therefore, this hypothesis addresses segregation by age as well as by sex. In Alpine ibex, Bon et al. (2001) found the least segregation during the rut, and outside the rut the degree of segregation increased with male age. The segregation into age groups continued even in the older age classes, where differences in body size would be insignificant. They argue, therefore, that sexual segregation of male ibex from female groups may be due to behavioural incompatibilities between males and females and social affinities between males of the same age classes.

The 'activity budget hypothesis' (Ruckstuhl & Neuhaus 2000), which could more descriptively be termed the activity asynchrony hypothesis, relates segregation to the timing of active and inactive periods between males and females (Conradt 1998, Ruckstuhl 1998). Ruckstuhl and Neuhaus (2000) suggest that differences in foraging behaviour and movement rates between males and females in body size dimorphic species will result in activity asynchrony and thus lead to social segregation. Ruckstuhl and Neuhaus (2002) suggest that activity differences would become apparent at approximately a 20% difference in body size. The nutritional requirements of males and females will also contribute to differences in activity budgets, due to the increased energetic costs of gestation and lactation for females (Robbins 1983). Most ungulates do show a difference

in activity budgets between males and females, where females forage for longer than males (Owen-Smith 1988). If as a result of these differences males and females are unable to synchronise their activities, then over time they should segregate, as demonstrated by Ruckstuhl (1998, 1999) for bighorn sheep and Conradt (1998) for red deer.

For my work on African buffalo (*Syncerus caffer*), I chose to test if the activity budget hypothesis could explain why male buffalo segregate from females during the mating season. All of the hypotheses for segregation described above are designed to explain sexual segregation in non-reproductive periods. Sexual segregation during the mating season has been suggested as a recovery period from reproductive activities for male wood bison (Komers et al. 1992) and related to changes in body condition in male African buffalo (Prins 1989). This study seems to be the first to test a current hypothesis explaining sexual segregation outside the mating season for its validity in explaining segregation during reproductive periods.

When adapting hypotheses on sexual segregation to African buffalo in the mating season, I selected a hypothesis for social segregation, as I saw no evidence of habitat segregation in Hluhluwe-Umfolozi Park (HUP). The importance of social segregation has been highlighted in recent studies by Conradt (1999) on red deer and Soay sheep and Bon et al. (2001) on Alpine ibex. Both studies examined the degree of social, habitat and spatial segregation, and found that sexual segregation was more likely due to social segregation than to spatial or habitat segregation. Of the hypotheses on social segregation, I selected the activity budget hypothesis, for it seemed the most plausible. The social

factors hypothesis seemed inappropriate as I observed few agonistic interactions between segregated males, and the social affinity hypothesis is not easily adapted to mating periods as the drive for reproduction should override male preference for other males. The idea of asynchrony in activity patterns seemed plausible for the buffalo in HUP as adult males move little when in male groups (pers. obs.). Therefore, it seemed likely that a mixed group would have higher levels of activity than an adult male could maintain, causing the male to eventually leave the herd. African buffalo also have a mean difference in adult body weight of 25% (Owen-Smith 1988), so sex differences in activity budgets should be apparent.

During the mating season, adult male African buffalo move repeatedly between mixed groups and male groups (Prins 1989, W. Turner & A. Jolles unpubl. data), a pattern we term alternating sexual segregation. Buffalo adult females, subadults of both sexes and juveniles live in mixed groups throughout the year. Outside the mating season, all adult and some subadult males segregate into male groups (Sinclair 1977; Mloszewski 1983; Prins 1996). During the mating season in my study area, most conceptions occur between December and May with a peak in February and March (Jolles, in prep).

In order to test the activity budget hypothesis, I examined activity patterns of adult buffalo in mixed groups and male groups (objectives A and B, section 1.2). Activity patterns of African buffalo have been studied in other populations, but never to compare male activity in different group types, or to address sexual segregation. Sinclair (1977) used activity patterns of lone males to determine diurnal grazing patterns, Stark (1986) examined individual females to gain an

understanding of daily movement, grazing patterns and diet of mixed groups, Prins and Iason (1989) examined activity of subadult and adult buffalo in mixed groups in relation to vigilance for predators, and Winterbach and Bothma (1998) examined seasonal activity patterns of mixed herds pooling all individuals.

Prins (1989) suggested that bulls moved between herd types due to a combination of factors including body condition changes, dominance relationships and breeding opportunities. Bulls can move in and out of mixed groups within a few days (Turner & Jolles, unpubl. data), a time span in which a measurable change in body condition is unlikely to occur. Therefore, this study looked at male behaviour to determine potential causes for the movement between group types. Behaviour is a more sensitive measure with which to examine males, for changes in behaviour will occur before changes in body condition. If males are indeed under nutritional stress while in mixed groups, then their feeding behaviour will be different from males in male groups. As males in mixed groups have many potential distractions from foraging, like assessing mating opportunities and competing for dominance, they would be expected to allocate less time to foraging than males in male groups. A change in male activity in the presence and absence of females has been observed in wood bison, where bulls in male groups spent relatively more time feeding and resting than bulls in mixed groups during the rut (Komers et al. 1992). During the breeding season in particular, pursuing reproductive opportunities has high energetic and time costs for male mammals (Bunnell & Harestad 1989), so males may forage and rest less in mixed than in male groups.

In addition to examining activity budgets, I planned to assess the degree of synchrony within mixed groups (objective C, section 1.2). The activity budget hypothesis states that differences in foraging behaviour and movement rates between males and females will lead to activity asynchrony, and thus social segregation (Ruckstuhl 1998). Therefore, in order to support this hypothesis as a cause of sexual segregation, differences in activity budgets as well as activity asynchrony between males and females must be demonstrated. I recorded activity budgets of three size classes of male buffalo to determine if the ability of males to synchronise activities with females decreased with increasing body size dimorphism. Ruckstuhl (1999) found that subadult bighorn males, with a body size similar to adult females, could synchronise their activity with females, but that larger adult males could no longer synchronise with females. I expected to find differences in activity budgets between the male size classes, with younger males grazing for more time than mature males, as the energetic requirements may be higher for growth than for maintenance of body size (Bunnell & Gillingham 1985).

Finally, I controlled for differences in food intake between mature males in mixed groups and male groups (objective D, section 1.2). It is possible that males in male groups, with fewer potential interruptions from foraging, could have a more relaxed intake rate than males in mixed groups. If the intake rate varied by group type, it could confound differences observed in total grazing time. Previous studies have examined the details of foraging behaviour in order to determine foraging efficiency (Owen-Smith 1994, Parker et al. 1995), which is defined as the rate of energy intake in relation to energy expenditure by Parker et

al. (1995). These were detailed studies of feeding behaviour, which examined the plant species and quantity of forage consumed for hand-reared kudu (Owen-Smith 1994) and black-tailed deer (Parker et al. 1995). The feeding behaviour of free-ranging wild ungulates cannot be studied in such precise detail, therefore, various measures of approximating intake can be used: the steps taken per second, feeding time per step, feeding time per site accepted, the proportion of time spent feeding, and the proportion of sites accepted (Underwood 1983). For buffalo the best approximation of food intake is feeding per unit time, for they often graze in tall grass which can obscure individual bites and steps (pers. obs.).

1.5 Hypotheses

- A. Mature males forage less and rest more than adult females and younger males while in mixed groups.
- B. Mature males forage less, rest less, and cover greater distances in mixed groups than in male groups.
- C. a. In mixed groups, adult females are more synchronised in their activities than are mature males with adult females.
b. Subadult males are more synchronised with adult females than are young adult or mature males.
- D. Mature males in mixed groups feed less while foraging than mature males in male groups.

1.6 Justification

This study evaluates whether the activity budget hypothesis, which has been suggested as the most general cause of sexual segregation outside the mating season (Ruckstuhl & Neuhaus 2002), can explain the segregation of African buffalo during the mating season. Most studies have evaluated social segregation during the non-reproductive period, as they have focused on temperate ungulates (Komers et al. 1992, Miquelle et al. 1992, Villaret & Bon 1995, Côté et al. 1997, Conradt 1998, Ruckstuhl 1998, 1999, Conradt et al. 1999, Conradt & Roper 2000, Bon et al. 2001, Lei et al. 2001, Weckerly et al. 2001). As species in temperate regions generally have very short mating periods (Owen-Smith 1988), males only briefly coexist with females. Therefore, many studies look for social mechanisms that would drive segregation when males and females are not interacting. Mature male buffalo alternate between mixed groups and male groups during the extended mating season (Prins 1989), which makes this system particularly appropriate for studying social segregation. By studying segregation in buffalo, I can assess how male activities and behaviour change when males are and are not segregated from females.

This study took place in Hluhluwe-Umfolozi Park, in the KwaZulu-Natal province, South Africa, as part of a study on disease ecology. The Buffalo Tuberculosis (TB) Research Project has two main facets: working with park management during the annual disease testing programme and twice weekly observations of 30 collared buffalo throughout HUP. TB is controlled in the population to reduce the prevalence in the buffalo population and to prevent the disease from moving into more endangered species. This work contributes to the disease study by providing additional data about the movement and motivation of

mature males, who we believe may be the main vectors spreading TB between otherwise discrete buffalo herds. This information may help optimise HUP's disease control programme, by focusing more attention on male groups where the disease may be residing.

