The effects of sexual dimorphism on the movements and foraging ecology of the African elephant

By

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ABSTRACT

Large herbivores are key components of terrestrial biomes because of their relative abundance and pronounced influence on ecosystem functioning and habitat structure. To manage and conserve these species effectively, requires greater understanding of their distribution and use of resources at varying spatial and temporal scales. Sexual dimorphism is one aspect of large herbivore ecology likely to have a significant effect on resource use and community level interactions. Elephants present an ideal species to test the influence of sexual dimorphism due to their marked body size and pronounced behavioural differences. This study used location and behavioural data collected over an 8 year period in five different South African reserves, all of which had well documented elephant populations. The reserves were relatively small (<1000 km^2) and had augmented water supplies so analyses were not influenced by surface water availability. Results indicated that male and female elephants resolve their available range at distinctly different scales. Both sexes were shown to expand their ranges with increasing forage quality, however males were the most flexible in their temporal and spatial response during periods of low resource availability. Females were more selective than males, targeting higher quality forage and being less destructive in their feeding approach. This may be due to females' higher mass specific energy requirements associated with their smaller body size and substantial reproductive investment. They were also constrained by the costs of group living compared to male elephants which range independently. Sexual segregation is a consequence of body size dimorphism and was investigated at both the habitat and plant scale to elucidate the mechanism driving the separation of the sexes. Whilst individual habitat preferences exist, these are not sufficient to segregate the sexes. At the plant scale, significant differences were shown with regard to foraging duration, tree size and plant parts eaten. Further investigation of sexual segregation involved testing the recently proposed activity budget hypothesis. Males and females have similar daily activity budgets and relatively high levels of behavioural synchrony, which is not sufficient to explain segregation. Instead, the marked sexual segregation appeared to be caused by social organisation, reproductive strategies and the divergent foraging behaviour of males and females at the plant scale. This research highlights the importance of considering male and female dimorphic herbivores as ecologically distinct species. For example, male elephants are likely to be driving the majority of destructive foraging bouts and this will often be in a heterogeneous manner, especially during periods of resource scarcity. Therefore, the effective management of elephants requires considering population structure, individual behaviour and population size.

PREFACE

The fieldwork described in this dissertation was carried out in the Pongola Game Reserve; Pilansberg National Park; Phinda Private Game Reserve; Tembe Elephant Park and Hluhluwe imfolozi Park in South Africa, through the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban from November 2002 to December 2005. This work was performed under the supervision of Professor Rob Slotow and the co-supervision of Mr Bruce Page.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others, it is duly acknowledged in the text.

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ANOVA	analysis of variance
D	drinking
F	feeding
FSH	forage selection hypothesis
GC	gut capacity
GPS	global positioning system
HiP	Hluhluwe imfolozi Park
M	body mass
MR	metabolic rate
PAs	protected areas
PGR	Pongola Game Reserve
PNP	Pilansberg National Park
PPGR	Phinda Private Game Reserve
R	resting
SCH	scramble competition hypothesis
TEP	Tembe Elephant Park
W	walking

CHAPTER 1

GENERAL INTRODUCTION

Introduction

Large herbivores (distinguished herein as >5 kg) are a major component of terrestrial ecosystems, influencing vegetation community dynamics, nutrient cycling, disturbance regimes and biomass availability through their foraging, trampling, urination and defecation (Gross et al., 1995; Hobbs, 1996; Boyce et al., 2003; Gordon et al., 2004). They exhibit pronounced diversity and are widely distributed in all of the major biomes (excluding the poles) and are considered to be one of the main drivers in habitat structure and ecosystem functioning (Gordon et al., 2004). Their relatively high abundance and large body size means that they require extensive ranges and abundant forage to satisfy their energy demands (Owen-Smith, 1992). Large herbivores exist at population densities which far exceed that of other similar sized mammals (e.g. carnivores), due to the nature of energy flow in the ecosystem, with the largest portion of available resources being at the plant level (Begon et al., 1996). This abundant food source and its heterogeneous nature, both in distribution and chemical composition, has enabled large herbivores to evolve diverse morphological and physiological adaptations (Van Soest, 1996; Shipley, 1999).

Large African Herbivores

Sub Saharan Africa has a diverse compliment (n =90) of large herbivore species which are distributed across the continent, from the open grasslands and savanna of the east and south to the rain forests in central and western Africa (McNaughton & Georgiadis, 1986; Owen-Smith, 1992). The savanna biome supports the greatest species richness of large herbivores, one that is unparalleled in any other bio-geographic region of the planet, even when taking the Pleistocene extinctions into account (Fritz et al., 2002). This is due to the high level of spatial and temporal heterogeneity that typifies savanna habitats (Bell, 1986; du Toit & Cumming, 1999). Large herbivores are predicted to exhibit the greatest diversity in areas with intermediate plant moisture and high nutrient availability, as this will maintain sufficient high quality forage for small herbivores, whilst being productive enough to support larger herbivores that require greater abundance of plant material (Olff et al., 2002).

The total biomass of large herbivores in the savanna biome also exhibits pronounced fluctuations which have been estimated to vary by as much as two orders of magnitude (Fritz et al., 2002). Rainfall and soil nutrient status are predicted to be the most influential factors in determining the densities of large herbivores (Coe et al., 1976; East, 1984). These two variables have been shown to account for 80% of the variation observed in African savannas (Fritz & Duncan, 1994). Despite these relationships, large African herbivores have a dominant role in ecosystem functioning and are likely to be major regulators. It

is estimated that large herbivores consume up to half of the plant production in Africa, giving an indication of their important role (du Toit & Cumming, 1999).

High densities of large African herbivores also provide a substantial resource, which if managed well, can yield significant economic and subsistence benefits (Leader-Williams et al., 2001; Gordon et al., 2004). However, despite the relatively low human population density, protected areas (PAs) are fast becoming the only refuges available to many African species, which are unable to compete with overexploitation, agriculture and human habitation (Thouless, 1994; Hoare, 1999; Sitati et al.,, 2003). The loss of habitat is now arguably the most critical issue facing many African species. This is especially pertinent for large herbivores, which require extensive ranges and the ability to disperse during seasonal changes in forage or water availability (Western, 1975; Thouless, 1995; Illius & O'Connor 2000). Many of the PAs have now become separate islands that are prone to problems associated with isolated populations including stochastic events, inbreeding, genetic drift and disease (Caughley, 1994). Whilst the restriction of movement and dispersal within reserves, either through fencing or human barriers (Hoare & du Toit, 1999) has led to the compression of many large herbivore populations, the resultant high densities have been linked to the degradation of vegetation and subsequent loss of biodiversity, especially with regard to the elephant (Van Wyk & Fairall, 1969; Laws, 1970; Owen-Smith, 1992; Moolman & Cowling, 1994; Johnson et al., 1999; Tedonkeng Pamo & Tchamba, 2001). The effects of smaller herbivores are often less obvious due to their feeding selectivity. However, it is believed they can impact the recruitment of woody plants (Belsky, 1984; Prins & Van der Jeugd, 1993; Van de Koppel & Prins, 1998).

Heterogeneity and Scale

Understanding the responses of individual species at different scales has far reaching implications for the effective management and conservation of large herbivores (Gordon et al., 2004). Scientific research attempts to answer the complex questions relating to the movement and foraging ecology of these species at different spatial and temporal scales (Senft et al., 1987). Heterogeneity has largely been ignored by ecologists until relatively recently, but it is in fact likely that heterogeneity, both in time and space is central to understanding the functioning of ecological systems (Pickett & Cadenasso, 1995, du Toit & Cumming, 1999; Illius & O'Connor, 2000). It has even been suggested, that the behaviour of an individual at small spatial scales can be extrapolated to understand patterns and interactions at larger, more complex scales, which has direct relevance to the management of species (Etzenhouser et al., 1998; Morales & Ellner, 2002).

The spatial scales of resolution range from the chemical composition of individual plant parts which are foraged upon, to the habitat patch, the landscape and the regional system which contains the entire range of a particular animal (Senft et al., 1987; Seagle & McNaughton, 1992; Ball et al., 2000; Skarpe et al., 2000). The temporal scale is equally broad from the amount of time spent feeding on a particular plant (Brown, 2000) up to the seasonal shift in range and foraging behaviour (Wilmshurst et al., 1999).

According to optimality theory, the main objective of a herbivore is to maximize energy and nutrient intake whilst balancing risk (e.g. predation and competition) (Stephens & Krebs, 1986, Brown, 2000). This takes place in spatially heterogeneous landscapes that contain abundant low quality forage and limited patches of higher quality forage, presenting the herbivore with a series of foraging decisions relating to the time spent searching for and feeding on particular plants and plant parts (McNaughton & Georgiadis, 1986; Senft et al., 1987; Owen-Smith, 1992; Brown, 2000). This contrasts sharply with predators that feed on discrete prey items, which have a relatively constant and high nutritional value (Senft et al., 1987; Choat & Clements, 1998). The strategy of searching out and feeding on higher quality food items will provide the animal with greater nutrient intake (Van Soest, 1996). However, the time spent searching for these relatively rare resources may prove prohibitively expensive, especially for animals with sizeable energy demands. It may therefore be more optimal to target the abundant lower quality forage and spend more time feeding and less time searching for high quality food sources (Demment & Van Soest, 1985; Krebs & Davies, 1993). In addition to consuming enough plant material to satisfy energy demands, the individual needs to eat a balanced diet and avoid ingesting toxic secondary compounds such as tannins which inhibit digestion (Belovsky, 1984; Ward & Saltz, 1994). Feeding behaviour is therefore closely linked to the heterogeneous nature of the system and as such, animals can adapt their behaviour according to costs (e.g. predation and competition) and benefits (e.g. high quality food patches, shelter) (Brown, 2000).

The decision making of an individual is likely to vary at the different scales and understanding the interactions between scale and heterogeneity will provide a much greater insight into ecosystem processes and community composition (Senft et al., 1987). For example, savanna ecosystems are defined by their climatic variability, experiencing comparatively wet and productive summer periods and dry winters. During the summer, food abundance and quality is at its highest but will change dramatically during the winter season, when plant growth rates are reduced and rainfall becomes rare and sporadic. This temporal heterogeneity in food availability and quality requires herbivores to adapt their foraging behaviour between seasons. Impala (Mcnaughton & Georgiadis, 1986) and elephants (Owen-Smith, 1992, Spinage, 1994) respond to seasonal variation by switching their forage selection from predominantly grass in the

summer to browse in the winter. In contrast, other herbivores such as the Thomson's gazelle (Fryxell et al., 2004) and wildebeest (Wilmhurst et al., 1999) migrate over large distances to target better foraging opportunities. It is apparent that there are various responses to this large scale temporal shift in forage abundance and quality, from foraging approach to ranging behaviour. These responses are linked to the biology of the particular herbivore species and the evolution of optimal behaviour. Ultimately, heterogeneity in the environment facilitates flexible feeding behaviours, physiological adaptations and resource partitioning, and in turn enables co-existence (du Toit & Cumming, 1999; Brown, 2000).

Competition and Coexistence

The mechanisms that have driven diversity and the subsequent coexistence of species have been of central interest to ecologists for many years and a number of hypotheses have been developed (Amarasekare & Nisbet, 2001). One of the main theories that has been debated at length, postulates that interspecific competition has resulted in coevolutionary divergence of species (Diamond, 1978; Schoener, 1983; Jenkins & Wright, 1988). It is based on the premise that species which have very similar resource requirements will not be able to persist over time, as one will eventually out compete and exclude the other. Therefore, competition is seen as an evolutionary driver, selecting adaptations that enable niche separation and ultimately facilitating species coexistence (Schoener, 1982). There are two distinct modes of competition: exploitation competition, where dominant species are expected to monopolize a given resource and interference competition where one species will actively deny another access to resources (Branch, 1985). Patchy environments such as those found in the African savanna, will have a diverse range of niches and exploitation competition is believed to play a major role in the evolution of large herbivore diversity (Sinclair, 1985; Fritz et al., 2002).

The interspecific competition theory provides a good case for niche separation. However, there are a number of cases indicating that even in situations of intense competition, animals are using similar habitats and experiencing large scale over-lap in resource use. One particular study was that of Sinclair (1985) who investigated the impact of the wildebeest migrations on the spatial distribution and association of other large grazing herbivores. Interestingly, he found continued association of the Thompson's gazelle and Grant's gazelle with wildebeest, despite the sudden increase in competition. This was due to the influence of predation pressure overriding possible interspecific competition. Wildebeest are the favoured prey of large carnivores and therefore other herbivore species can reduce their predation risk by associating with them (Sinclair, 1985). Consequently, it has been suggested that in the presence of intense predation, competition may actually be of little consequence as populations are held well below the level where resources become limited (Schoener, 1982). Facilitation is another mechanism, by which

the actions of one or more species enable others to coexist (Huisman & Olff, 1998, Farnsworth et al., 2002). It has been suggested in the case of African megaherbivores (herbivores >1000 kg), which are believed to facilitate the feeding of smaller grazers by removing large quantities of low quality forage, thus creating higher quality feeding patches (Fritz et al., 2002). The final hypothesis regarding coexistence, is the theory that species respond to environmental gradients and adapt to these rather than competition (Jenkins & Wright, 1988). The extensive body of research carried out on the mechanisms behind coexistence has shown that, as with many ecological situations, there is more than one process at work depending strongly upon the nature of the system being studied. Competition however is clearly an important factor in the structure of many ecological communities (Sinclair, 1985; Jenkins & Wright, 1988; Dublin et al., 1990a, Forsyth, 2000).