Studying buffalo behaviour is not an easy task, as many buffalo populations have extremely large herds. Buffalo can occur in herds of 1000 individuals in Lake Manyara National Park, Tanzania (Prins 1996) and in Kruger National Park, South Africa (P. Cross pers. comm.) and up to 1500 individuals in the Serengeti National Park, Tanzania (Sinclair 1977). Trying to evaluate the activity of a large mixed group would be nearly impossible, particularly on savanna terrain which generally has very little relief. HUP is an ideal place to study buffalo behaviour, for the mixed groups are comparatively small and the terrain is very hilly. The average discrete mixed group in HUP is 100 individuals, but groups often break up into smaller fragments (A. Jolles in prep.). The terrain in HUP allowed me to observe buffalo herds from an opposite hillside without disturbing their activity. This was very important to the success of this study, for buffalo are quite wary. If they were aware of my presence, they would either watch me continuously or run away, neither of which is conducive to behavioural observations.

1.7 Methods

1.7.1 Study Design

My field season lasted from September 2001 to May 2002. The mating season in HUP is mainly between December and May (A. Jolles in prep.), but

mature males start appearing in mixed groups in mid-September and are generally all in male groups by the end of May (pers. obs.). The Nqumeni section of HUP was the main study area, as this section of the park was the best for observations. The terrain in Nqumeni has many hills with open grasslands and bushlands which turn into thickets and closed woodlands in ravines and valleys. This section also contains ten radio-collared adult females (in six distinct herds) and nine radio-collared mature males. I initially attempted individual focal animal sampling on collared individuals, but the group sizes and vegetation types made this method impractical.

To address my hypotheses, I observed buffalo mixed groups and male groups throughout the day. These groups were located either by chance or by radio-tracking collared individuals. Observations were performed using binoculars and a spotting scope from distances of 300-1500 meters. As hiking in HUP requires the accompaniment of an armed guide, all sightings had two observers. My guard, Nobuhle Zodwa Mnyandu, helped collect and record data.

My funding for this study came from the Buffalo TB Research Project, so I worked half-time collecting my data, and half-time as a field assistant and project coordinator of the main project. A typical work week included five days of fieldwork, dividing my time equally between my work and the main project, and two days of office work, entering my data and performing administrative duties.

1.7.2 Data Collection as Planned and Conducted for Each Hypothesis

A. Daily activity in mixed groups: proposed methods

The differences in activity budgets between mature males and females will be studied through daytime activity watches of mixed groups. Scan samples of the group will be performed to collect activity data on all target individuals (after Altmann 1974). As herds contain many more adult females than males (by up to a factor of 10), scan samples will need to be performed more frequently for males in order to represent male activity more accurately. Therefore, scan samples of adult female activity will be recorded every 30 minutes, and every 15 minutes for mature males. The activities recorded during a scan sample will be the actions observed at the moment when an individual is first seen, before age and sex are identified. This is better than using the moment of age-sex identification, which could create a bias towards activities where an individual's head is up (Komers et al. 1993). Adult females, mature males, young adult males and subadult males will be identified in the field by body size and shape, coat condition, horn wear and the presence or absence of horn bosses (Sinclair 1977). The size classes were correlated to age based on incisor wear. A detailed description of how I identified sex and size classes and how they correlate to age can be found in section 2.3.1.

During the scan samples, the actions recorded within the active state will include travelling (moving from a resting area to a feeding area), grazing (head down or chewing with head up), moving (searching for forage), watching (standing vigilant), nursing (including all mothering activities), courting (any male reproductive activities), sparring (any playing or fighting), and other (scratching, grooming, defecating, urinating). The actions to be recorded in the inactive state will include ruminating (either while lying down or standing),

sleeping, resting (when lying down and not sleeping or ruminating) and lying (when lying down but due to vegetation or animal position the head is obscured from view).

Many observations will be needed of mixed group activities for a variety of reasons. First, male activity should vary greatly depending on whether or not oestrous females are present in the herd. To help understand the effect an oestrous female could have on male activity patterns, the presence or absence of oestrous females will be recorded. It is not difficult to identify oestrous females, for they are surrounded by eager subadult and adult males. Second, weather affects the activity of buffalo. In order to account for weather variability, the maximum temperature, cloud cover and precipitation will be recorded during observations. The maximum daily temperature will be recorded from a weather station in Nqumeni, cloud coverage will be recorded as clear, partly cloudy, or overcast, and precipitation will be recorded as either no rain or light rain as changes occur. Observations will be abandoned in heavier rains, when buffalo often seek shelter in woodlands and visibility through optical equipment is poor. Finally, different seasons may affect activity, due to changes in forage quality and availability. I will therefore divide the field season into the early- (September-November), mid- (December-February), and late-wet seasons (March-May). In order to help account for these different confounding variables, I plan to collect one all-day observation per week, with 32 all-day observations interspersed throughout the field season. In order to reduce pseudoreplication (Hurlbert 1984), every attempt will be made to rotate weekly observations through different mixed groups.

A. Daily activity in mixed groups: changes in methods

I planned on performing scan samples every 15 minutes on males, and every 30 minutes on females, but changed to every 15 minutes for both sexes. It made sense to record female activity as often as male activity, as I already had to distinguish the age and sex of each individual during a scan. I was concerned that recording all adult animals in each scan sample would not leave enough time between scans to collect additional data for hypothesis D (section 1.5). However, as scans generally took between two and 10 minutes to complete, there was enough time for other data collection. For analysis I treated days with 30-minute and days with 15-minute scan samples for females equally, as the 30-minute scan are just a slightly rougher measure of female activity.

I also made small changes to the activities recorded. I eliminated travelling, for it was difficult to differentiate between the travelling and moving actions as defined. Buffalo rarely moved without some grazing, so there was no travelling action separate from foraging movements. I also separated the ruminating category into standing-ruminating, lying-ruminating, and moving-ruminating, as buffalo would sometimes continue ruminating while active. The category 'up' was also added, for times when buffalo were clearly active but out of sight, moving through a forest patch, for example. The addition of the 'up' category enabled me to have a more accurate estimation of active time, but as I cannot say whether or not the buffalo were grazing, it could cause an underestimate of grazing time. Therefore, when determining grazing proportions, I used the number of animals observed, and not the total which includes unseen animals.

B. Daily activity of mature males: proposed methods

I will conduct observations on male groups in order to compare the activity of mature males in mixed and male groups. The scan samples will be performed at 15-minute intervals to match the sampling interval for males in mixed groups. The activities recorded will be the same as for observations on mixed groups. Observations on male groups will not need as many replicates as for mixed groups, for the activity of bachelors is less variable (pers obs). Therefore, three all-day observations are planned per month for a total of 21 samples. The male groups chosen for observation will include many of the collared males as well as groups seen opportunistically in the study area. When possible, I will try to do observations on mixed groups and male groups on the same day (if both groups are visible from the same observation point) to account for weather variability.

Distance travelled for mixed and male groups will be determined by recording a location at the beginning and end of the observation period with a GPS, and tracking the path of movement between the two locations on a topographical map.

B. Daily activity of mature males: changes in proposed methods

The only changes include alterations to the actions I recorded (as described in section 1.7.2 A for mixed groups). I was ultimately unsuccessful at sighting more than one group in a day.

C. Synchrony in mixed groups: proposed methods

No additional data collection is needed in order to address this hypothesis. Ideally I would have recorded the exact length of activity bouts for focal animals, in order to directly examine how synchronous males are with females in the timing of their activities. When piloting the study, however, I discovered that the group sizes were too large to enable successful focal animal sampling. Therefore synchrony will be evaluated relatively by looking at differences in the proportion of animals active from each age-sex class recorded during the scan sampling. The three age classes of males will be compared with adult females to determine how male ability to synchronise changes with increasing body size.

C. Synchrony in mixed groups: changes in proposed methods

There were no changes to data collection for this hypothesis.

D. Foraging efficiency data: proposed methods

The foraging efficiency of mature males will be measured by recording time spent feeding during a five-minute foraging interval. This will be recorded on all mature males once per sighting, for mixed and male groups. One observer will keep the time for the five-minute interval, and another observer will watch the focal animal and use a stop-watch to record the exact time spent feeding (time with the head down). The number of mature males sampled should be between one and 12 in mixed groups and one and seven in male groups (pers. obs.). Times chosen for observation will be when the buffalo are at their peak feeding time; the beginning and end of a foraging bout will be avoided. When time

allows, replicates of individuals will be recorded to determine variability in feeding time.

D. Foraging efficiency data: changes in proposed methods

I changed when I was collecting samples from the proposed peak feeding time to any active period. By waiting for a 'peak feeding time' I was not collecting any data on males in mixed groups, as they were very distracted from feeding while active. I also recorded what activities the bulls were doing when they were not feeding.

1.7.3 Data Analysis for Each Hypothesis

A. Daily time allocation in mixed groups

I chose to use proportions when evaluating activity budgets, as visible group size varied. Using the number of animals observed would create a bias for samples when more buffalo were visible, and thus underestimate resting time. I assumed, therefore, that the activities of the animals in view were representative of the entire group. When animals were obviously obscured while resting, by tall grass on an otherwise open hillside, for example, I extrapolated the number of each age-sex class obscured by using a count of the age-sex structure of the group when they became fully visible. This kept me from over-estimating the proportion of active animals.

I observed groups for as long as possible during daylight hours, but they often moved into low-lying woodlands and ravines to wallow at mid-day. In order to utilise the resulting partial-day samples, I divided the day into morning (6:00-12:00) and afternoon (12:00-18:00) time periods for analysis. Within these

periods I only used samples greater than three hours in duration, as shorter samples could omit the active periods. I calculated the proportion of each age-sex class performing a target activity for each scan sample, and then averaged the proportions within the morning and afternoon period. I assumed independence of morning and afternoon samples collected on the same group in one day, as the active periods within samples were discrete. I collected 37 half-day observations on mixed herds. I checked that the results for half-day observations were comparable with daytime activity budgets by presenting activity proportions from samples greater than 10 hours.

I used two-tailed comparisons when testing for differences in active time. When testing for differences in grazing time, I used one-tailed analyses, as most female ungulates forage for longer than males (Owen-Smith 1988) and the feeding time of males should decrease with increasing age and body size (Bunnell & Gillingham 1985). I square-root transformed the time spent grazing and active to approximate a normal distribution. For comparisons between age-sex classes in mixed groups, I performed paired *t* tests, as the activity data from each age-sex class were obtained during the same observation periods. This procedure reduced extraneous variability affecting activity levels. The groups of pairs tested were adult females with mature males, and all combinations of male classes: mature males with young adult males, mature males with subadult males, and young adult males with subadult males.

Before performing *t* tests, I used an ANOVA to test if extraneous factors altered the relative differences in active time (or grazing time) between each pair. I controlled for the following categorical variables: the presence of oestrous

females, cloud cover, maximum daily temperature (above and below 32°C), season and time of day. (For more information on why temperature was analysed categorically, see section 2.3.2). The *t* tests presented in results (sections 2.4.1 and 2.4.2) indicate which variables had significant influences on activity. For example, if time of day had a significant effect on the relative difference in active time, I would perform *t* tests on morning and afternoon samples separately.

The only extraneous factors which had an influence on active or grazing time were temperature and time of day. Therefore, the presence or absence of oestrous females, season, cloud cover, and precipitation were eliminated from further consideration. As I terminated observations in sustained rain, it is not surprising that the light rain recorded had no influence on behaviour. Season is clearly related to maximum daily temperature, and when it was significant, it was strongly correlated with temperature. As temperature was a better predictor of activity differences and the seasonal distinctions were subjective, I chose to use temperature and not season in analyses. It was surprising that the presence of oestrous females had no influence on male activities. However, while in mixed groups mature males continually evaluate females to determine their oestrous status, which may explain why the time spent grazing or active does not change.

B. Daily time allocation in mature males

The preparation of scan samples for analyses was the same as for mixed groups, using proportions and half-day samples. I collected 36 half-day observations on male groups and 37 half-day observations on mixed groups. I did comparisons of grazing and active time between mature males in mixed and

male groups using ANOVA. The grazing and active time data were square-root transformed to approximate normality. I controlled for extraneous factors in the ANOVA, including oestrous females, different seasons, cloud cover, maximum daily temperature and time of day. As for mixed groups, the only factors that had significant effects on male activity budgets were temperature and time of day. All other factors were excluded from further analysis.

I analysed the distance travelled per observation time for mixed groups versus male groups using a two-sample t test. Samples shorter than four hours in length were excluded from analysis. The rate of movement was square root transformed to approximate a normal distribution. The analysis was one-tailed as I expected mixed groups to move further per hour than male groups. Sinclair (1977) noted that buffalo male groups seemed to have much smaller home ranges than adult females, Ruckstuhl (1998) found that mixed groups of bighorn sheep moved much further per time than male groups, and prior observations in HUP indicated that male groups moved very little per day.

C. Activity synchrony in mixed herds

Through my field season, it became clear that buffalo mixed groups had very low activity synchrony. At any given time a number of buffalo would be active or inactive. The only time I observed what one could call complete female synchrony was in the early morning or late afternoon when groups would sometimes move together to a new feeding location. How I evaluated the activity asynchrony of adult females is described fully in section 2.3.2. I chose not to

evaluate male synchrony with females, as females had low activity synchrony amongst themselves.

D. Foraging efficiency of mature males

For each 5-minute feeding sample, I calculated the proportion of time spent grazing. When multiple feeding times of one individual were recorded within a day, I averaged the grazing times to get one value. After averaging replicates, I had 63 samples from mixed groups and 65 from male groups. The data for the proportion of time spent feeding were not normally distributed, for I had sampled feeding bouts and non-feeding active bouts. In Figure 1.1, the upper end of the distribution more likely shows grazing bouts, while the heavy tail at the lower end of the distribution shows non-foraging active bouts.

I had planned to analyse the differences in feeding times between mixed and male groups, but as Figure 1.1 indicates, the type of data recorded in each group was not analogous. Therefore, based on the non-grazing actions I had recorded, I labelled each sample as part of a foraging bout or a non-foraging active bout. I distinguished the two types of samples using the occurrence of other activities recorded during sampling. The non-grazing actions which could be considered part of foraging bouts were moving and vigilance, and those which terminated a foraging bout were courting, sparring, standing-inactive, alarmed, scratching, urinating and defecating.

I tested for differences between males in mixed and male groups in feeding time using only foraging samples with a Wilcoxon Rank Sum Test.

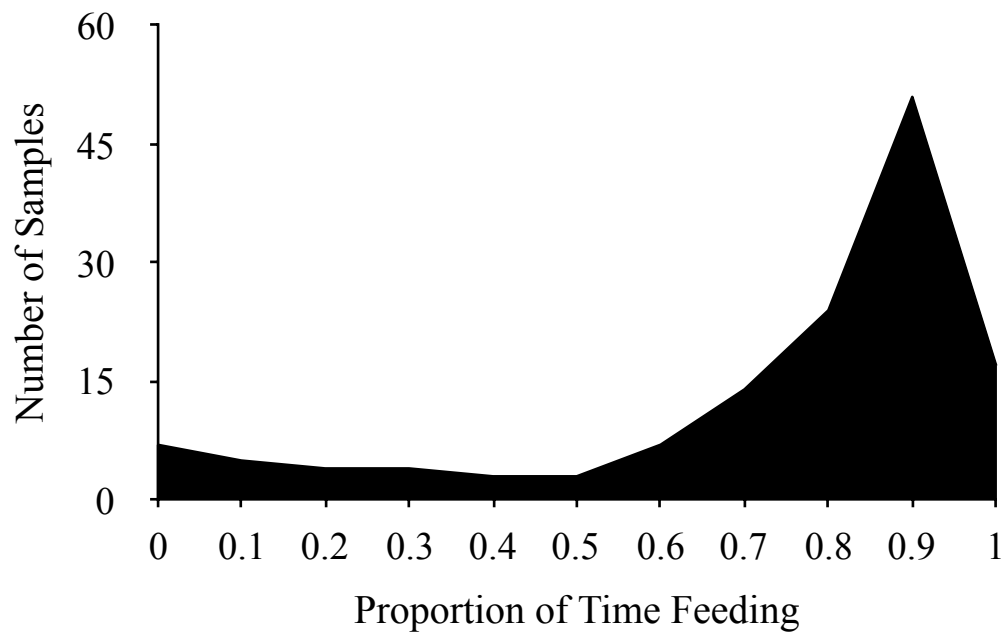


Figure 1.1: The distribution of feeding time while active for mature males combining observations from mixed groups and male groups.

There was no significant difference in the proportion of time spent feeding (mixed groups: 85.1%±4.3%, male groups: 92.8%±1.3%). I further performed Chi-Squared tests on the number of foraging versus non-foraging samples. There were significantly more non-foraging samples recorded in mixed groups ($\chi^2_1=12.8$, $p<0.001$). Therefore, males in mixed groups were as efficient at foraging as males in male groups when they did forage, but they had significantly fewer foraging bouts while active.

2 TIME COST AND NOT ACTIVITY ASYNCHRONY EXPLAINS ALTERNATING SEXUAL SEGREGATION DURING THE MATING SEASON IN AFRICAN BUFFALO

2.1 Abstract

Ruckstuhl and Neuhaus (2000) suggest that differences between males and females in time budgets and movement rates result in asynchronous activity bouts and thus sexual segregation. This study tested this activity budget hypothesis in African buffalo (*Syncerus caffer*) in Hluhluwe-Umfolozi Park, South Africa, during their six-month mating season. During this period, mature male buffalo alternated between joining large mixed groups including female and young, and small all-male groups. Assuming the activity budget hypothesis to be valid, we expected that (1) males would have different activity budgets from females and that as a result (2) males would have difficulty synchronising their activity budgets with females. We found that mature males did forage for less time than adult females and younger males when they were in mixed groups. However, the activity of female buffalo in mixed groups was only weakly synchronised, so that asynchrony between males and females did not seem to be a factor in sexual segregation. Mature male buffalo showed no significant difference in total time spent active between mixed groups and male groups, and their active time was constrained in temperatures above 32°C in both group types. In male groups, males spent most of their active time grazing. In mixed groups, mature males spent less time grazing, courted females, and moved at a

greater rate than when in male groups. These results suggest that within the available active time, reproductive activities may come at the expense of foraging time. We conclude that alternating segregation of male buffalo was due to the time cost of reproductive activities.