Resource Partitioning

It is evident that a number of mechanisms are involved in the coexistence of large herbivores and ultimately all lead to the partitioning of resources at both a spatial and temporal scale. This is facilitated through evolutionary adaptation (Schoener, 1974; McNaughton & Georgiadis, 1986; Jenkins & Wright, 1988). There are two major physiological adaptations that can be used to classify herbivore species on the basis of resource partitioning. The first is forage selection and whether grass (grazer), woody plants (browser) or both (mixed feeder) are targeted (McNaughton & Georgiadis, 1986). Grasses and woody plants are very different with regard to architecture, distribution and plant chemistry, with grasses having thicker cell walls, whilst woody plants contain greater quantities of indigestible fibre within the cell. Woody plants also have more secondary compounds than grasses, reducing the efficiency of digestion and are heterogeneous in structure, whilst grasses are more homogeneous (Shipley, 1999). The levels of protein are on average significantly higher in browse than grass and last longer into the dry season. This is one reason why mixed feeders such as impala and elephant shift their focus from grass to woody plant species with the onset of the dry season (McNaughton & Georgiadis, 1986).

The second major physiological adaptation is the method of digestion. All large herbivores require micro-organisms to digest plant material because they lack the specific enzymes which are required for effective digestion of fibrous carbohydrates (Van Soest, 1996; Shipley, 1999). As a result, fermentation chambers are needed to ensure the survival and continued growth of symbiotic microbial populations (Van Soest, 1996). On this basis, herbivores are classified as either pre-gastric fermenters (e.g. ruminants) or post-gastric fermenters (e.g. non-ruminants). Pre-gastric fermentation involves the use of microbes to break down plant material prior to the ingesta reaching the true stomach and being absorbed into the blood stream. This occurs in a pouch called the reticulum, which is effective in breaking down plant material, as

food particles are retained until they are reduced to a certain size. This is the reason that ruminants regurgitate and re-masticate the ingesta, thus helping the effective digestion of fibre within the diet (Demment, 1983). However, in order to maintain efficient digestion, the animal needs to be relatively selective with regards to the particulate size and the quantity of fibrous material ingested, as the rate of food intake is directly related to the break down of plant material (Demment, 1983). African ruminant species include the entire range of medium to large sized antelope (30-250 kg) and also giraffe and buffalo. Post gastric fermentation occurs after the ingesta passes through the stomach, in enlarged sections of the large intestine, this method of digestion allows the animal to process greater quantities of fibrous plant material as it is not limited by the narrow aperture of the reticulum (Shipley, 1999). The efficiency of digestion is unlikely to be as high as for pre-gastric fermentors since the caecum and large intestine do not retain the ingesta for the same time periods as the reticulum of ruminants (Demment & Van Soest, 1985). Non-ruminants include the warthog, zebra, elephant and both rhinoceros species.

In the savanna biome, vegetation quality and quantity vary at relatively small spatial scales due to the sharply contrasting seasons and the change in plant moisture and soil nutrient status (Bell, 1986; du Toit & Cumming, 1999). The resulting myriad of habitat patches, with varying plant structure and height classes, allows for diversification amongst herbivore species and effective resource partitioning, reducing competition between species and ultimately encouraging diversity of the magnitude observed in the African savanna (McNaughton & Georgiadis, 1986). Resource partitioning amongst herbivores in the African savanna, occurs principally in three main ways: the spatial and temporal composition of species, the seasonal variation in species composition in a particular habitat and the differentiation in feeding approaches that are a result of the diet, season, forage strategy, food availability and body size (McNaughton & Georgiadis, 1986).

The Biology of Body Size

African large herbivores range in body size from the 5 kg dik-dik to the 6000 kg elephant. Body size is one mechanism by which species have diversified and targeted distinct niches, due to the stratification in feeding height, tolerance to differing food quality, mobility and physiological adaptations (Demment, 1983; McNaughton & Georgiadis, 1986; du Toit, 1990; Van Soest, 1996; Fritz et al., 2002). Body size is a key determinant in animal biology and has been shown to have direct influence on a range of physiological and ecological factors, including metabolism (Demment, 1983; Demment & Van Soest, 1985), ranging behaviour (Jetz et al., 2004; Carbone et al., 2005), temperature regulation (Calder, 1984), population density (Peters, 1983; Owen-Smith, 1992) and reproductive success (Møller, 1991; McElligott et al., 2001). This aspect of biology is referred to as allometry and the size differences between or within

species and the resulting ecological and physiological responses have been well researched (Demment & van Soest, 1985; du Toit, 1990; Van Soest, 1996).

Body Size and Feeding Ecology

It is evident that body size has wide ranging implications for the biology of herbivore species and in this study we focus on the influence that body size has on foraging and ranging behaviour. Body size acts in two main ways: firstly it determines the energy demands of an individual and secondly the methods of energy extraction from the environment (McNaughton & Georgiadis, 1986). Larger herbivores have greater absolute energy requirements than smaller species and therefore must process a greater quantity of forage per unit time (Demment, 1983, Van Soest, 1996). Despite this relationship, large herbivores have lower mass specific energy demands due to their metabolic rate scaling with a coefficient of $M^{0.75}$ (M= body mass) (Peters, 1983, Demment & van Soest, 1985; Owen-Smith, 1992). This non-linear relationship results in smaller species having higher relative energy requirements than larger species due to their greater associated heat loss and muscle inefficiency (Peters, 1983). A second allometric relationship that influences foraging behaviour is the linear relationship between body size and gut capacity (Demment & Van Soest, 1985). Therefore, larger bodied herbivores have a metabolic rate to gut capacity ratio (MR/GC) which is lower than that of smaller herbivores, this enables them to ingest larger quantities of forage and achieve more complete digestion in order to satisfy their higher absolute energy demands, whilst small herbivores are constrained by gut sizes that are proportional to their body size and high relative energy demands (Demment, 1983, Stokke & du Toit, 2000). Retention of food in the gut is also linearly related to body size, thus large herbivores have significantly longer retention times than smaller herbivores. Increased retention time allows food to be digested for longer, resulting in greater nutritional benefit to the animal (Owen-Smith, 1992) and this relationship between herbivore size and the tolerance of bigger species to a wider range of forage quality is known as the Jarman-Bell principle (Bell, 1971; Jarman, 1974). However, it is important to note that elephants and other large hind gut fermenters do not exhibit the predicted mean retention times based on their body sizes. It is suggested that this is due to the limits of forage fermentation and the potential loss of energy through methanogenic bacteria. Therefore it is suggested that large hind gut fermenters have evolved accelerated passage rates of ingesta to maximize efficiency of digestion (Clauss et al. 2003).

The variability in the chemical and structural composition of plants has also played a significant role in driving the anatomical and behavioural diversity of large herbivores (Shipley, 1999). The availability of nutrients is based both on the chemical composition of the food resources and their spatial distribution (Demment & van Soest, 1985). Foraging herbivores perceive the food quality as a function of

digestibility. The cell contents of a plant are the most readily digestible and consist predominantly of sugars, proteins and storage carbohydrates (Demment & van Soest, 1985). However, the cell wall must be broken down to release these nutrients. The cell wall consists of complex structural carbohydrates that require microbial and mechanical action to be digested effectively (Van Soest, 1996). The cell wall also contains varying proportions of lignin. The amount of lignin varies throughout the plant and can not be digested by the herbivore or the symbiotic microbes (Demment, 1983). Ingesting high levels of lignin, serves only to reduce gut capacity and the efficiency of digestion. However due to its abundance in the majority of plant material, it is a trade off faced by larger herbivores as they need to consume significant quantities of forage to meet their absolute energy demands (Owen-Smith, 1992; Van Soest, 1996).

There is also a relationship between body size and digestive anatomy. Medium size herbivores are most likely to be ruminants as they can maximize the efficiency of pre-gastric fermentation by being relatively selective with regard to the forage ingested and having a large enough reticulum to process the food effectively. The retention of food in the reticulum and the microbial digestion prior to absorption in the gut, means that ruminants will exhibit greater digestive efficency than similar sized non-ruminants (Demment & Van Soest, 1985; Owen-Smith, 1992). Small herbivores on the other hand can not afford the delay in the processing of food, due to their relatively high energy demands. These herbivores are more likely to utilise post-gastric fermentation (non-ruminants). At the other end of the scale, large herbivores are unlikely to be ruminants as they have greater absolute energy demands which require the processing of significant quantities of forage. This forage is generally much lower in quality than the one selected by smaller herbivores and would be unsuitable for the rumination process due to particle size, fibrous content and absolute quantity. In addition, large herbivores have gut retention times much greater than those of smaller species, allowing them to break down the food without having to selectively retain it (Van Soest, 1985; McNaughton & Georgiadis, 1986).

These body size relationships and the heterogeneity in forage quality and abundance enables larger herbivores to target vegetation of a lower quality to meet their substantial absolute energy demands, whilst smaller herbivores adopt a strategy of searching out the higher quality plant parts such as roots, new leaves, fruits and flowers (Demment & Van Soest, 1996; McNaughton & Georgiadis, 1986). Body size therefore, partitions resources on the basis of the most effective strategies that allow individual herbivores to meet their daily nutrient and energy demands. Larger herbivores are more likely to be generalist in their foraging approach as opposed to small herbivores which feed selectively and may target only a few particular species of plants in a well defined range.

Sexual Dimorphism

The majority of large herbivore species exhibit sexual dimorphism, with the adult male being significantly larger than the adult female (Abouheif & Fairbairn, 1997; Ruckstuhl & Neuhaus, 2000; Le Blanc et al., 2001). This dimorphism is believed to have evolved due to divergent reproductive strategies and sexual conflict which ultimately lead to sexual selection (Darwin, 1871) although it has also been suggested with little evidence that ecological differences in the sexes drive dimorphism (Shine, 1989). Males generally have a relatively low investment in reproduction, their input ending after a successful mating (Mysterud et al., 2004). They are limited by the availability of receptive mates, whereas females have much greater reproductive investments, including gestation and weaning, and are not limited by the availability of males. In fact, females actively select mates on the basis of strength and dominance. Female choice is therefore believed to be the dominant factor in determining mating systems (Alonzo & Warner, 2000). In many ungulate species, the female benefits from polygynous reproductive strategies and this results in an immediate advantage being conferred to the larger and more powerful males who out-compete smaller males (Poole, 1989; McElligott, et al., 2001). This selection pressure is likely to drive body size dimorphism, especially in species which exhibit polygynous breeding systems, as body size is one of the most important factors in individual reproductive success (Clutton-Brock & Harvey, 1978; Poole, 1989; McElligott et al., 2001). It is believed that the greater the polygynous nature of the breeding system, the more pronounced the dimorphism in body size between the two sexes, whilst body size in females is not correlated to the overall extent of dimorphism (Loison et al, 1999). Larger body size in males has also been linked to the number of sperm produced per ejaculate, which is likely to lead to greater reproductive success for larger individuals (Møller, 1991).

Despite the apparent benefits of increased body size, pronounced sexual dimorphism between males and females coupled with high variability in mating success are often associated with higher male mortality rates (Owen-Smith, 1993; McElligott et al., 2001; Moss, 2001). For example, male kudu in the Kruger National Park were found to have notably higher mortality rates than females from the age of 3 years onwards, with the maximum longevity being approximately 10 years, compared to 14 years for females (Owen-Smith, 1993). This disparity in mortality rates was due to increased predation of males by lion, greater susceptibility to malnutrition and conflict with other males when competing for access to females (Owen-Smith, 1993). These negative aspects of increased body size are probably counter-balancing the selection pressure for increasingly larger males and therefore establish an evolutionary compromise due to both the costs and benefits associated with large body size (Blanckenhorn, 2000).

Pronounced sexual dimorphism is likely to have a significant influence on the spatial and foraging ecology of the two sexes due to the differences in physiology that are related to body size (Ruckstuhl, 1998; Stokke & du Toit, 2000; 2002). Females and males may therefore perceive their environment and foraging opportunities at different scales of resolution (Houston & Shine, 1993; Ruckstuhl, 1998; Kie & Bowyer, 1999). This is likely to have implications for the effective conservation of dimorphic species (Bowyer, 2004). Populations are often viewed as generic units and foraging behaviour, habitat use and movements are likely to be determined on the basis that a single animal is representative of the population. Realistically males and females may well be dramatically different in their life strategies, from reproduction through to foraging behaviour. Effective management would benefit from looking at the existence of dimorphic species as being ecologically defined on the basis of sex (Bowyer, 2004). This is particularly pertinent for the African megaherbivores (>1000 kg) as they exhibit pronounced sexual dimorphism, are bulk feeders, range extensively and remove substantial quantities of vegetation (Owen-Smith, 1992). They have the potential to alter habitat structure and impact on the associated biodiversity through their foraging behaviour (Laws, 1970; Dublin et al., 1990b; Owen-Smith, 1992; Cumming et al., 1997; Bond & Loffell, 2001; Mapaure & Campbell, 2002).