2.2 Introduction

Sexual segregation has been widely studied, in order to explain why male and female ungulates commonly occur in separate groups. Three forms of sexual segregation have been identified, including habitat segregation, spatial segregation and social segregation. Clearly these forms of sexual segregation are not mutually exclusive, as even the definitions require clarification in terms of the other forms: (1) habitat segregation occurs when males and females differ in their habitat use, or at smaller scales, diet choices (called ecological segregation by Mysterud 2000), (2) spatial segregation occurs when males and females utilise exclusive ranges without necessarily using different habitats, and (3) social segregation occurs when males and females segregate for socially mediated reasons, without requiring differences in area or habitat use. Depending on the scale used, however, both habitat and social segregation demonstrate spatial segregation. These terms are misleading for they blend functional and mechanistic explanations for sexual segregation, and hence the occurrence of more than one form is often reported (Miquelle et al. 1992, Villaret & Bon 1995, Cransac et al. 1998, Conradt 1999, Bon et al. 2001, Ruckstuhl & Neuhaus 2002). Fortunately, several authors have quantified the influence of these three forms of segregation to ascertain which form represents a stronger determinant of sexual

segregation (Conradt 1999, Bon et al. 2001) which helps clarify their relative importance if not the terminology. These studies concluded that sexual segregation was most strongly influenced by social segregation, and thus behavioural differences between males and females. Additional support for the general importance of social segregation was found in studies by Cransac et al. (1998) and Ruckstuhl and Neuhaus (2002) where sexual segregation was influenced more by social than habitat segregation.

Social segregation has been attributed to a number of behavioural differences between males and females as described by the social factors hypothesis (Main et al. 1996), the social affinity hypothesis (Bon et al. 2001) and the activity budget hypothesis (Ruckstuhl & Neuhaus 2000). The ‘social factors hypothesis’ (Main et al. 1996) suggests that males join all-male groups to develop fighting skills, establish a dominance hierarchy, learn the location of potential mates, and avoid costly interactions in the presence of females. The ‘social affinity hypothesis’ (Bon et al. 2001) suggests that males tend to interact with other males through play or pseudo-sexual behaviours and females may avoid these type of interactions. The cohesion of social groups is thus facilitated by the grouping of individuals with similar social behaviours. Sexual segregation would thus occur when individuals differ in their ability or motivation to interact with individuals of the opposite sex. Males would be less motivated to interact with females outside the rut than during the rut, resulting in sexual segregation outside the mating season (Bon et al. 2001).

The ‘activity budget hypothesis’ (Ruckstuhl & Neuhaus 2000), perhaps better labelled the activity asynchrony hypothesis, relates segregation to the

timing of active and inactive periods between males and females (Conradt 1998, Ruckstuhl 1998). Ruckstuhl and Neuhaus 2000 suggest that differences between males and females in the length of foraging bouts and movement rates, expected for species which are sexually dimorphic in body size, cause activity asynchrony and thus lead to social segregation. Activity asynchrony occurs when some animals remain ruminating while others move off to forage, thus creating multiple groups. Generally, differences in grazing time between mature males and females are expected due to the added energy requirements of gestation and lactation incurred by females (Robbins 1983) even without size differences between the sexes. Ruckstuhl (1998) found that mixed groups of bighorn sheep moved much further per time than male groups, and Sinclair (1977) noted that male African buffalo seemed to have much smaller home ranges than mixed groups.

It is not clear at what degree of body size dimorphism differences in activity budgets between the males and females would be apparent. Ruckstuhl and Neuhaus (2002) suggested that a 20% difference in body mass between males and females was the threshold at which physiological differences in digestive efficiency would translate into differences in activity budgets. Results from Barboza and Bowyer (2000), where they modelled cervid digestion with males 20% and 70% larger than females, suggest that differences in digestive efficiencies would be visible at 20% dimorphism. They found that even at 20% dimorphism, males differed from non-reproductive, gestating and lactating females in metabolic and protein requirements and total retention time in the rumen, and different considerably from lactating females in energy obtained from

digesta. Although these models were done for cervids, the results suggest that African buffalo (*Syncerus caffer*) males and females would have differences in digestive efficiency which could be manifested in differences in activity budgets, as adult male African buffalo are on average 25% heavier than adult females (Owen-Smith 1988).

During the mating season, adult male buffalo move repeatedly between mixed groups and male groups. We term this pattern alternating sexual segregation. Buffalo adult females, subadults of both sexes and juveniles live in mixed groups throughout the year. Outside the mating season, all adult and some subadult males remain segregated in male groups (Sinclair 1977; Mloszewski 1983; Prins 1996). During the mating season in our study area, Hluhluwe-Umfolozi Park (HUP), most conceptions occurred between December and May with a peak in February and March (A. Jolles, in prep). Within this reproductive period, adult males are found in both mixed groups and male groups and individuals move between the two group types at time scales varying from weeks (Prins 1989) to days (W. Turner & A. Jolles, unpubl. data).

Different factors are likely to influence segregation in ungulates during mating and non-mating periods. During reproductive periods, males would be socially motivated to remain with females. Accordingly, Conradt (1999) and Bon et al. (2001) show that males and females are the least segregated during the rut. The periodic occurrence of segregation within the mating season in African buffalo indicates that there must be a strong pressure on males to cause them to presumably forgo mating opportunities. Evaluating differences in male

behaviour between mixed groups and male groups may illuminate the cause of this unexpected segregation.

Most past studies on social segregation among ungulates have been done in temperate regions (wood bison: Komers et al. 1992; moose: Miquelle et al. 1992; Alpine ibex: Villaret & Bon 1995, Bon et al. 2001; muskoxen: Côté et al. 1997; red deer/Soay sheep: Conrads 1998, Conrads et al. 1999, Conrads & Roper 2000; bighorn sheep: Ruckstuhl 1998, 1999; Przewalski's gazelle: Lei et al. 2001; Roosevelt elk: Weckerly et al. 2001), where ungulates generally have narrowly defined mating seasons (Owen-Smith 1988). Ruckstuhl and Neuhaus (2002) investigated activity budgets of oryx and zebra in a subtropical region within the context of sexual segregation, but both these species show no body-size dimorphism, and live in mixed groups year round. Hence, our study seems to be the first to examine the cause of social segregation in a dimorphic ungulate species under tropical or subtropical conditions. To fully understand the causes of segregation, species exhibiting segregation need to be examined in different climatic regions where the proportion of the year males interact with females can vary considerably.

This study focused on social segregation during the mating season in African buffalo. Spatial and habitat segregation were not considered, as preliminary observations showed that male groups and mixed groups utilised overlapping ranges and habitats. It seemed that the hypothesis of activity asynchrony and not social factors or social affinity would explain why males periodically segregate from females during the mating season. Males should clearly prefer to be where there are breeding opportunities, and we saw no

evidence that male dominance interactions or female aggression could be driving segregation. Fighting among buffalo is rare and males are seldom excluded from groups through acts of dominance or aggression (Sinclair 1977, Mloszewski 1983, Prins 1996).

The aim of our study was to evaluate whether the activity budget hypothesis explained the pattern of sexual segregation shown by mature male buffalo. We recorded daily activity patterns and movement rates for mixed groups and male groups. If activity asynchrony caused sexual segregation, we expected that within mixed groups (1) the larger males would forage for less time than smaller males and females and (2) male activity bouts would be out of synchrony with those of females. We further expected that males in male groups would be less active, forage more, and cover smaller distances than males in mixed groups.

2.3 Methods

2.3.1 Study Area and Animals

The study was conducted in Hluhluwe-Umfolozi Park (HUP) in KwaZulu-Natal, South Africa between September 2001 and May 2002. The specific study area was the Nqumeni section of Hluhluwe Park between 28°10' and 28°14'S, and 31°54' and 32°03'E. The mean annual rainfall in Nqumeni is 782 mm. Rainfall is strongly seasonal with most rain falling between October and March. The mean maximum daily temperature in HUP during the main conception period (December to May) was 30.7°C and 31.5°C during the peak in conceptions (February and March) of our field season. HUP contains savanna

vegetation comprising open fire-maintained grasslands, open woodlands, densely encroaching woodlands, thicket and closed woodlands. Buffalo often utilise open hillsides enabling observations from an opposite hillside without disturbing their activity. Observations were made using a spotting scope from distances of 300-1500 meters.

Male groups in HUP vary in size from 1-12 males with most groups containing 2-5 males. Discrete buffalo mixed herds in HUP vary in size from 30 to 250 individuals and periodically break up into two to three smaller subgroups. The mixed groups observed within our study area ranged from sub-groups of 30 individuals to entire herds of 150 individuals.