Sexual Segregation

One of the main consequences of sexual dimorphism is the spatial segregation of males and females outside of the breeding season (Bon & Campan, 1996; Ruckstuhl, 1998; Conradt, 1999; Barboza & Bower, 2000). In large herbivores, the more pronounced the body size dimorphism, the greater the frequency of sexual segregation (Mysterud, 2000). This suggests that body size differences have indeed a significant influence on the spatial and foraging ecology of the two sexes, as a greater occurrence of segregation would tend to indicate a larger incompatibility between the biology of the two sexes. Understanding sexual segregation has important implications for the conservation and management of large herbivores due to its influence on spatial use, foraging behaviour, population dynamics and sociality (Conradt, 1998a; Bowyer, 2004; Yearsley & Perez-Barberia, 2005).

Whilst the majority of large herbivore species exhibit sexual segregation, this phenomenon has also been observed in whales, seals, primates and a number of bird and fish species (Ruckstuhl & Neuhaus 2000). Sexual segregation has been separated into two distinct components: social segregation and habitat segregation. Social segregation involves the separation of males and females into single sex groups on the basis of social cohesion and conflict avoidance (Conradt, 1998b; Ruckstuhl & Kokko, 2002; Michelena et al., 2004; Perez-Barbeira et al., 2005), whereas habitat segregation involves the sexes utilising different areas of their range due to physiological adaptation and ecological preferences (Conradt, 1998b;

Mysterud, 2000; Stokke & du Toit, 2002). There has been debate as to whether these two forms of sexual segregation are inextricably linked, or act independently (Conradt, 1999; Mysterud, 2000; Ruckstuhl & Neuhaus, 2002; Bowyer, 2004). Despite the many field studies that have attempted to explain sexual segregation, there is no unifying theory or direct evidence as to how sexual segregation provides fitness advantages and reproductive success (Perez-Barbeira et al., 2005). It is however reasonable to assume that sexual segregation occurs because the costs of remaining as a mixed sex group exceed those of being in a sexually segregated group. There are currently four main hypotheses regarding the cause of sexual segregation.

(1) The predation risk hypothesis states that females will choose safer habitats with lower incidence of predation at the expense of nutritional quality, and in doing so will increases their reproductive success due to the greater survival rate of their offspring (Ruckstuhl & Neuhaus, 2000; Corti & Shackleton, 2002). Males on the other hand, are likely to select habitats with high food availability, in order to maximize their fitness and body size, as this is directly related to reproductive success (McElligott et al., 2001). This hypothesis is supported by research on Dall's sheep, which showed males and females using different areas on the basis of predation by wolves (Corti & Shackleton, 2002). Males often take greater risks than females when foraging and this is believed to be due to males exhibiting less predator avoidance (Sukumar & Gadgil, 1988). As mentioned above, sexually dimorphic animals which exhibit sexual segregation, often experience higher rates of mortality associated with predation when compared to females (du Toit, 1990; Owen-Smith, 1993). However, it is also important to remember that many predators have been systematically eradicated from their original ranges and it is questionable whether in these situations, current behaviour would still be so strongly defined by past adaptations (Ruckstuhl & Neuhaus, 2000). This relationship was studied by Kie & Bower (1999) who recorded a reduction in the sexual segregation of white-tailed deer when predator numbers dropped. The predation risk hypothesis also suggest that females without offspring would associate with males as they do not experience the same pressures to find safe habitats and would therefore select habitats on the basis of forage availability (Frid, 1994; Ruckstuhl & Neuhaus, 2000).

(2) The forage selection hypothesis states that males and females are segregated due to sexual dimorphism which leads to differing energy demands and diet selection (Ruckstuhl & Neuhaus, 2000, Stokke & du Toit, 2000). As discussed above, the metabolic rate of a mammal scales with a factor of $M^{0.75}$ (M = body mass) resulting in larger herbivores having lower relative energy demands per kg mass, whilst gut capacity scales in direct proportion to body size (Bell, 1971; Jarman, 1974; Demment & Van Soest, 1985). Therefore, the larger the individual the lower the metabolic rate to gut capacity ratio

(MR/GC). This results in large herbivores being able to tolerate lower quality diets to meet their absolute energy demands (Peters, 1983; Owen-Smith, 1992). Smaller herbivores are constrained by size and high relative energy demands and need to forage more selectively. This has been shown to operate across the species divide and is believed to play a key ecological role between male and female herbivores exhibiting dimorphism (Barboza & Bowyer, 2000). Essentially, males will be able to tolerate a greater proportion of fibre in the diet as they have lower relative energy demands and greater digestive efficiency (Demment, 1983; Demment & Van Soest, 1985). It is postulated that males and females will select different plant species and/or habitats on the basis of their nutritional quality and abundance, and this will ultimately lead to segregation (Stokke & du Toit, 2000). Female nutritional demands are compounded further by reproductive investment, i.e. gestation and lactation, with peak lactation increasing energy requirements for an individual by as much as 150% (Dunbar et al., 2002; Blanchard, 2005). Previous research on the forage selection hypothesis has produced mixed results with some studies showing that females select higher quality habitats than males (Putman et al., 1993; Corti & Shackleton, 2002) whereas others have shown the converse relationship (Bleich et al., 1997; Ruckstuhl & Neuhaus, 2002) or no relationship (Ginnet & Demment, 1999; Ruckstuhl, 1998).

(3) The social preference hypothesis states that sexual segregation is driven by differences in the ontogenetic behaviour of males and females, resulting in differing levels of activity and interaction (Bon & Campan, 1996; Perez-Barberia; 2005). Males are likely to show social affinity for same sex groups as they learn to fight and establish hierarchies amongst individuals of the same age. These interactions will be important determinants when they reach breeding age and compete directly for females (Ruckstuhl & Neuhaus, 2000). It is therefore suggested that individuals may segregate on the basis of age as well as sex (Bon & Campan, 1996). However, whilst males and females may interact more with members of their own respective sex, segregation will not necessarily ensue, especially if they share similar nutritional demands and activity budgets (Ruckstuhl & Neuhaus, 2000).

(4) The activity budget hypothesis is the most recent theory to be put forward as an explanation of sexual segregation (Ruckstuhl, 1998, 1999; Ruckstuhl & Neuhaus, 2000, 2002; Ruckstuhl & Kokko, 2002). It states that if the synchronisation and duration of activities (e.g. feeding and walking) vary between the sexes, then segregation will occur over time (Conradt, 1998b; Ruckstuhl, 1998). Segregation will be spatial and temporal but not necessarily based on the use of different habitats. In fact, it is postulated that the two sexes would segregate within the same homogeneous habitat if their activity budgets varied significantly enough, because the costs of remaining within a mixed sex group would exceed the benefits. There are two main assumptions on which this hypothesis is based. The first is that females are not as

efficient at digesting forage as males due to their smaller body size and the subsequent allometric relationships (Demment & Van Soest, 1985, Owen-Smith, 1992; Stokke & du Toit, 2000). The second is that significant differences in the activity budgets make synchronisation of behaviour costly and are likely to result in individuals segregating (Conradt, 1998a; Ruckstuhl & Neuhaus, 2000; Yearsley & Perez-Barberia, 2005). It is therefore predicted that females will feed for longer than males because of decreased digestive efficiency and to meet their higher relative energy demands. Females may also walk at greater rates than males to reduce the chance of predation (Ruckstuhl, 1998, Rusckstuhl & Neuhaus, 2000). As this theory predicts that activity budgets will vary on the basis of body size, it also applies for cohorts of the same sex (e.g. adolescent males) due to their energy demands and similar physiology (Yearsley & Perez-Barberia, 2005).

Even though the causes of sexual segregation are not fully understood, it evidentially leads to a partitioning of resources in space and time. In addition to being a result of sexual selection, it may also reduce the competition for limited resources between males and females.

Study Animal: Elephant

This study focuses on the spatial and foraging behaviour of male and female African elephants (*Loxodonta africana*) in five distinct South African populations. The African elephant exhibits marked sexual dimorphism with adult males weighing in excess of twice the weight of an adult female (Poole, 1994; Spinage, 1994). Elephants are also sexually segregated throughout the year, except when males enter musth (Hall-Martin, 1987). During this time, the male experiences elevated hormonal (testosterone) levels and associates with females in order to reproduce (Poole & Moss, 1981; Poole, 1987, 1989). The musth period is highly variable but lasts on average 2-3 months of the year and varies in intensity (Poole, 1987). Younger males (<30 years of age) will only come into musth for short periods of time as there is an established hierarchy dominated by the older and larger individuals (Poole, 1989, 1994). Outside of the musth period, male elephants range independently or in loosely associated same sex groups (Owen-Smith, 1992). Females live in defined family groups of 4-12 adults and their offspring (Poole, 1994). These family groups are closely related and are generally led by the oldest member, the matriarch (Moss & Poole, 1983; McComb et al., 2001). Elephants have a very developed social system and during the wet season family groups often merge into large herds, which can number in excess of 200 individuals (Owen-Smith, 1992). Young males are forced out of the family groups when they reach adolescence (approximately 10-15 years old), probably a mechanism by which inbreeding is prevented.

Male and female elephants are long lived and show divergent growth around their late teens, where males accelerate their growth, whilst females channel resources into reproduction (Lee & Moss, 1995). Females reach their maximum height at around 25 years of age, whereas males will continue to grow throughout their life time, although slowing down appreciably after 30-35 years of age (Lee & Moss, 1995). This continued investment in growth suggests that there has been strong selection pressure for large body size in male elephants (Poole, 1994). Females who reproduce at an early age (12-15 yrs) may well trade off against growth as lactation costs are high in young females (Lee & Moss, 1995). Due to their comparatively large size, elephants have evolved as large generalist herbivores, targeting both grass and browse. They are non-ruminants, using post-gastric fermentation to break down and digest the sizeable quantities of plant material that they ingest (Owen-Smith, 1992). Their relatively low MR/GC ratio allows them to target low quality forage. Foraging is their dominant activity, taking up to 18 hours per day to satisfy substantial energy requirements. In the wet summer seasons elephants concentrate their foraging on grass but switch to browse during the dry winter season (Owen-Smith, 1992).

Aims and Objectives

The aims of this study are as follows: (1) Investigate the influence of sexual dimorphism on the spatial ecology of the African elephant in relation to resource heterogeneity. (2) Explore the role of sexual dimorphism on the segregation of the two sexes at various spatial and temporal scales. (3) Apply the concept of 'distinct ecological species' to the two sexes, with a view to effective management and conservation of dimorphic herbivores. The elephant provides an ideal species on which to test theories of sexual dimorphism due to its gregarious nature, large size and relative abundance in the savanna ecosystem. Males and females also exhibit markedly different reproductive strategies, different body sizes and are segregated most of the year (Moss & Poole, 1983; Hall-Martin, 1987; Poole, 1994). Research on sexual segregation and the influence of body size dimorphism has received significant attention over the past 10 years. However, 98% of the studies carried out on sexual segregation deal solely with ruminants, temperate cervids and bovids in particular (Bowyer, 2004), probably because their biology has been well researched and they exhibit pronounced sexual dimorphism (Bowyer, 2004). In this study, we tested a number of ecological theories that have been developed from the studies of temperate ruminants, on a large African non-ruminant, the elephant.

The first objective of this study was to establish the basic spatial patterns of elephant behaviour and is detailed in Chapter 2. It was carried out in the Pongola Game Reserve and involved the analysis of home range and habitat utilisation data for female and male elephants in a simplified, closed population. This enabled preliminary differences between the sexes to be investigated and the hypotheses and methods to

be developed for the next four chapters. As such, the approach was relatively descriptive. The objectives of Chapter 3 were to quantify the influence of changing vegetation quality and abundance on the ranging behaviour of female and male elephants. This was carried out at different spatial and temporal scales to elucidate the responses of the two sexes to heterogeneity in the ecosystem. The first objective of Chapter 4 was to establish whether habitat segregation was a significant causal effect in the social segregation of elephant and to apply this across three distinct populations using habitat maps and accurate location data of known individuals. The second objective was to test whether habitats were also segregated on the basis of foraging preference. In Chapter 5, the focus shifted to the temporal and spatial scale of foraging events. The objectives were to quantify the foraging behaviour of the two sexes at the plant level and to ascertain whether foraging differences could lead to social segregation. Our results were also compared with those from an earlier study of elephant foraging behaviour carried out by Stokke & du Toit (2000). Chapter 6 assesses the most recent theory with regard to sexual segregation, the activity budget hypothesis. The main objectives of this chapter were to investigate the daily activity budgets of male and female elephants to determine whether they were significantly different and thus lead to segregation of the sexes, to establish whether the onset and timing of certain key behaviours was asynchronous and if these patterns were repeated across populations or were site specific. The final chapter brings all the chapters together to draw conclusions on the influence of sexual dimorphism on elephant spatial and foraging ecology. It assesses the responses of the sexes at different temporal and spatial scales in an attempt to elucidate the key factors driving segregation. Finally this research attempts to provide answers to some of the current challenges facing conservation of large sexually dimorphic herbivores and gives an insight into the potential benefits of managing the sexes as two ecological species.