Our study focused on the daily activities of adult females and three size classes of males. Adult females were identified in the field by body size, coat condition and an absence of bosses. The male classes were distinguished through differences in body size and shape, horn wear and coat condition. Subadult males have hair between their bosses, their horns are unridged, their coats are sleek, their shoulders are the same height as adult females, and their body shapes are indistinguishable from females. Young adult males have very little hair between their bosses, the distal area of their bosses show wear, their coats have small patches of mange at the shoulder, they are slightly larger than adult females, and the signs of shape dimorphism, i.e. a dewlap and thickening neck and shoulders, emerge. Mature males have no hair between their bosses, their bosses show wear throughout, their coats have substantial mange, they are larger than adult females and have large dewlaps and thick shoulders and necks. The size classes were correlated to age using mean incisor height: adult females (6+ years), subadult

males (5-6 years), young adult males (7-9 years), and mature adult males (10+ years) (A. Jolles unpubl. data).

2.3.2 *Data Collection and Analyses*

We recorded activity patterns of mixed groups and male groups using scan samples at 15-minute intervals (after Altmann 1974). The behaviours categorised as active included grazing, moving, reproductive activities (including courting, testing and tending females), sparring, nursing, vigilance and other activities (including scratching, grooming, defecating and urinating). Inactive behaviours included ruminating, standing-motionless, and lying.

We observed buffalo for as long as possible during daylight hours. The length of observations was often limited by buffalo moving into low-lying woodlands and ravines to wallow at mid-day. In order to utilise partial-day samples, we divided the day into morning (6:00-12:00) and afternoon (12:00-18:00) time periods. Within these morning and afternoon time periods we used samples containing observations greater than three hours in duration. A mean proportion of animals performing the target activity was calculated from the scan samples for each half-day sample, and these mean proportions were the sample unit analysed. We analysed a total of 37 half-day observations on mixed herds, and 36 half-day observations on male groups for differences in time spent active and grazing. We also present the proportion of a full day spent in each of the activities recorded, using observations of 10 hours and longer (mixed groups: n=10, male groups: n=6) to compare with our half-day observations and other studies.

When comparing the activity patterns of mixed groups with male groups, we used ANOVA. Data on the two group types were collected from different groups on different days and we further let at least one week pass between repeated observations on a particular mixed or male group. For comparisons between age-sex classes within mixed groups, we used paired *t* tests, as the activity data from each age-sex class were obtained during the same observation periods. This procedure reduced the effects of extraneous variability on activity levels.

When testing for differences in total time spent active, we used two-tailed comparisons. When testing for differences in grazing time, we used one-tailed comparisons, because female ungulates invariably forage for longer than males (Owen-Smith 1988). Furthermore, feeding time of males is expected to decrease with increasing age and body size, as growth is more energetically costly than maintenance (Bunnell & Gillingham 1985). We also expected males in male groups to forage more than males in mixed groups, as they have fewer potential distractions from foraging. In the results, means are reported together with standard errors.

All of these comparisons were checked for the influence of extraneous factors which could affect activity budgets. These factors included the presence of oestrous females, different stages of the wet season (early, mid, late), cloud cover (clear, partly cloudy and overcast), maximum daily temperature and time of day (morning or afternoon). When comparing male groups with mixed groups, these factors were incorporated in the ANOVA. Time spent active and grazing both required a square root transformation to approximate a normal distribution.

When doing comparisons within mixed groups, we initially performed ANOVA on the difference in total active or grazing time between the age-sex classes.

When certain factors had significant effects on active or grazing time, the data were analysed separately for different ranges in condition.

We terminated observations during heavy rain. We noted the presence or absence of oestrous females by observing male courtship behaviour (Sinclair 1977). Maximum daily temperature data was obtained from a weather station of the Zululand Grassland Project located within our study area. Previous studies of activity patterns on African ungulates have found that activity levels decreased above 32°C, including eland (Lewis 1977), giraffe (Leuthold & Leuthold 1978), impala and blesbok (Klein & Fairall 1986). Therefore, we used temperature categories of 32°C and above, and below 32°C when investigating temperature effects.

Distance travelled was determined by recording a GPS location at the beginning and end of the observation period and tracking the path of movement between the two locations on a topographical map. The rate of movement was compared for mixed groups and male groups using a one-tailed *t* test, as we expected mixed groups to move further per hour than male groups. Sinclair (1977) noted that male groups tended to have smaller home ranges than mixed groups, and male groups in HUP seemed to move much less than mixed groups (pers. obs.). Movement rates were square root transformed to approximate a normal distribution. Samples shorter than four hours were excluded from analysis.

The large herd sizes prevented us from recording activity bouts of individual animals in order to assess activity synchrony directly. In order to estimate female synchrony, we categorised each individual scan sample as part of an active or inactive period. Samples were categorised as active when greater than 50% of females were active. A series of consecutive active or inactive observations were then divided into 1-2 hour bout segments, and a mean value of female activity was calculated for each segment. The bout segments were further subdivided by the proportion of females grazing while the majority were active or inactive. We had 166 bout segments which span the range of female activity levels. Since we found a low degree of synchrony among females, we did not attempt to calculate the synchrony between males and females.

2.4 Results

2.4.1 Grazing Time and Movement

Mature males in mixed groups grazed for significantly less time than mature males in male groups (one-way ANOVA: $F_{68}=8.5$, $p<0.003$, Figure 2.1a). Mixed groups also travelled further per observation time than male groups; mixed herds moved at a rate of 159 ± 97 m/hr and male groups at 51 ± 40 m/hr ($t_{43}=4.1$, $p<0.001$). The main periods of movement occurred in the early morning and late afternoon. During mid-day, there was very little distance covered by either mixed herds or male groups.

Within mixed groups, adult females spent more time grazing than mature males at temperatures above 32°C ($t_{12}=4.9$, $p<0.001$, Figure 2.1b). At temperatures below 32°C , mature males grazed for significantly less time than

adult females in the morning (females: 31.4%±4.4%, males: 22.6%±2.9%, $t_{11}=3.8$, $p<0.002$) but the difference was smaller and not quite significant in the afternoon (females: 20.1%±4.6%, males: 17.6%±6.1%, $t_7=0.9$, $p=0.195$). There were significant differences in grazing time between all male age classes, where the younger males spent more time grazing than older males (Figure 2.1a). Mature adult males grazed for less time than both young adult males ($t_{32}=2.7$, $p=0.005$) and subadult males ($t_{30}=4.4$, $p<0.001$). Young adult males also spent significantly less time grazing than subadult males ($t_{32}=2.3$, $p=0.014$).

2.4.2 Active Time

At temperatures below 32°C, mature males and adult females showed no significant differences in total active time ($n=20$, Figure 2.2b). Above 32°C, the activity of mature males was depressed and males were less active than adult females ($t_{13}=5.1$, $p<0.001$). There were no significant differences when comparing the time spent active of mature males versus young adult males or subadult males versus young adult males (Figure 2.2a). Subadult males were more active than mature males during afternoon periods at temperatures above 32°C (subadult males: 24.7%±3.0%, mature males: 16.6%±2.5%, $t_5=2.9$, $p=0.032$) and in mornings at temperatures below 32°C (subadult males: 26.9%±4.4%, mature males: 22.6%±2.9%, $t_{11}=2.4$, $p=0.039$). Differences in active times seemed to depend more on relative body size and temperature than

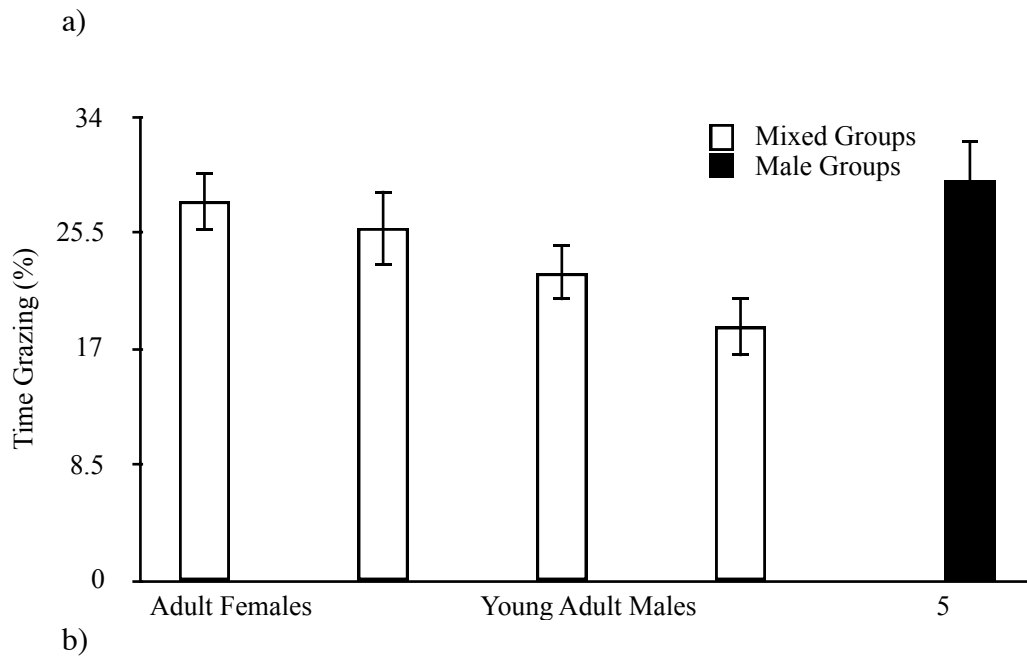
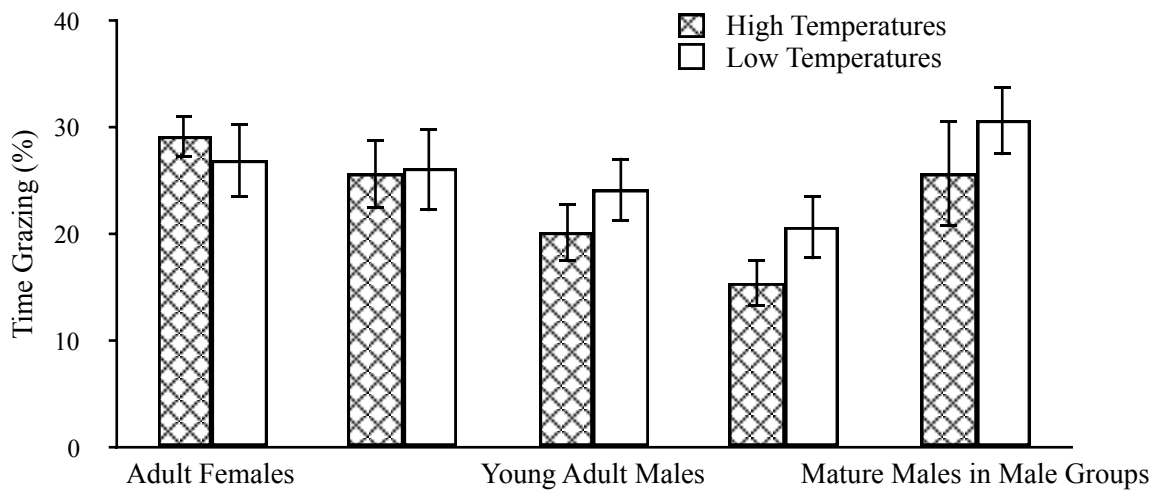