CHAPTER 2

AFRICAN ELEPHANT HOME RANGE AND HABITAT SELECTION IN PONGOLA GAME RESERVE, SOUTH AFRICA

Abstract

The ranging behaviour and habitat occupancy of three elephant groups (cow herd, three adult males, and a female orphan group) were studied over a two-year period in a small fenced reserve. No summer dispersal was observed. Distinct seasonal home ranges were exhibited for all groups, with the summer (wet season) ranges being smaller than the winter (dry season) ranges. Home range size was much smaller than in other locations. The lake and surrounding high density of vegetation patches of high nutritional quality are thought to be the reason. Habitat selection was strongly evident with all of the elephant groups selecting River Line habitats in the dry season. In the wet season, the cow herd and orphans selected the more open *Acacia* habitats and the males exhibited no significant habitat preference.

Introduction

The non-random use of space and differential habitat selection is a longstanding basic tenet of ecology (Rosenzweig, 1981). Energetic constraints, social factors and the abundance and distribution of resources, influence the size, shape and location of seasonal ranges. These constraints determine which resources are limiting and their influence on demographic parameters. Understanding seasonal range dynamics and what drives it, is therefore of critical importance in understanding how populations are limited and how the different sexes respond. This is especially pertinent in large herbivores which generally exhibit body size dimorphism and are sexually segregated outside of the mating season (Ruckstuhl, 1998; Conradt, 1999; Mysterud, 2000; Bowyer, 2004)

It is generally accepted that in semi arid environments, an expansion of the distribution range occurs at the beginning of summer and results in the entire elephant population of a region dispersing over a wider area than during the dry winter season when sub-populations, sometimes referred to as clans or bond groups, are restricted to much smaller areas close to rivers and waterholes (e.g. Jarman, 1972; Williamson, 1975; Norton-Griffiths, 1975; Leuthold, 1977; Western & Lindsay, 1984; Merz 1986; Ottichilo 1986; Lindeque & Lindeque, 1991; Chase, 2003). This summer dispersal gives rise to distinct summer and winter ranges for the sub-populations.

Precisely how this sub-population summer range expansion is linked to changes in the seasonal home range of individual males or family units, is not clear. The literature provides contradictory data. Jachman (1983) suggested that dry season ranges for females were larger than wet season ranges. The results were

however based on a small sample. Viljoen (1988) showed that of the four female herds studied, two had larger dry season core areas and two had smaller dry season core areas. Similarly, one of two males had a larger dry season core area and the other the reverse. De Villiers and Kok (1997) stated that the wet season ranges that they identified for seven elephants were larger than the dry season ranges. However, closer examination of their data indicates that the statement is not as clear-cut as suggested.

In De Villiers and Kok's study (1997) seasonal home range size was examined in three different phenological seasons: a wet season when both trees and grasses had green leaves (about November to March), a transitional season when the trees had green leaves but the grasses were senescent (about April to August) and a dry season when trees had lost their leaves and the grasses were senescent (August/September to October/November). For five of the six home ranges the intermediate season (mid to late winter) home range was larger than the summer range, and thereafter decreased to an area smaller than during the wet season. However, their dry season, which was shorter is likely to have fewer sightings, and this may have affected the results. The single bull monitored in their study showed a consistent decrease in the size of its home range from the wet to dry period. Osborn (2003) working with bull elephants in the Sengwa Wildlife Research area in Zimbabwe, showed precisely the same pattern as observed by De Villiers and Kok (1997). Ntumi (2003) found that the dry season ranges of four female groups were smaller than the wet season ranges, but the single male had a larger dry season range. Similarly, Chase (2003), in an unpublished report, describing the results of an analysis of movement of 6 female elephants indicated that the wet season ranges were larger. Clearly, more detailed data on elephant movement and the factors affecting it are required to properly understand how and why these discrepancies arise.

Relatively few studies have quantified habitat occupancy and use by male and female elephants, particularly on a seasonal basis. All authors, for example, Viljoen (1989), Babassa (2000), De Boer et al., (2000), Stokke & du Toit (2002), Osborn & Parker (2003) have found strong selection of some habitats and avoidance of others, especially in the dry season. Riparian and low lying habitats on relatively nutrient rich soils are strongly selected for at these times.

This study had three main objectives: (1) to determine whether the elephants in the Pongola Game Reserve dispersed away from water in summer, (2) to determine whether they used distinct home ranges and if these were different according to seasons and sex, (3) to determine habitat preferences and whether these were different in summer and winter, for males and females.

Methods

Study Site

The Pongola Game Reserve (PGR) was established in 1993 and covers an area of approximately 82 km^2, on the western shore of the Jozini Dam. The lake forms the entire eastern and northern boundary. A railway line bisects the reserve from the southern border to the northwest (Fig. 1). The climate is hot and arid with an average rainfall of 400-600mm per annum. The annual rainfall for the two years of this study was however well above average, with 1220 mm in 2000 and 780 mm in 2001. The vegetation falls into three of Acocks (1988) veld types: Zululand Thornveld, Lowveld and Arid Lowveld. The last two cover the southern and central portions of the Kruger National Park and adjoining reserves, making these results of interest in the management of these areas. Canonical Correspondence Analysis and Two Way Indicator Species Analysis of woody species densities in randomly located transects identified seven vegetation types (Page and Duffy unpublished data), the limits of which can be seen on the habitat map (Table 1 and Fig. 1).

Table 1. Link between habitat types, topography, soils and dominant woody species of the Pongola Game Reserve. Numbers in brackets indicate the number of woody species recorded in the type.

Habitat Type	Topographic Position and Soils	Dominant Species
Combretum Woodland	Rocky, well drained soils of upper slopes and tops of highest hills	*Combretum apiculatum, A. nigrescens, Ozoroa engleri, Gymnosporia buxifolia, Grewia villosa, Grewia hexamita, Grewia caffra, Sclerocarya birrea, Ziziphus mucronata (17)*
River Line Thickets	Clay rich deep soils of drainage lines	*Ehretia rigida, Capparis tomentosa, Salvadora australis, Gymnosporia senegalensis, A. nilotica, A. tortilis, Schotia brachypetala, Rhus guenzii, A. luederitzii, A. senegal, Gymnosporia buxifolia, Dichrostachys cinerea (28)*
Flood Plain Grassland	Deep alluvial clay soils of lake shore	*Mixed grasses and forbs*
Mixed Acacia Woodland	Higher nutrient soils on lower slopes	*A. nilotica, A. tortilis, A. luederitzii, Dichrostachys cinerea, Ehretia rigida, Capparris tomentosa, Rhus guenzi, Spirostachys africana (25)*
Acacia & Marula Woodland	Shallow soils of mid to upper slopes on higher hills.	*A. nigrescens, Sclerocarya birrea, Ziziphus mucronata, A. tortilis, Grewia flava, Gymnosporia buxifolia, Grewia villosa, Dichrostachys cinerea, Ozoroa englerii, Canthium inerme (38)*
Euclea Thickets	Alluvial soils on flat areas close to water at lower altitudes.	*Euclea racemosa, Euclea divinorum, Euclea natalensis, Pappea capensis, Gynmosporia nemorosa, A. nilotica, Capparis tomentosa, Salvadora australis, A. luederitzii, Ehretia rigida (31)*
Old Land	Soils and elevation correspond to adjacent habitat type	*Mixed Acacias & Dichrostachys cinerea*

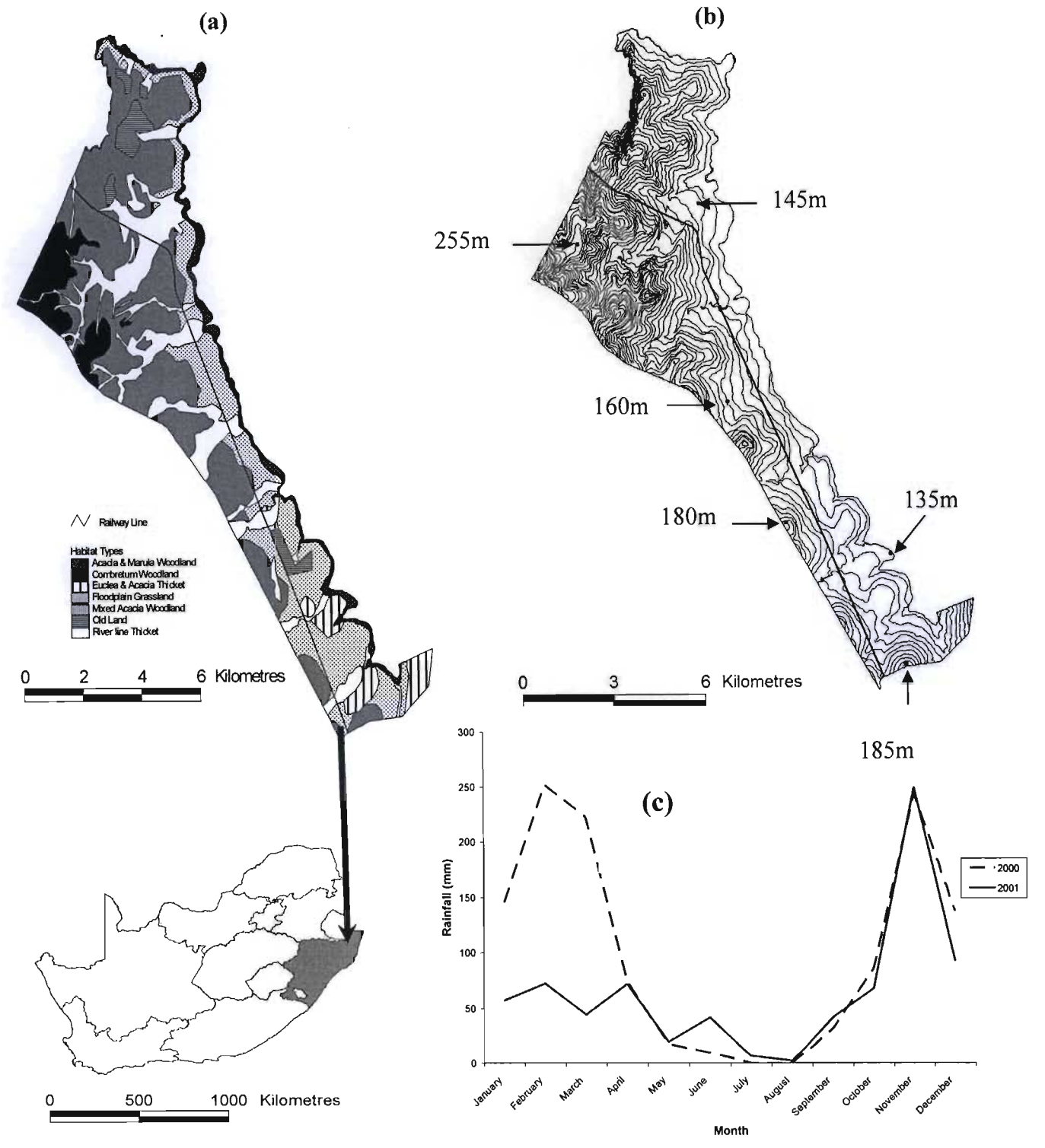


Figure 1. (a) Habitat map of the Pongola Game Reserve with an arrow indicating the geographic position of the reserve in South Africa (KwaZulu Natal is highlighted) (**b**) Contour map of the reserve, exhibiting the hillier relief of the northern section. Altitude and relief are directly linked to the spatial distribution of the habitat types within the reserve. (**c**) The rainfall figures for 2000 and 2001, clearly showing the seasonality in precipitation.

Seventeen elephants in two family groups were translocated from Kruger National Park to PGR during June 1997. Six males were also introduced: Three in 1998 (of which one died and one was shot) and three in 2002 (of which one died). The population in 2000 and 2001 consisted of two permanently associated family units in a group of 28 to 30 individuals and 4 adult males. Five orphan elephants (four females and one male), all approximately ten years old, broke into PGR from a nearby reserve in July of 2000 and remained together as a separate group. The term "orphan elephants" refers to young elephants between the ages of 5 and 10 that were captured during culling operations and translocated in small groups to reserves without elephants for the purpose of restocking. The practice has been discontinued.

Data Collection

Elephants were located two or three times a week from March 2000 to February 2002. Locations were aided by radio collars on one adult female and one adult bull. On sighting, a GPS (Global Positioning System) was used to record the position of the group from a vehicle. Observations were made from the reserve's extensive road and track network and off-road, from a position that did not influence the movement of the elephants.

Data Analysis

In order to avoid the effect of spatial and temporal autocorrelation the first location recorded each day was used for this analysis. The seasons were based on rainfall data (Fig. 1c) and defined as summer between 1st November and 30th April and winter between 1st May and 31st October.

Distributions were overlayed on the habitat type map (Fig. 1) using ArcView® 3.2a and each location was assigned to a habitat type. Elephant home ranges based on minimum convex polygons have been shown to be strongly dependent on the number of points used (Whyte 2001). Therefore, kernel analysis was used in this study (Hooge & Eichenlaub, 1997) and 50 % kernels and 95 % kernels calculated (Worton 1989) using distance units of 500m. Separate analyses were run for each of the three groups of elephants in each season in each year.

Whilst preference ratios lack statistical precision, they still provide a crude but easily understood comparison of the use of particular habitat types. Preference ratios were therefore calculated as the proportion of locations in a particular habitat type divided by the proportional area of that habitat type i.e. (number of locations in a specified habitat / the total number of locations) / (the area of the specified habitat type / the total area).

Chi-squared tests were used to establish statistical differences in the occurrence of elephants in the different habitats. The railway acted as a functional barrier for the cow herd (see Results below). Therefore the analyses were performed using an area value of 36.8 km^2 for the cow herd, and the total extent of the reserve (73.6 km^2), for the males and orphan group.

Results

Dispersal

No indication of dispersal away from water in summer or contraction of the range toward water in winter was noted (Fig. 2).

Individual Home Range Analysis

The cow herd only utilised the area east of the railway line despite the fact that it does not present a physical barrier. Both the orphan group and the males crossed the railway line freely (Fig. 2 and Table 2). Equivalent vegetation types are found for at least a kilometre on either side of the railway line along its entire route (Fig. 1) and there is surface water on both sides of the line. No observation or sign from the cow herd was ever recorded on the west of the line. The herd was however observed on several occasions approaching the line and then turning away.

The home ranges of the males, cow herd and orphan group showed strong seasonal shifts (Fig. 2). In both years the summer home ranges of all three elephant groups, had the core home range (50% kernel) located over the northern lake shore and the surrounding *Acacia*-Marula Woodland (Fig. 1a). The males and orphan group occupied a larger range than the females. During both winter seasons there were two core ranges for all three groups, in the north and south of the reserve, in both years, with the northern core shifting slightly south.

Larger areas were used in the winter compared to the summer (Table 2). In 2000, the winter total range for the herd was 1.78 of the summer range and the winter core home range was 2.33 of the summer range. In 2001, the winter range was 2.10 of the summer total range and 4.40 of the summer core range. In 2000, the winter total home range of the males increased to 1.79 of the summer range and the winter core home range increased to 2.92 of the summer range. The orphans only entered the reserve in July 2000 so their winter 2000 range is not comparable to the other distributions. In 2001 the winter total home range was 2.26 of the summer range and the winter core range 1.40 of the summer range. The cow herd and males had smaller seasonal ranges in 2001 compared to 2000 (Table 2).

Habitat Occupancy

All three elephant groups used different habitats with varying intensity from one season to the next (Table 3). In summer, the males used the habitats in proportion to their area (χ^2_6= 9.776 P>0.1) but in winter, there was a significant difference (χ^2_6= 44.498 P<0.001). The herd strongly selected for particular habitats in both seasons (summer: χ^2_6= 11.603 P<0.05; winter: χ^2_6= 31.808 P<0.001). The orphans also exhibited heterogeneous habitat use throughout the year (summer: χ^2_6= 28.205 P<0.001 winter: χ^2_6= 33.376 P<0.001). *Acacia*-Marula Woodland was selected for by both the cow herd and males in summer and avoided in winter. In the winter River Line Thickets were heavily used. All three groups showed increased use of *Euclea* Thickets during winter. The mixed *Acacia* Woodland was selected for by the orphans in both seasons, and by the males in winter.

Table 2. The home ranges of elephant groups in the Pongola Game Reserve, 2000-2001

Elephant Group	Season	Year	Total home range (95% Kernel) (Km^2)	Core home range (50% kernel) (Km^2)
Males	Summer	2000	40.0	10.8
	Summer	2001	33.6	19.4
	Winter	2000	71.5	31.5
	Winter	2001	61.2	18.7
Herd	Summer	2000	20.6	9.0
	Summer	2001	17.5	4.3
	Winter	2000	36.7	21.0
	Winter	2001	36.7	18.9
Orphan	Summer	2000	40.6	13.8
	Summer	2001	26.8	8.1
	Winter	2000	10.5	1.7
	Winter	2001	60.5	11.3

Table 3. Habitat selection of the herd, males and orphans.

		Summer		Winter	
Vegetation	**% of Total Area**	**% of Total Sighting No. (=n)**	**Preference Ratio**	**% of Total Sighting No. (=n)**	**Preference Ratio**
Cow Herd					
Acacia & Marula Woodland	26.5	37 (45)	1.40	14 (17)	0.53
Mixed *Acacia* Woodland	32.8	31 (38)	0.95	36 (45)	1.10
River Line Thicket	13.7	16 (20)	1.17	29 (36)	2.12
Combretum Woodland	0	0 (0)	0	0 (0)	0
Flood Plain Grassland	11.9	11 (13)	0.92	6 (7)	0.50
Euclea & *Acacia* Thicket	8.5	2 (3)	0.24	13 (16)	1.53
Old Land	6.6	3 (4)	0.45	2 (3)	0.30
Males					
Acacia & Marula Woodland	39.8	50 (57)	1.26	24 (26)	0.60
Mixed Acacia Woodland	21.9	19 (22)	0.87	30 (32)	1.37
River Line Thicket	17.8	17 (19)	0.96	37 (40)	2.08
Combretum Woodland	7.0	6 (7)	0.86	0 (0)	0
Flood Plain Grassland	6.0	3 (3)	0.50	2 (2)	0.33
Euclea & Acacia Thicket	4.2	0 (0)	0.00	7 (7)	1.67
Old Land	3.3	5 (6)	1.52	0 (0)	0.00
Orphans					
Acacia & Marula Woodland	39.8	32 (31)	0.80	16 (14)	0.40
Mixed Acacia Woodland	21.9	34 (33)	1.55	33 (28)	1.51
River Line Thicket	17.8	15 (15)	0.84	27 (23)	1.52
Combretum Woodland	7.0	0 (0)	0	0 (0)	0
Flood Plain Grassland	6.0	16 (16)	2.67	6 (5)	1.00
Euclea & Acacia Thicket	4.2	1 (1)	0.24	15 (13)	3.57
Old Land	3.3	2 (2)	0.61	3 (2)	0.91

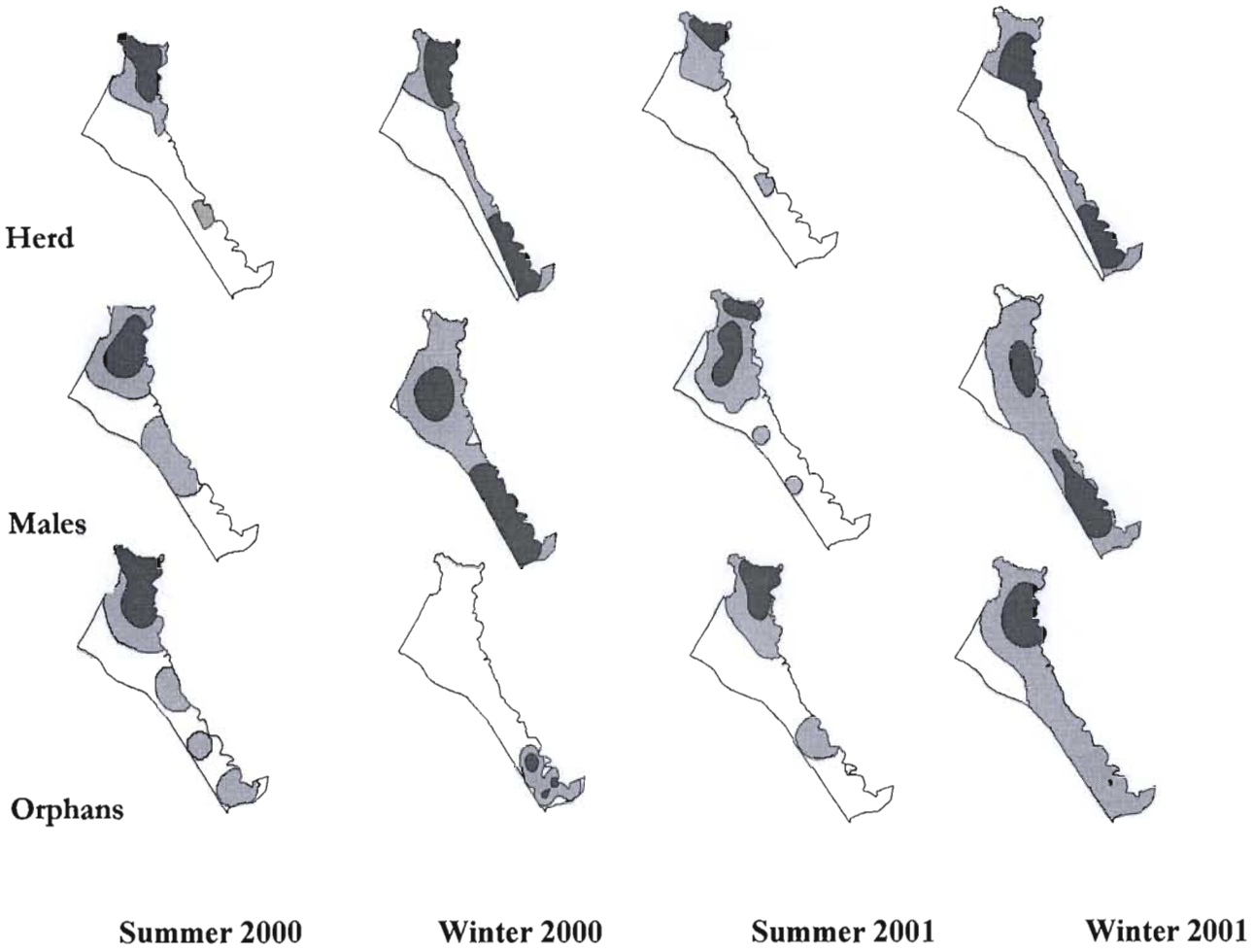


Figure 2. Home ranges of the herd, males and orphans in different seasons and years. Dark shading indicates core home range (50% kernel) and light shading indicates total range (95% kernel).

Discussion and Conclusions

Dispersal

There are two possible explanations for the lack of dispersal in the reserve: either the small size of the area or the constant availability of water and forage on the lakeshore.

Home Ranges

The results from several studies appear to indicate that boundaries to home ranges often lie along rivers or roads that can easily be crossed (Leuthold, 1977; Thouless, 1996; Whyte, 2001). However, the ability of elephants to recognise these features in the landscape and respond to them in terms of defining home range boundaries has not previously been emphasized in the literature. It is worth noting that it is unlikely that every elephant in the group responds in the same way to these features, which suggests that the size and configuration of the home range may be strongly determined by the matriarch.

The size of home ranges reported in the literature for cow herds vary widely from 240 km^2 in the Kruger National Park, South Africa, to 1800 km^2 in Tsavo East National Park, Kenya (Owen-Smith, 1988). The maximum area of the range for the cow herds reported in this study (36.7 km^2 for 95 % kernel) is therefore considerably smaller. The 95% ranges of males are slightly larger than those described at Addo Elephant National Park (100% range based on minimum convex polygon = 52.8 km^2; reserve area = 103km^2) (Whitehouse & Schoeman, 2003) but smaller than those described for males in Pilanesberg National Park (95% range based on Kernel Analysis = 99.7 km^2; reserve area = 500 km^2) (Slotow & van Dyk, 2004). Apart from the fact that the males in PGR cross the railway line freely, their ranges may also be larger than that of the female groups due to their greater body size, independent ranging behaviour and their reproductive strategy of actively seeking females during musth periods (Owen-Smith, 1992; Poole, 1994).

The distribution of water is known to affect home range size (Osborn, 2004). The permanent widespread supply of drinking water and the abundance and clustering of relatively high nutritional quality forage in small patches of different vegetation types (Fig 1), probably account for the relatively small ranges observed in PGR for both males and females. This was further influenced by the abnormally high rainfall during both years of the study, which led to abundant forage availability during the wet summer season and therefore enabled the elephants to satisfy their energy demands in very limited ranges. The larger winter range could be explained in either of two ways. Food availability may be limited compared to the abundant summer season, thus forcing animals to move over a wider area in search of foraging opportunities. Alternatively, the spatial distribution of habitat types of higher nutritional quality may

result in a wider area being traversed in winter. In the dry season, lake levels drop and a narrow band of comparatively good quality grazing becomes available on the lake edge. At the same time, away from the lake, there is a reduction in the quality and availability of forage. The River Line and *Euclea* thickets that are the preferred habitats in winter (Table 3) lie perpendicularly to the lake edge and are widely separated (Fig 1). The combination of these three factors appears to result in the elephants covering a greater area in order to satisfy their nutritional demands during winter.