Figure 2.1: The proportion of half-day observation time buffalo spent grazing, combining morning and afternoon samples. a) mean time spent grazing for age-sex classes in mixed groups and male groups, and b) mean time spent grazing in mixed groups and male groups subdivided by the daily temperature maximum of above or below 32°C. Mixed groups: n=37, Male groups: n=36.



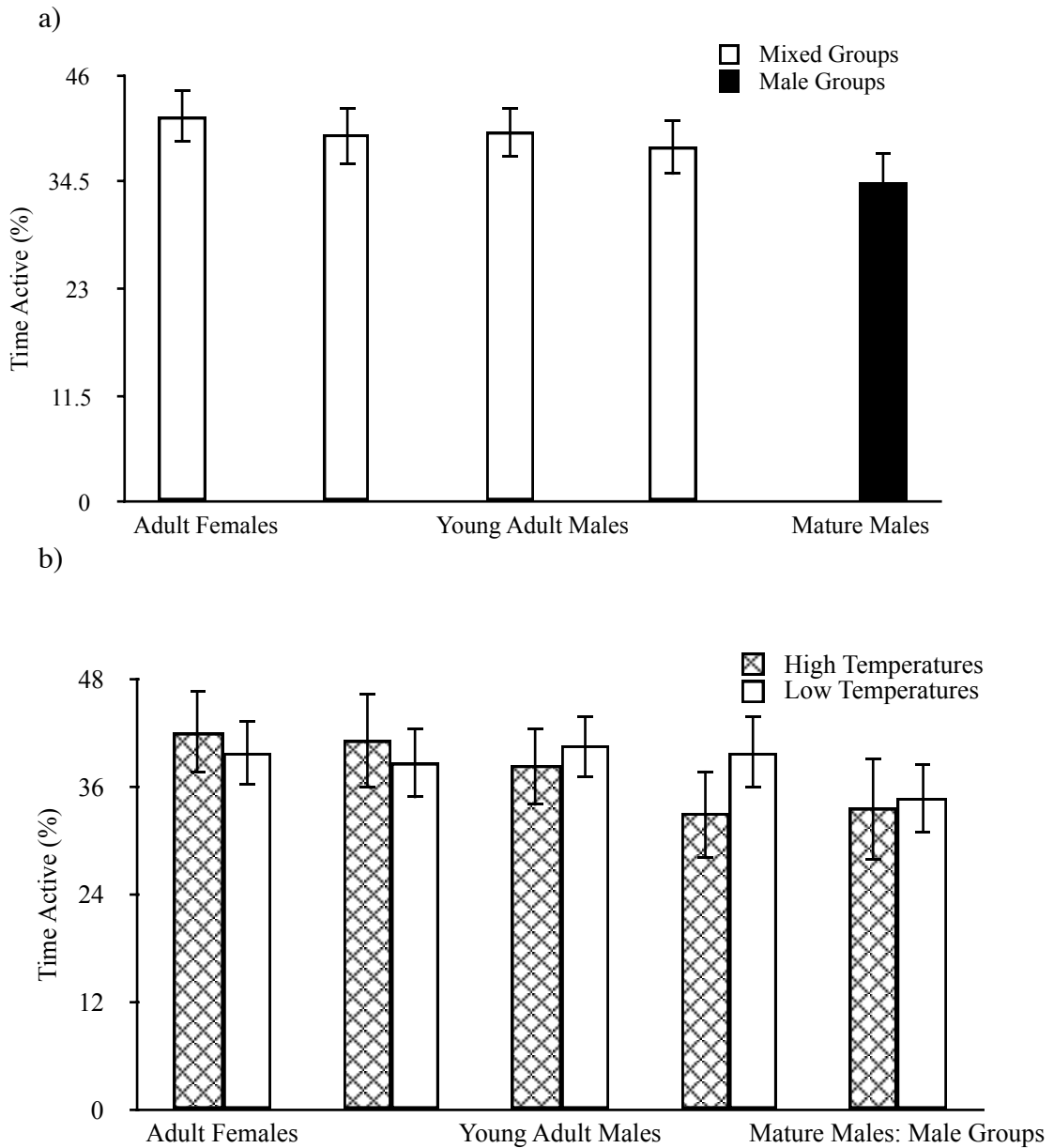


Figure 2.2: The proportion of half-day observation time buffalo spent active, combining morning and afternoon samples. a) mean time spent active for age-sex classes in mixed groups and male groups, and b) mean time spent active in mixed groups and male groups subdivided by the daily temperature maximum of above or below 32°C. Mixed groups: n=37, Male groups: n=36.

on sex differences.

In the morning mature males were more active in mixed groups than in male groups, but the differences were not quite significant as the active times were rather variable (mixed groups: $46.4\% \pm 4.5\%$ male groups: $36.0\% \pm 3.9\%$, two-way ANOVA: $F_{46}=3.7$, $p=0.060$). There was no difference in active time of mature males in mixed groups versus male groups in the afternoon (mixed groups: $29.7\% \pm 3.8\%$, $n=13$; male groups: $30.0\% \pm 5.3\%$, $n=9$).

The results presented above based on morning and afternoon periods are consistent with the activity budgets of buffalo over a full day (Table 2.1). The total activity time shows the same relative pattern among age-sex classes, but the percentages of active time are less for the all-day samples. The relative differences in grazing times between age-sex classes are equivalent above 32°C . Below 32°C the grazing pattern is equivalent with the exception of the subadult male class which has a low mean grazing time with high variability. At temperatures above 32°C , when mature male activity was already depressed, mature males in mixed groups were moving much more than other age-sex classes (Table 2.1). If the movement of mixed groups is determined by females, then the increased movement observed in mature males is beyond what would be necessary to maintain group cohesion. Mature males in mixed groups also courted females, an activity which encompassed roughly 10% of their active time. Much of the extra movement by mature males is likely an effect of manoeuvring through the herd to assess reproductive opportunities and rival males.

Table 2.1: Allocation of active time to particular activities by buffalo in mixed groups and male groups during all-day observations, taking into account the daily temperature maximum. Includes samples of 10 hours and longer in duration. Values reported with mean±SE

Temp	Group	Age-Sex Class	% Active (of day)	n	Active proportion spent in different activities (%)						
					Grazing	Moving	Courting	Sparring	Vigilant	Other	Nursing
T>3 2 C	Mixed Groups										
		Adult Females	34.1 ±3.2	5	83.1±4.1	11.6±3.7	-	<0.1	1.8±0.2	2.5±0.2	1.0±0.4
		Subadult Males	30.6 ±6.0	5	77.0±4.9	13.6±3.4	<0.1	1.8±1.1	1.0±0.7	6.5±2.0	-
		Young Adult Males	27.9 ±5.3	5	70.9±4.9	16.4±4.3	2.9±1.0	2.0±1.1	3.4±1.1	4.3±0.9	-
		Mature Males	26.3 ±4.6	4	52.7±3.5	30.4±5.4	7.0±2.4	2.0±1.2	3.9±1.4	4.1±2.9	-
		Male Groups									
		Mature Males	30.0	1	87.6	10.9	-	-	1.4	-	-
T<3 2 C	Mixed Groups										
		Adult Females	34.2 ±4.4	5	58.5±8.9	25.4±7.1	0.2±0.1	0.2±0.1	8.7±1.9	5.7±2.1	1.3±0.6
		Subadult Males	31.9 ±5.7	5	50.4±13.9	28.6±13.1	1.8±1.6	8.1±3.6	7.6±3.0	3.6±1.5	-
		Young Adult Males	35.7 ±4.0	5	55.5±5.6	22.8±6.4	6.0±2.8	4.4±1.3	6.9±2.4	4.4±1.6	-
		Mature Males	32.8 ±4.6	5	50.3±11.4	27.2±7.0	11.2 ±4.1	<0.1	4.9±1.8	6.4±2.6	-
		Male Groups									
		Mature Males	30.5 ±5.6	5	93.6±2.2	1.6±0.9	-	1.0±0.6	0.5±0.3	2.4±1.3	-

2.4.3 *Activity Synchrony*

During active periods in mixed groups, adult females showed little activity synchronisation amongst themselves (Figure 2.3). If females were highly synchronised in the timing of their activities, then most bout segments should be concentrated around 0% and 100% activity. The occurrence of grazing throughout most inactive bouts indicates that even while the majority of females are inactive, some individuals are still foraging. Where greater than 90% of females were active, nearly half of observations show less than 50% of females grazing. These observations correspond to times when mixed groups moved location in the early morning and late afternoon.