Naturally occurring lakes are rare in Africa. However, there are many man made dams in conservation areas, along which subpopulations of elephants occur. The effect of these water bodies on the movement of elephants has not been established but it appears from this study that there may be negative impacts on vegetation because of reduced home range size around lakes and dams. When there is no shift in the seasonal range, impact is likely to be higher than when movement occurs. The similarity in position of the core home ranges in both seasons in both years (Fig. 2), indicates that there may be cause for concern.

Habitat Occupancy

As water availability in PGR is not limiting, it is likely that nutritional demand and social factors drive elephant ranging behaviour. Over the period of the study, both wet seasons were well above average, so resources were most likely abundant. Lake levels were high in summer and a large proportion of the floodplain grasslands were covered. *Acacia* – Marula woodland which is dominated by a wide range of highly palatable species (Table 1), was heavily used for in both summers (Table 3 and Fig 2). The Mixed *Acacia* woodlands have fewer palatable species. In addition the Lower lying areas in the Mixed *Acacia* woodlands and Drainage Line Thickets might have been avoided because they were relatively muddy, compared to the *Acacia* – Marula woodlands that occur on steeper slopes (Fig 1). Females exhibited greater habitat selectivity in the summer, when compared to males. This may indicate either a more selective foraging approach or avoidance of habitats due to perceived risk. Male elephants are more likely to forage in 'riskier' habitats than females as their priority is to maximize nutritional return, whilst the females' strategy is to protect their offspring (Sukumar & Gadgil, 1988). Habitat types selected for during the winter season are all located in lower lying regions (Fig. 1). It is well established that soils in bottomlands have a higher nutrient status and moisture-holding capacity than soils at the tops of hills (Schimel et al., 1985; Nellemann et al., 2002). Elephants of both sexes are therefore probably selecting for nutritional quality during the winter period. Several studies in semi-arid environments have characterised elephants as riparian species and invoked both the availability of palatable plants and water as explanatory factors (Viljoen, 1989; Ottichilo, 1986; Sommerlatte, 1976). This study suggests that nutritional quality is important.

CHAPTER 3

THE INFLUENCE OF FORAGE ABUNDANCE AND QUALITY ON THE RANGING BEHAVIOUR OF MALE AND FEMALE AFRICAN ELEPHANTS

Abstract

Spatial and temporal heterogeneity in food availability influences foraging and ranging behaviour of large herbivores. This is especially pertinent in savanna ecosystems, which have well defined climatic seasons varying greatly in biomass productivity and quality. Phenological analysis and rainfall data were used to investigate how male and female elephants respond to changes in vegetation quality over space and time when the availability of surface water is not a limiting factor. Elephants exhibit pronounced sexual dimorphism which is believed to have a strong influence on their spatial ecology. Location data were recorded in five reserves over an 8 year period for both males and females with their family groups (1998-2005). VHF and GPS collars were used to monitor movements at a range of spatial and temporal scales. Both sexes expanded their annual ranges during years of above average rainfall and exhibited seasonal patterns in their ranging behaviour. Males exhibited the strongest relationship, with a positive relationship between the residuals of range size and increasing annual rainfall. Males also responded at daily and hourly temporal scales, reducing their displacement distances in dry winters whilst increasing their movement rates. This is consistent with their response at the home range scale, which suggests they focus their ranging behaviour when forage quality and abundance is limited. Movement rates increased during periods of resource scarcity as foraging became more time consuming. Males are likely to focus their ranging behaviour during resource scarcity and this may lead to heterogeneous impacts on vegetation. Females did not show the same flexibility, this is probably due to their greater energy demands per kg body mass and the constraints of group living. Females were unlikely to meet their energy demands with the same efficiency as males and therefore adopted a different strategy: maintaining ranging patterns that allowed them to seek out higher quality forage. This study highlights the important role that sexual dimorphism plays in behaviour and how sex differences can have implications (e.g. habitat utilisation and influences on vegetation) for conservation planning and management implementation.

Introduction

Large herbivores experience wide scale temporal fluctuations in forage availability and quality (Owen-Smith, 1994; Illius & O'Connor, 2000). This is especially pronounced in savanna ecosystems where variation in productivity is determined by two distinct seasons (summer and winter), yearly rainfall and soil type (McNaughton & Georgiadis, 1986; East, 1984). The abundance of forage in the summer season is contrasted by scarce resource availability in the winter, which may lead to nutritional stress amongst

herbivores (Illius & O'Connor, 2000; Redfern et al., 2003). In semi arid areas (< 700 mm) rainfall has long been considered the major predictor of productivity with direct relationships between rainfall and total herbivore biomass (Coe et al., 1976). Biomass productivity also varies on an annual basis due to fluctuations in yearly rainfall, with episodic droughts occurring relatively regularly in savanna biomes (Rouault & Richard, 2003). In addition to temporal fluctuations in resource quality, spatial heterogeneity exists at a range of scales from habitat structure and species composition at the landscape level, down to the chemical composition of an individual plant (Pickett & Cadenasso, 1995; Ball et al., 2000; Skarpe et al., 2000).

This spatial and temporal heterogeneity presents the herbivore with key foraging decisions, as most herbivores are attempting to maximize the intake rate of nutrient rich or energy digestible plant parts (Stephens & Krebs, 1986; Ward & Saltz, 1994; Brown, 2000). Herbivores must also resolve their ranges at appropriate scales depending upon body size, energy requirements and mobility (Jetz et al., 2004). As body size increases so does the total energy required. However, due to greater efficiency and lower heat loss, the energy required per unit mass is in fact reduced (Owen-Smith, 1992; Van Soest, 1996). Large herbivores are also able to tolerate lower quality diets due to larger gut capacity and increased retention times (Demment & Van Soest, 1985; Ginnett & Demment, 1997). The body size hypothesis has been shown to predict differences in energy requirements and foraging behaviour among species and is also predicted to play a significant role in sexually dimorphic species (Ruckstuhl, 1998; Stokke & du Toit, 2000). African elephants (*Loxodonta africana*) exhibit pronounced sexual dimorphism and this is likely to influence the patterns of foraging and ranging behaviour (Poole, 1994; Stokke & du Toit, 2000; Stokke & du Toit, 2002). Adult males commonly exceed twice the weight of a fully-grown female (3000 kg) and range independently (Spinage, 1994).

As foraging decisions and movement are inextricably linked, ranging behaviour is a key ecological correlate by which to study the interactions between an individual and its environment (Stephens & Krebs, 1986). Effective decision making becomes critical during resource scarcity as poor strategies can lead to reduced individual fitness, lower reproductive output or even death (McNaughton & Georgiadis, 1986; Mysterud et al., 2001a). Therefore, as plant biomass and quality changes between seasons and years, an individual herbivore will adapt its ranging behaviour to respond to these changes. These responses have been studied in a number of large herbivore species including the wildebeest (Wilmhurst et al., 1999), Thompson's gazelle (Fryxell et al., 2004), red deer (Mysterud et al., 2001a), reindeer (Van der Wal et al., 2000; Marell, et al., 2002) and elk (Boyce et al., 2003), all of which exhibit seasonal habitat selection and change in movement behaviour based upon plant phenological development. In the

case of wildebeest in the Serengeti, this involves a large-scale migration over thousands of kilometres (Mduma et al., 1999). Red-deer and elk migrate at smaller scales, moving up mountain slopes in summer to target new plant growth (Mysterud et al., 2001a; Boyce et al., 2003). This is a common response of cervids in temperate regions, where food quality is the main driver behind seasonal migration (Fryxell & Sinclair, 1988). Reindeer in the Arctic exhibited the opposite response, selecting biomass over forage quality. This may be a strategy to optimise the short Arctic growth season (Van der Wal et al., 2000).

Elephant home ranges have been well documented but most studies concentrate on large spatial and temporal scales (Leuthold, 1977; Owen-Smith, 1992; Thouless, 1995; de Villiers & Kok, 1997; Osborne & Parker, 2003) whilst daily movements are rarely investigated. Home range variation has mainly been linked to resource availability (food and water), although this remains relatively untested (Thouless, 1995; Viljoen, 1989). Elephants are water dependent and as such their ranges are predicted to be strongly influenced by the availability of suitable drinking points (Western, 1975; Owen-Smith, 1996; Redfern et al., 2003). However, this variable was factored out of our analysis due to the abundance of permanent water sources in the reserves we studied.

Four temporal scales were examined in this study, (1) yearly range, based on a biological year (single continuous wet and dry season), (2) summer and winter seasonal range (Mysterud et al., 2001b), (3) daily displacement and (4) movement rate per hour (Galanti et al., 2000; Chamberlain et al., 2003). The spatial scales included the 95% kernel (total range) and the 50% kernel (core range) in km^2 (Worton 1989). Kilometres were also used as a measurement of displacement and movement rate. The large scale is important in understanding the broad spatial ecology of large mammals, while daily ranging behaviour provides a finer scale to assess foraging decisions (Carborne et al., 2005). Researching five distinct populations prevented the bias of localised effects that are commonly associated with one study site.

The aim of this study was to investigate the influence of forage quality and abundance on the ranging behaviour, and ultimately decision making processes, of a large sexually dimorphic herbivore. Elephants provide ideal study animals due to the pronounced behavioural and physiological differences between the sexes (Moss & Poole, 1983; Poole, 1994; Stokke & du Toit, 2000), their size, gregarious nature (Owen-Smith 1992; Spinage 1994; Charif et al., 2005) and role in ecosystem functioning (Laws, 1970; Owen-Smith, 1992; Mapaure & Campbell, 2002).

Three hypotheses were tested: (1) An individual's ranging behaviour will be positively correlated with rainfall. (2) Sexual dimorphism will result in females and males responding differently to fluctuations in

resource quality and availability. (3) These responses will occur at different temporal and spatial scales. Specific objectives were: (1) Verify the correlation between rainfall and forage abundance. (2) Compare male and female ranges (total and core) with reserve size, season and rainfall. (3) Contrast male and female displacement distance (24 hour period) with season, rainfall and reserve size. (4) Contrast male and female movement rates with reserve size, season and rainfall. (5) Assess the influence of four temporal scales on ranging behaviour: year, season, day and hour. (6) Outline the implications of the results for elephant conservation, management and research.

Methods

Study Sites

The Pongola Game Reserve (PGR) has a total extent of 82 km^2 and is situated on the western side of the Jozini Dam in Northern Zululand (27°54′ -27°35′ S; 32°01′-31°86′ E). The climate is hot and arid with an annual average rainfall of 650 mm and a range of 350-1000mm. The vegetation is classified under three broad types: Zululand Thornveld, Lowveld and Arid Lowveld (Acocks, 1988) and is of relatively high nutritional quality. Surface water is abundant with the dam forming the eastern boundary of the reserve and a number of pumped drinking points throughout the western section. The maximum distance from water is 5 km. PGR has three distinct elephant groups, a large herd (n=38) which only utilises the east of the reserve (40 km^2), an orphan group (n=7) and three adult males. The males and orphan group range across the whole reserve. During the study at least one of the males was collared throughout, the herd had two collars from 1997-2002 and third was deployed in 2004. The orphan family group had a collar on at least one individual from 2002 onwards.

Phinda Private Game Reserve (PPGR) was 150 km^2 in extent until August 2004, at which time the boundaries were expanded to 180 km^2 (27°92′ -27°68′ S; 32°44′-32°20′ E). PPGR has a diverse range of habitat types, from sand forest to the sweet lowveld bushveld, Natal low bushveld and the coastal bushveld of the savanna biome (Low & Rebelo, 1996). The reserve has an average rainfall of approximately 750 mm (averaged over 10 years) and a range of 350 mm to 1100 mm. The maximum temperature of 35°C occurs during the summer months. The minimum winter temperature is approximately 10°C. There is one river in the southern section of the reserve and 6 pumped dams situated throughout PPGR. Twenty four males and 34 females were introduced during 1992-1994, four were subsequently culled and four died of natural causes. In 2003, 37 elephants were removed and 3 adult males were introduced from Kruger National Park. Two males and one female were collared with GPS/GSM collars during 2003.

Pilansberg National Park (PNP) is a 500 km^2 reserve in the North West Province and is approximately circular in shape (25°8′ -25 °22′ S; 26 °57′-27 °13′ E). It is located in the crater of an extinct volcano and as such has hilly savanna relief. Acocks (1988) classifies the vegetation as sour bushveld, which is considered less nutritious than the vegetation of PGR. The average yearly rainfall is 630 mm with a range of 480mm to 1000 mm, which mainly falls in the summer (November-April) (Slotow & Van Dyk 2004). During the period of 1979-1998, 58 male and 37 female elephants were introduced. Fourteen of the males were culled and 15 elephants died between 1979 and 2001 of other causes. In 1998, six adult males, all fitted with radio collars, were introduced from Kruger National Park. During September 2002, 12 females from separate family groups were collared. Two satellite GPS collars were fitted to females in early 2004 and a further four GPS/GSM collars to females from different family groups in late 2004.