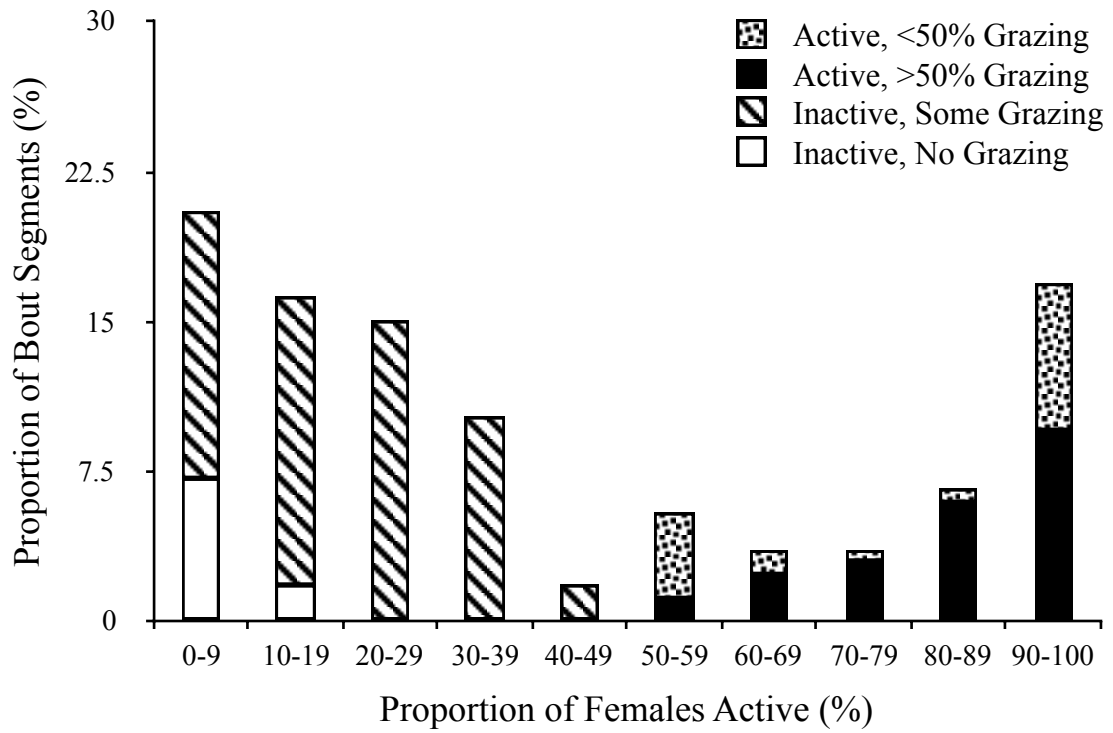


Figure 2.3: The proportion of bout segments occurring across the range of activity levels for adult females, from fully inactive to fully active.

2.5 Discussion

2.5.1 Activity Asynchrony and Sexual Segregation

Ruckstuhl and Neuhaus (2002) argue that the activity budget hypothesis, which states that males and females segregate due to differences in activity budgets, is the general cause for sexual segregation in ruminants. Ruckstuhl (1998) explained that in order to stay in female groups, males would have to synchronise their foraging behaviours and movement patterns with those of females. However, the activity budget hypothesis is dependent on the assumption that the activities of females are highly synchronised. Buffalo females in HUP were able to maintain group cohesion without a high degree of activity synchrony. During the mating season, which coincides with the rainy season, there is abundant high-quality forage available. Groups could remain in a feeding location throughout the day, allowing some animals to rest while others fed without affecting group stability. If females are not highly synchronised, then group cohesion can be maintained even with large sex differences in grazing bout lengths. We recommend that female activity synchrony should be evaluated before concluding that sex differences in activity budgets lead to segregation.

2.5.2 Time Costs and Sexual Segregation

If activity asynchrony does not lead to social segregation in African buffalo, the question remains: what causes the alternating sexual segregation of mature males? Prins (1989) found for buffalo in Manyara, Tanzania, that segregation was related to body condition changes of males, where they lost condition in mixed groups and regained condition in male groups. In HUP,

condition changes in bulls were not readily apparent, for during the mating season forage was abundant and most animals were in good condition. The movement between mixed groups and male groups could also happen over a period of a few days, before visible changes in body condition would be evident.

We suggest that alternating sexual segregation may result from the time and energy costs of reproductive activities incurred by males. Mature males showed no significant difference in total time active between mixed groups and male groups, but the allocation of active time in each group differed considerably. In male groups, active time was spent mainly grazing, and other activities, including movement, made up a small proportion of active time. Mature males in mixed groups spent time pursuing reproductive activities, including searching for receptive females and watching rival males, at the expense of grazing time. They grazed for considerably less time than males in male groups, they courted females and they allocated more time to moving and vigilance. These results suggest that within the available active time, males in mixed groups select reproductive activities over feeding. Komers et al. (1992) suggested, similarly, that male wood bison leave breeding herds during the mating season for a recovery period rather than to search for other breeding opportunities. Male buffalo did not rest significantly more while in male groups, but their grazing time was considerably higher than mature males in mixed groups.

The grazing and active times we report for the half-day and full-day observations are within the range of daytime activity patterns reported for buffalo in other studies (Stark 1986, Prins & Iason 1989, Winterbach & Bothma 1998). Our study did not look at night activity patterns, and it is possible that males

could make up for deficits in their daytime grazing time budget by foraging at night. As daytime matings are rarely witnessed (Prins 1996, pers. obs.), however, heightened reproductive activities after dark may prevent males from compensating for reduced daytime grazing.

Mature males in mixed groups grazed for less time than adult females, young adult males and subadult males in these same groups. This is consistent with patterns seen in most ungulates due to the increased energy demands of lactation and gestation on females (Robbins 1983) and growth for immature animals (Bunnell & Gillingham 1985). The gestation period for buffalo females is 11-11.5 months and many adult females have two calves within a three year period (Pienaar 1969), so most females will be gestating, lactating or both throughout the year. Due to these high energy demands on females, it is not surprising that adult females grazed more than mature males in mixed groups. Mature males in male groups, however, spent as much time grazing as adult females. The elevated grazing times of these males suggests that alternating sexual segregation may facilitate maintenance of their competitive ability during the extended mating season. Male buffalo should clearly join mixed herds to pursue reproductive opportunities, and their respites in male groups may be to maintain their competitive ability (Prins 1989).

As smaller animals conduct more heat to the external environment than larger animals due to their relatively larger surface to volume ratio (Parker & Robbins 1985), in high temperatures male buffalo may be less efficient at dissipating heat than females. This may explain the decrease in active time of mature males compared with adult females and subadult males in temperatures

above 32°C. As the peak of the mating season in HUP had mean temperatures of 31.5°C, temperature and body size differences may have a larger influence on activity time than sex differences. Therefore, the restriction of activity budgets through male heat sensitivity may be an additional factor which could influence the importance of alternating sexual segregation for males. Male active time is constrained by higher temperatures, and the peak of the mating season occurs around the hottest part of the year. In mixed groups males exhibited a decrease in time spent grazing in higher temperatures, but the time allocated to other activities remained the same. Therefore it seems that males are choosing reproductive activities over foraging. These temperature effects may be relevant to many other segregating species, for most polygynous ungulates occur in tropical and subtropical environments. Generalisations on sexual segregation from temperate species will not necessarily be appropriate for tropical species.

The results of this study suggest that during the mating season males join mixed groups for mating opportunities and move into male groups periodically to increase their grazing time. Cross and Getz (in review) show that within mixed groups African buffalo preferentially associate with individuals of the same sex and age cohort, with the exception of cow-calf pairs. Segregation outside the mating season may be due to a combination of these factors, where males prefer to interact with individuals of their same age and sex and would suffer from reduced grazing if in the presence of females. Further research should be directed towards examining male behaviour and the occurrence of segregation during the mating season in species which vary in the length of the mating period. The causes of sexual segregation may be further elucidated by examining

how male behaviour can change when inside and outside of female groups, and between the mating and non-mating periods.

3. CONCLUSIONS

3.1. Summary of Research Findings

This study achieved my research aim: to help understand why male buffalo leave mixed groups during the mating season. The time and energy costs of reproductive activities incurred by mature males when in mixed groups may lead to alternating sexual segregation. This is reflected in the dramatic rise in grazing time for mature males in male groups versus mixed groups (objective B, section 1.2). I evaluated the activity budget hypothesis for African buffalo, and found that although there were differences in activity budgets between males and females in mixed groups (objective A, section 1.2) and differences in the movement rates in mixed and male groups (objective B, section 1.2), activity asynchrony was unlikely to be causing the observed sexual segregation (objective C, section 1.2). Finally, I established that males in mixed groups do not correct for the reduction in grazing time by increasing their intake rate when feeding (objective D, section 1.2).

I selected my objectives in order to evaluate the details of the activity budget hypothesis, and as my results do not support this hypothesis, not all of the planned analyses were feasible. I did not evaluate the degree of activity asynchrony between females and the male age classes. Females exhibited such low activity synchrony that males would not need to constrain their activity budgets to synchronise with females.

My results may support the social affinity hypothesis, which suggests that behavioural compatibility between individuals contributes to group cohesion, and incompatibilities contribute to segregation (Bon et al. 2001). Although Bon et al. (2001) specify that this would explain segregation outside the rut, my results suggest that behavioural incompatibilities could also lead to segregation during reproductive periods. Mature males would be motivated to remain with females, but the time and energy costs of reproductive behaviours may be ‘incompatible’ with feeding in mixed groups.

The results of my study highlight the importance of focusing on different climatic regions. Most studies examining sexual segregation of body size dimorphic species, and all studies on social segregation, have focused on dimorphic species in temperate or arctic regions. These areas are relatively depauperate of ungulate species and tend to have extremely short mating periods. African buffalo have a long gestation period where parturition and conception both occur during the long breeding season (Pienaar 1969). Therefore parturition, when most sexually segregating species are at their greatest degree of segregation, coincides with the mating season, when males would have the greatest motivation to remain with females. Although the simultaneity of births and conceptions is unusual, in African ungulates a narrowly defined mating season is more the exception than the rule (Estes 1991). Additional research should be directed at African species to assess the generality of sexual segregation hypotheses. Tropical/subtropical regions are quite different from temperate/subarctic regions in the type of environmental variation, the occurrence of large predators, and the number of segregating ungulate species.

3.2 Applicability to Other Buffalo Populations

To assess the generality of my results, I investigated the occurrence of alternating sexual segregation in other buffalo populations. Considerable differences in social affiliation behaviour of buffalo males during the mating season have been documented. There is agreement that bulls past their reproductive prime will leave mixed groups permanently (Grimsdell 1969, Sinclair 1977, Prins 1989), and that reproductive males will leave mixed groups during the dry season (Grimsdell 1969) or during lulls in reproductive activity (Sinclair 1977). During the mating season, however, different behaviours have been documented: reproductive bulls remain with mixed groups in Uganda (Grimsell 1969), in the Serengeti National Park, Tanzania (Sinclair 1977), and in Kruger National Park, South Africa (P. Cross pers. comm.); bulls remain on the periphery of mixed groups in Zambia and south-western Kenya (Mloszewski 1983); and bulls will move between mixed and male groups over a period of weeks in Lake Manyara National Park, Tanzania (Prins 1989) or days in Hluhluwe-Umfolozi Park (HUP), South Africa (W. Turner & A. Jolles unpubl. data).

The occurrence of alternating sexual segregation may be influenced by the temporal and spatial distribution of oestrous females. If a male segregates, he must be able to relocate a mixed group or he loses all mating opportunities. The spatial distribution of oestrous females depends on the size of a group's home range and the distance they travel per day. The smaller the home range and the shorter the average distance travelled per day, the easier males can relocate mixed

groups. Whether or not a male segregates may also relate to the number of oestrous females in a group at any one time. The greater the number of oestrous females in a herd at a given time, and the shorter the intervals with no oestrous females in a herd, the greater the incentive would be for bulls to remain in mixed groups. Therefore, the temporal concentration of oestrous females depends on the number of reproductive-aged females in groups and the length of the mating season.

I compiled these spatial and temporal factors from buffalo populations in Hluhluwe-Umfolozzi Park and Kruger National Park in South Africa, and the Serengeti National Park and Lake Manyara National Park in Tanzania. Judging from the factors presented in Table 3.1, group size and home range size may have a greater influence on the occurrence of alternating sexual segregation than daily movement or length of the mating season. In Kruger and the Serengeti, the cost of leaving mixed groups for increased foraging may be higher than the cost of remaining with mixed groups. These populations both have considerably larger home ranges and group sizes than Manyara and HUP. Therefore, many oestrous females would be concentrated in large groups that could be difficult to relocate if alternating sexual segregation occurred.

The two populations that show alternating sexual segregation, HUP and Manyara, have smaller group sizes and home ranges than the Serengeti and Kruger.

Manyara may exhibit alternating segregation because the home ranges of herds are concentrated around the lake, and are therefore quite small. In HUP the number of oestrous females in a mixed group was generally zero or one, I rarely observed more than one female in oestrus simultaneously. The group sizes and

home ranges may be small because HUP is a comparatively small, well-watered reserve, with multiple rivers and hills that further subdivide the park. As Mloszewski (1983) detailed, group size and home range size depend on the distribution and quantity of food and water, as well as the physical geography, vegetation types and predation within an area.

Buffalo male behaviour varies between populations that are spatially quite close. HUP and Kruger are 300 kilometres apart, and the Serengeti and Manyara are only 60 kilometres apart. This suggests that behaviour is driven by the ecology of an area and not by genetic factors, as populations that are presumably more closely related do not have similar behaviour. Therefore, broad geographic location is a poor predictor of buffalo behaviour; the details of local resource distribution are more important.

Further research could be conducted on activity patterns and male behaviour within a buffalo population that does not exhibit alternating sexual segregation. I would expect that males in mixed groups would have to forage more in mixed groups or show a substantial decline in body condition as the mating season proceeds.

Table 3.1: The occurrence of alternating sexual segregation and factors affecting temporal and spatial distribution of oestrous females in different buffalo populations.

The numbers presented are an approximation as they were generally extrapolated from published data or from correspondence with researchers.

Location	Alternating Segregation?	Group Size Mean (Range)	Home Range Size (km ² /year)	Mating Season (# of months)	Daily Movement (km/12 hours)	Source
Hluhluwe-Umfolozi	Yes	100 (30-250)	50	6	1.3 (mean, wet season)	Jolles in prep., pers. comm., Turner unpubl. data
Lake Manyara	Yes	260 (12-980)	50	8	-	Prins 1996
Serengeti	No	350 (50-1500)	250	6	2.75 (minimum/year)	Sinclair 1977
Kruger	No	575 (200-1000)	256	5	2.5 (mean, wet season)	Cross pers. comm.

3.3 Implications for Conservation and Disease Management

The varying occurrence of alternating sexual segregation in buffalo populations has serious implications for disease management. In HUP, mature males move between mixed groups and male groups throughout the mating season. These males do not necessarily return to the same mixed group; I have observed known males in as many as three separate groups. Mixed groups in HUP are discrete, and despite often breaking into smaller fragments, each group has a stable home range that overlaps little with neighbouring groups (Jolles in prep.). The movement of males between mixed groups in HUP's population may have a greater effect on disease spread than in other populations where males remain with a mixed group throughout the mating season.

My master's research contributes to a collaborative study with Anna Jolles and Scott Creel, where we believe mature males are the most likely culprits for inter-herd transmission of TB. The adult male age-sex class has the highest prevalence of TB (Jolles and Cooper in prep.), which we think can be explained in two ways. First, males contact a greater number of individuals as they move between otherwise distinct herds, and therefore are more likely to encounter the disease. Second, high faecal cortisol levels found in males from mixed groups suggest that these males are significantly more stressed than adult females or males in male groups (Jolles et al. in prep). High levels of the stress hormone cortisol, can compromise immune function (Nelson 2000), and this may render males more susceptible to infection when they are exposed to *Mycobacterium bovis*, the causative agent of bovine TB. Observations from my research suggest that stress levels in buffalo may correlate closely with their grazing times:

females and mature male in male groups were much less stressed and grazed much more than mature males in mixed groups. Interactions with competitors and potential mates in mixed groups also likely contribute to high stress levels in these males. This collaborative study connects several levels of causality: social and feeding behaviour may influence stress levels in buffalo which in turn appear to affect susceptibility to disease.

It is important to understand the behaviour of populations when constructing management and conservation programmes. In HUP, the ongoing TB control programme has focused on testing and culling positive animals from mixed groups. This programme, however, takes place during the non-reproductive period, when most adult and subadult males are not with mixed groups. Therefore, despite the enormous success the programme has shown in reducing the TB prevalence in mixed groups, the disease may remain uncontrolled in male groups. If infected males enter mixed groups in the mating season they may re-infect controlled herds. My research has helped bring attention to the problem of TB in male groups, and wildlife managers at KwaZulu-Natal Wildlife, the provincial authority in charge of HUP, are considering how to incorporate this information into the disease control programme.

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