Tembe Elephant Park (TEP) is 300 km^2 in extent and is situated in northern KwaZulu-Natal on the border with Mozambique in an area known as Maputuland (27°07′ -26 °86′ S; 32 °59′-32°40′ E). Maputuland experiences a climate that is best described as humid and sub tropical (Schultze 1982). The average rainfall is 700 mm per annum with a range of 250 mm to 1400 mm. The substrate of the coastal plain is predominantly aeolian sands, which are layered and deposited by marine processes. The endemic sand forest of the Maputuland region is well represented in TEP but despite its high diversity, it is of relatively low nutritional quality. TEP is the only reserve in this study that maintains an original elephant population. The reserve was fully fenced in 1989, due to heavy poaching. The elephant population is believed to number between 155-185 with a sex ratio of 1:1.1 (male to female) (Matthews 2005). GPS/GSM collars were fitted to 3 females from separate family groups in 2004.

Hluhluwe imfolozi Park (HiP) is a 900 km^2 reserve situated in northern KwaZulu-Natal (28°42′ -28 °01′ S; 32 °15′-31°70′ E). It is the largest of all five study sites. The reserve has two distinct regions, varying in topography and rainfall. The northwest has an average altitude of 600m compared to 60m in the south. The rainfall gradient is also distinct with 990 mm/year in the northeast compared to 630 mm/year in the southwest. The majority of the yearly rainfall occurs during the warm summer months when temperatures reach up to 35 °C. Between 1981 and 1994, 184 juveniles were introduced to the reserve. During 2000, 10 radio collared adult males were introduced from the Kruger National Park. Two females were fitted with satellite collars in 2004.

Location Data

The elephants were located using radio telemetry or traditional tracking methods. Once sighted, a GPS position of the observer was recorded, along with date, time and habitat type. The precise location was

calculated by estimating the distance and bearing from the observer to the individual elephant or group. The elephants were then followed at a discrete distance until they moved out of sight, or the observation period ended. During this time, location points were repeatedly taken at approximately 20 minute intervals. Satellite GPS collars and GPS/GSM collars automatically recorded positional data throughout the day at pre-determined times. The data collection spans an 8 year period from 1998-2005, with each reserve being sampled at various intensities and times during this period. The longest continual data set was from PGR (1999-2004).

Climate Data

Rainfall data (mm) were collected in all of the reserves for management purposes and therefore historical data were available in addition to the actual study period. The rainfall data for the PGR were collected in the northern section of the reserve from 1999-2004. Data were also collected from 2003-2004 at another 4 locations throughout the reserve to measure localised variation. The regional ecologist supplied rainfall data for TEP, which was recorded daily at a weather station in the South of the reserve. Data for PNP was provided by the South African Weather Bureau and reserve management using a weather station in the reserve and one in Rustenburg. Data for PPGR were collected at the centre of the reserve since 1995. The HiP data were provided by the Zululand Grass Project (Botany Department, University of Cape Town) and were collected at 10 sites throughout the reserve.

Rainfall was highly variable with 2000 being the wettest year in all of the reserves (Fig. 1). The period of 2002-2004 was significantly drier and many regions of South Africa experienced prolonged droughts during this time. The pattern is evident across all the reserves providing an opportunity to assess the effect of changing rainfall on the ranging behaviour of the elephant. The average rainfall over the 6 years varied from 673-770 mm and TEP showed the greatest variation with 257 mm in 2002 and 1391 mm in 2000. Variation within PGR was marked, with the southern section receiving 24% (824 mm) more rainfall than the north (683 mm) during 2003-04. The lowest rainfall occurred in the northwest of the reserve (585 mm), and was 14% lower than the reserve average of 677 mm. HiP also exhibited spatial variation in rainfall. Annual variation was greatest during the drought year of 2002-2003 with a range of 349-471 mm (25%) compared to 733-845 mm (13%) in 2003-2004. During 2002-2003, there was significantly more rainfall in the northwest compared to the southeast of the reserve.

Temperature

The maximum and minimum daily temperatures were recorded throughout the study period and were augmented with local weather station data. The average maximum and minimum monthly temperature

were then calculated. These data were used to compare temperature patterns of wet (2000-01) and dry years (2003-04). The results indicate that monthly minimum and maximum temperatures were above average during the wetter years and below average during the drier years.

Phenological Data Collection

Phenological data were collected in both the PGR and PNP from 2002-2004. Trees were sampled throughout the reserve in all height classes above 1 metre. Individuals of the common species were selected at random in different parts of the reserve. The location of each sample point was plotted to ensure an even coverage of the reserve. The location of the tree was recorded using a GPS, along with aspect and topographic position. Basal diameter, height, height below canopy and diameter of longest and shortest canopy axis were measured. The available biomass was appraised and the percentage of old wood, new wood and non-woody biomass (leaves, fruit and flowers) were estimated as a percentage of the total biomass. A further breakdown of the non-woody biomass was done in order to calculate the relative proportions of new leaf, mature leaf, senescent leaf, fruits and flowers. These data were collected throughout both seasons in order to track the availability of forage over time.

The phenological variation in PGR and PNP was strongly correlated to season. There was a reduction in the new leaves at the end of the wet season and into the dry season, followed by an increase in the amount of senescing leaves. A broad measure of vegetation quality was established using a ratio of the percentage of mature leaf divided by the percentage of senescent leaf on the basis that green leaves will have higher nutritional value (protein content) than browning senescent leaves. The rainfall values used for the analysis were from the month prior to the collection of the data to account for the lag in growth response after rain. There was a positive correlation between biomass and rainfall in both PGR ($F_{1,20}$=18.02, $P<0.01$, r^2=0.47) and PNP ($F_{1,12}$=15.11, $P<0.05$, r^2 =0.55) (Fig. 2).

Spatial Analysis

To avoid autocorrelation, one location point was selected per day for each set of home range analyses. This ensured independence of one location from the next. This has been discussed at length in the literature (Swihart & Slade, 1985; Swihart et al., 1988; de Solla et al., 1999; Ramsey & Usner, 2003). The Animal Movement extension in ArcView® 3.2 (Hooge & Eichenlaub, 1997) was used to calculate the core home ranges (50 % kernel) and the total home range (95 % kernel) based on Worton (1989). The home ranges were then clipped according to the reserve boundaries and their size was calculated using the X-tools extension.

Home ranges were calculated for each biological year (complete summer and winter season) and separately for summer and winter seasons. The length of a season was defined by the rainfall of that year, with the summer beginning 10 days after >15mm of rain in September/October. Winter began when there had been no significant rainfall (<15mm) for two weeks, from 15 March to as late as mid May.

The location data were also used to generate the displacement distance from one day to the next using the Animal Movement extension. The straight line distance from one point to the next was calculated. These values provided the displacement distance for subsequent days. Points not in a 24 hour sequence were discarded. The remaining distances were summed and divided by the number of days in order to get an average straight-line displacement for each individual during different years and seasons. Movement rates were calculated using the same method. Days with regular location points (minimum of six for 12 hr period) for a group or individual were selected and the total distance covered was divided by the time during which the data were collected. This does not provide an exact rate of movement due to the coarse nature of the data, which are unable to detect the finer scale of elephant movements. However, this sampling error is repeated for all the data sets and therefore provides an index by which comparisons among seasons, years and sex can be made.

Statistical Analysis

All of the analyses were carried out in the statistical package SPSS 11. The Kolmogorov Smirnov test was used to establish whether data was normally distributed. A linear regression was used to investigate the relationship between rainfall and range size. To remove the effect of reserve size, the standardized residual was calculated for each point using a one-way ANOVA of range against reserve size, separately for each sex. The limited size of the PGR and PPGR prevented the results being included for further analysis as range expansion was constrained by reserve size and residuals remained relatively similar for all of the data points.

The reserves were therefore split into two distinct categories; small (<150 km^2), which included PPGR and PGR, and large (>300 Km^2), which included TEP, PNP and HiP. A two way ANOVA was used to investigate the influence of sex and rainfall on range size in the larger reserves. Annual rainfall was classified as low or high, depending whether it was above or below the long term mean for all five reserves (680mm). These results were compared with the long term data set collected from PGR to establish whether similar patterns of behaviour occurred in small and large reserves. The PGR data set was analysed using a Wilcoxon paired-sample test to establish whether winter and summer ranges were significantly different for males and females. The displacement analysis involved comparing all the male

and female results using a one-way ANOVA. The data were separated by sex and a two-way ANOVA was used to analyse the influence of season and rainfall. The influence of reserve size on displacement was also investigated using a one-way ANOVA. The movement rates were analysed in the same way.

Results

Home Range

The size and location of male and female home ranges varied seasonally and annually throughout all of the study sites. The linear regression of home range size against reserve size was significant for both males ($F_{1,44} = 134.79$, $P < 0.01$ $R^2 = 0.75$) and females ($F_{1,36} = 58.377$, $P < 0.01$ $R^2 = 0.62$), confirming the strong influence that reserve size has on range extent. After factoring out the reserve size effect, annual range size increased significantly with rainfall for both the total ($F_{1,44} = 4.56$, $P < 0.05$ $R^2 = 0.095$) and core male ranges ($F_{1,44} = 4.07$, $P < 0.05$, $R^2 = 0.097$) across all reserves (Fig. 3). The R^2 value is low, suggesting a high level of variation. This is to be expected, considering the myriad of factors that influence the movement of elephants and the differences between reserves and population size. Despite this variation, there is a positive effect of rainfall on the annual range size of male elephants. Females and their associated family groups do not exhibit the same relationship for the annual 95% range ($F_{1,36} = 0.65$, $P > 0.5$ $R^2 = 0.006$) or the annual 50% ranges ($F_{1,36} = 0.009$, $P > 0.9$ $R^2 = 0$).

In the large reserves both male and female elephants exhibit a positive relationship between range size and rainfall. This relationship is observed for both the total annual home range ($F_{1,54} = 4932.1$, $P < 0.01$) and the core annual range ($F_{1,54} = 778.5$, $P < 0.05$). The seasonal data were not as conclusive, with only winter providing a positive result for the total home range ($F_{1,53} = 944.5$, $P < 0.05$). This is due to the level of variation in the female response. The trend for males and females was to increase their range with rainfall. The variation in range size was also greater in years with above average rainfall. Summer ranges were consistently larger than winter ranges in all years (Fig. 4).

The smaller reserves did not exhibit a significant relationship between home range size and rainfall when analysed together (total range $F_{1,22} = 3.17$, $P > 0.25$ and core range $F_{1,22} = 0.63$, $P > 0.5$). The continuous data set from PGR enabled the ranges of males and females to be plotted against rainfall (Fig 5). As with the larger reserves, male range size tracked the drop in rainfall from 1999-2003 (Fig. 5a & b) for both the total and core range. The total range increased in 2004, which coincides with the end of a severe drought. The females in PGR did not exhibit the same relationship. Their total range expanded with reduced rainfall, whilst the core range remained constant throughout the study except during 2003 when it doubled in size (Fig. 5c & d).

The females in PGR exhibited a distinct relationship between season and range size despite fluctuating rainfall. The winter seasons for all four years had larger core ranges than the proceeding summers. Whilst not significant, the trend was evident ($Z=-1.826$, $P<0.1$). The males exhibited no relationship for the seasonal core range size ($Z=0$, $P>0.95$). However during the dry period of 2002-2004 they reduced their core range. These results are similar to those from the larger reserves, further indicating that male range size is positively correlated to rainfall.

Displacement

The annual displacement distance (24 hour) did not differ significantly between males and females ($F_{1,50}=0.26$, $P>0.5$). Male winter displacement distances were significantly lower than summer ones ($F_{1,52}=4.03$, $P=0.05$). Data for females were non-significant and season did not influence the displacement distances ($F_{1,52}=0.01$, $P>0.9$). Males had a significant interaction term for season and displacement ($F_{1,50}=4.81$, $P<0.05$), suggesting different seasonal responses (Fig. 6a). There was no influence of reserve size on the annual displacement distance of females, but males exhibited significantly greater average displacement distances in the larger reserves ($F_{1,25}=9.42$, $P<0.01$) (Fig. 6c).

Movement Rates

Males move at a significantly faster rate than females ($F_{1,37}=5.25$, $P<0.05$). Despite a low sample size, the males exhibit increased movement rates during wet summers and dry winters ($F_{1,10}=8.37$, $P<0.05$) (Fig. 7a). This relationship was not found for the females (Fig. 7b) ($F_{1,21}=0.25$, $P>0.75$). Females in small reserves had higher average movement rates (>0.5 km/h) compared to large reserves where movement rates did not exceed 0.3 km/h ($F_{1,23}=73.71$, $P<0.001$). This occurred in both seasons. Due to the limited size of the male data set, it was not possible to compare movement rates between the different sizes of reserves.

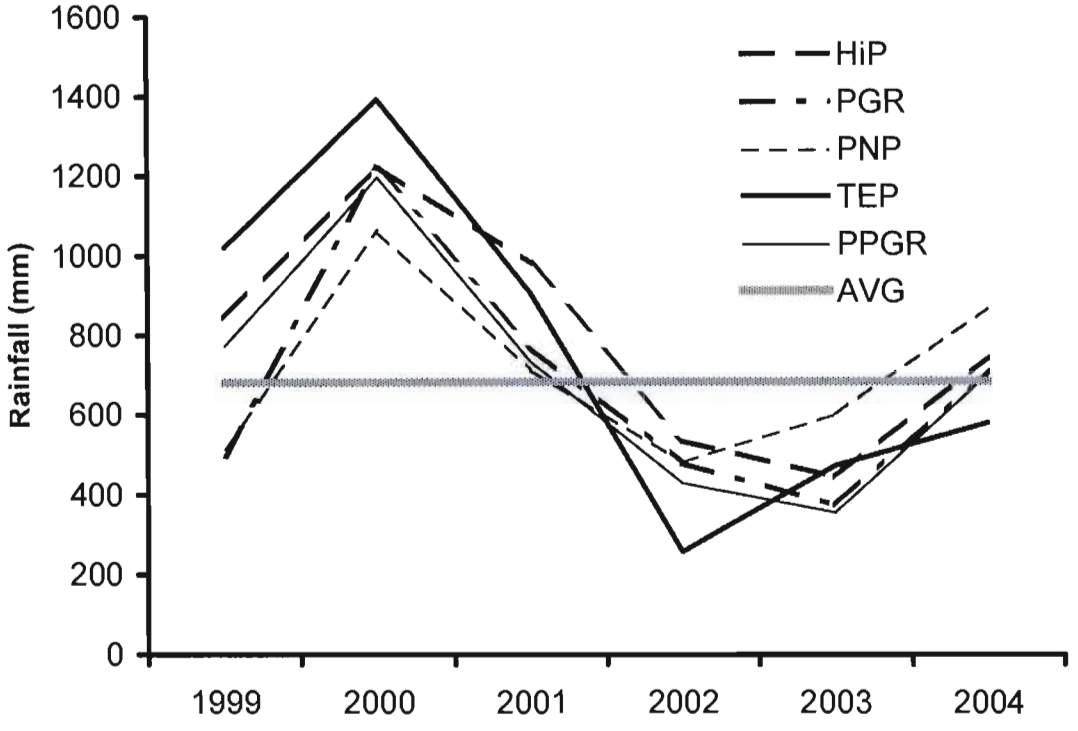


Figure 1. The variation in annual rainfall from 1999-2004 for the five reserves used in the study and the average long term mean (AVG).

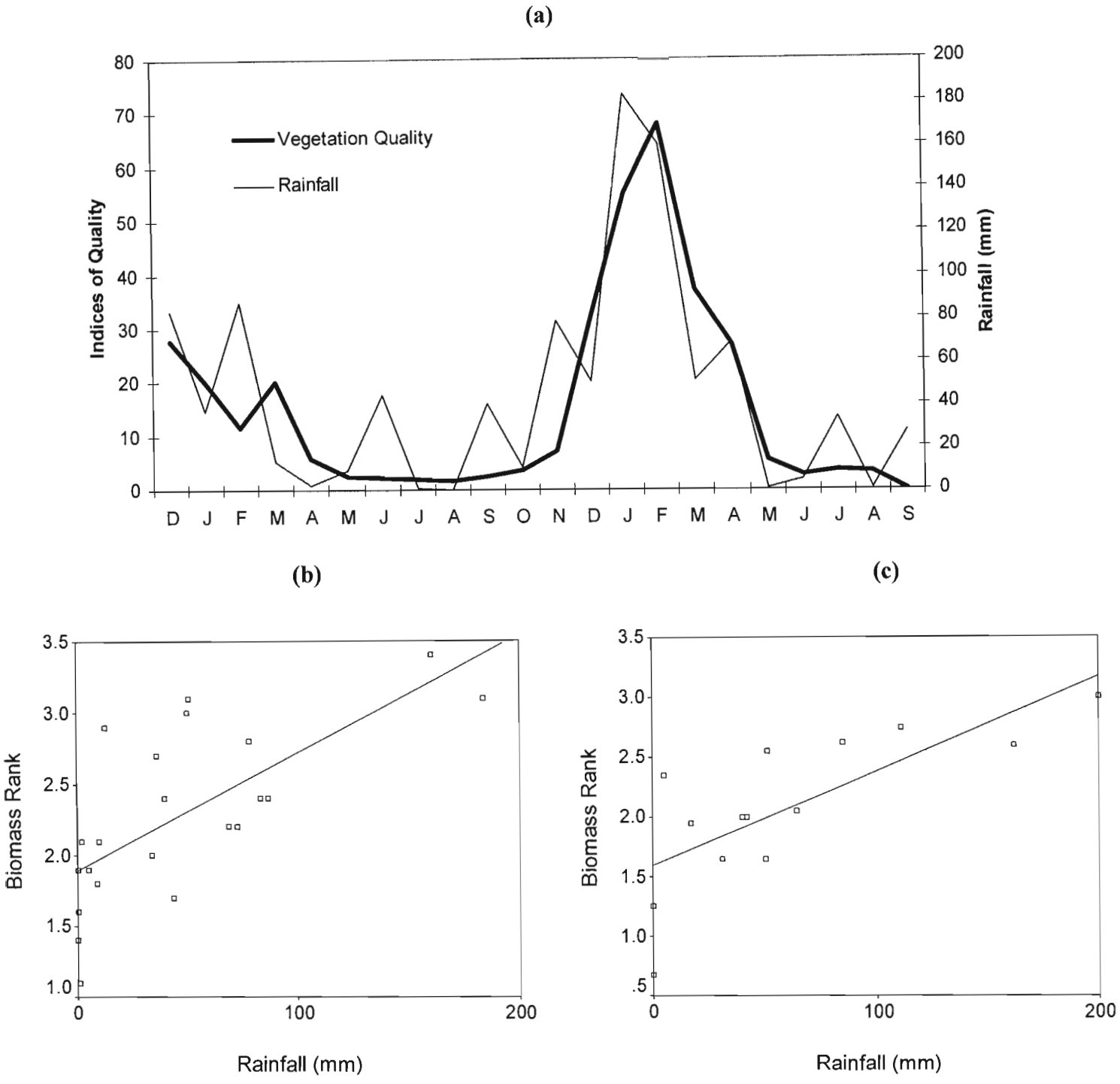
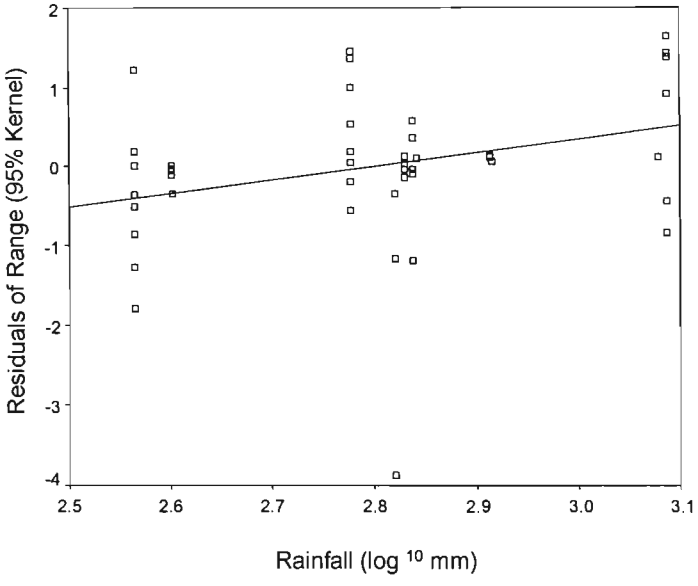


Figure 2 (a). The relationship between rainfall and vegetation quality (a ratio of mature leaf/senescent leaf) from 2002-2004. The relationship between the availability of non-woody biomass and monthly rainfall in (b) PGR and (c) PNP from 2002-2004. Both of these figures use rainfall from the preceeding month to account for the lag in vegetation growth response.



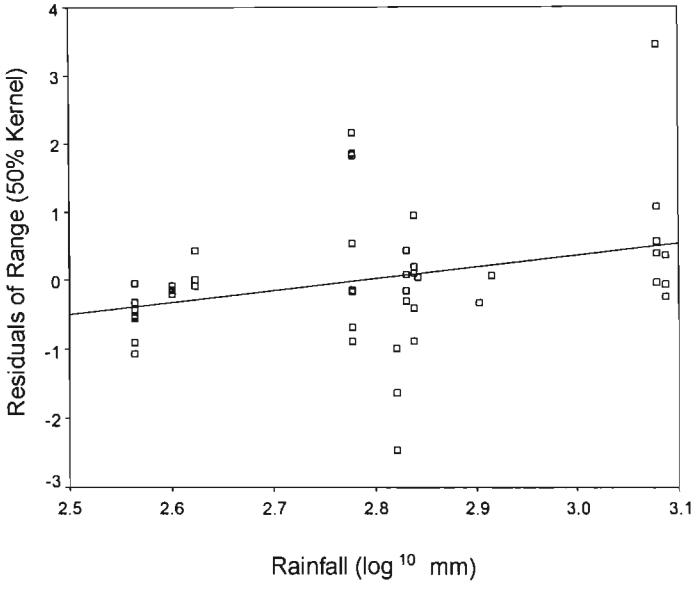


Figure 3. Effect of rainfall on range size (95% and 50%) of male elephants, using data from all five study sites. Residuals were calculated in order to remove the reserve effect which was shown to have a significant influence on range size.

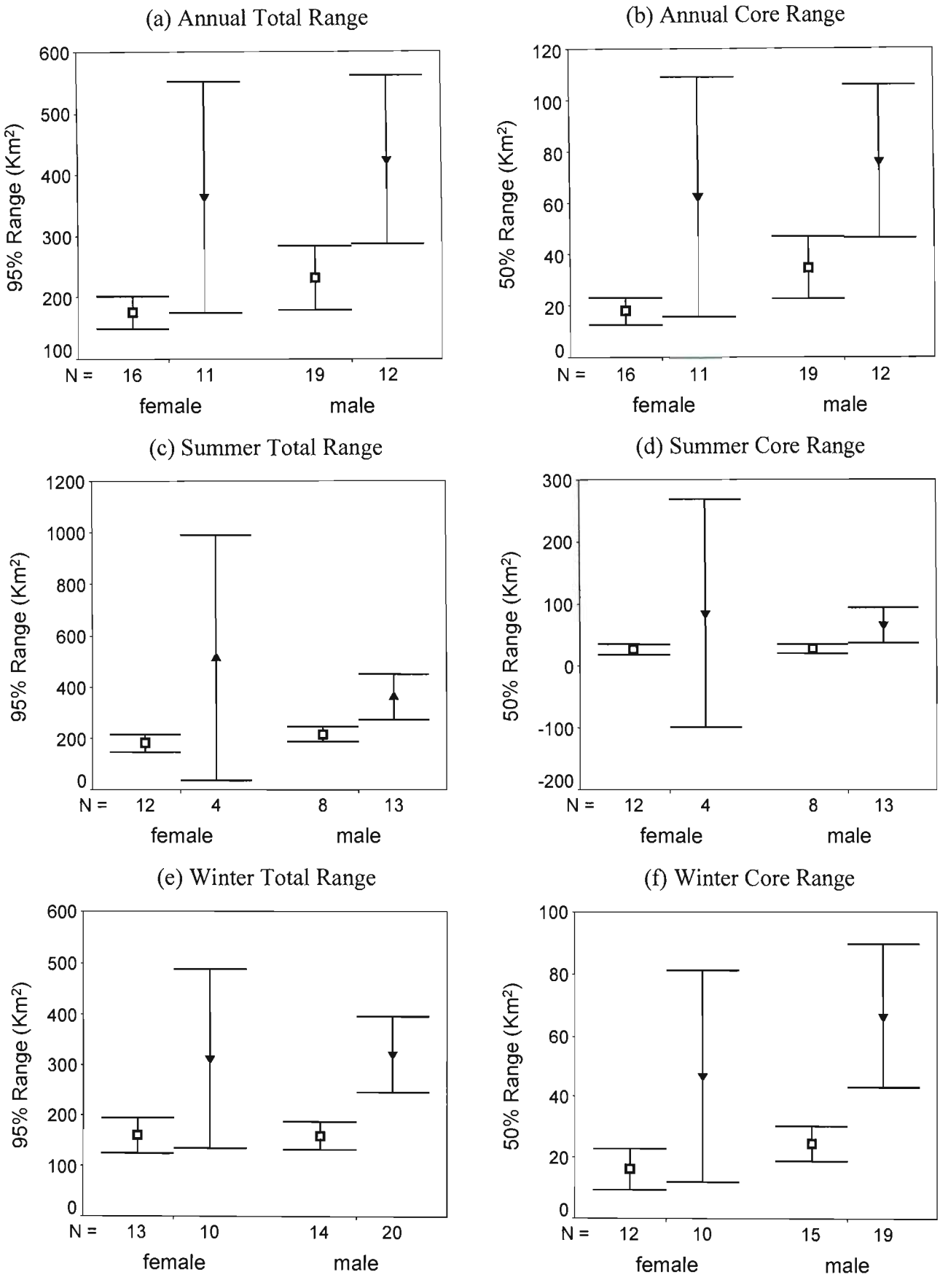


Figure 4. The effect of rainfall on range size for male and female elephants in large reserves, = □ low rainfall (<680 mm per year); high rainfall =▼ (>680mm per year) (Data are mean ± 95% CI).

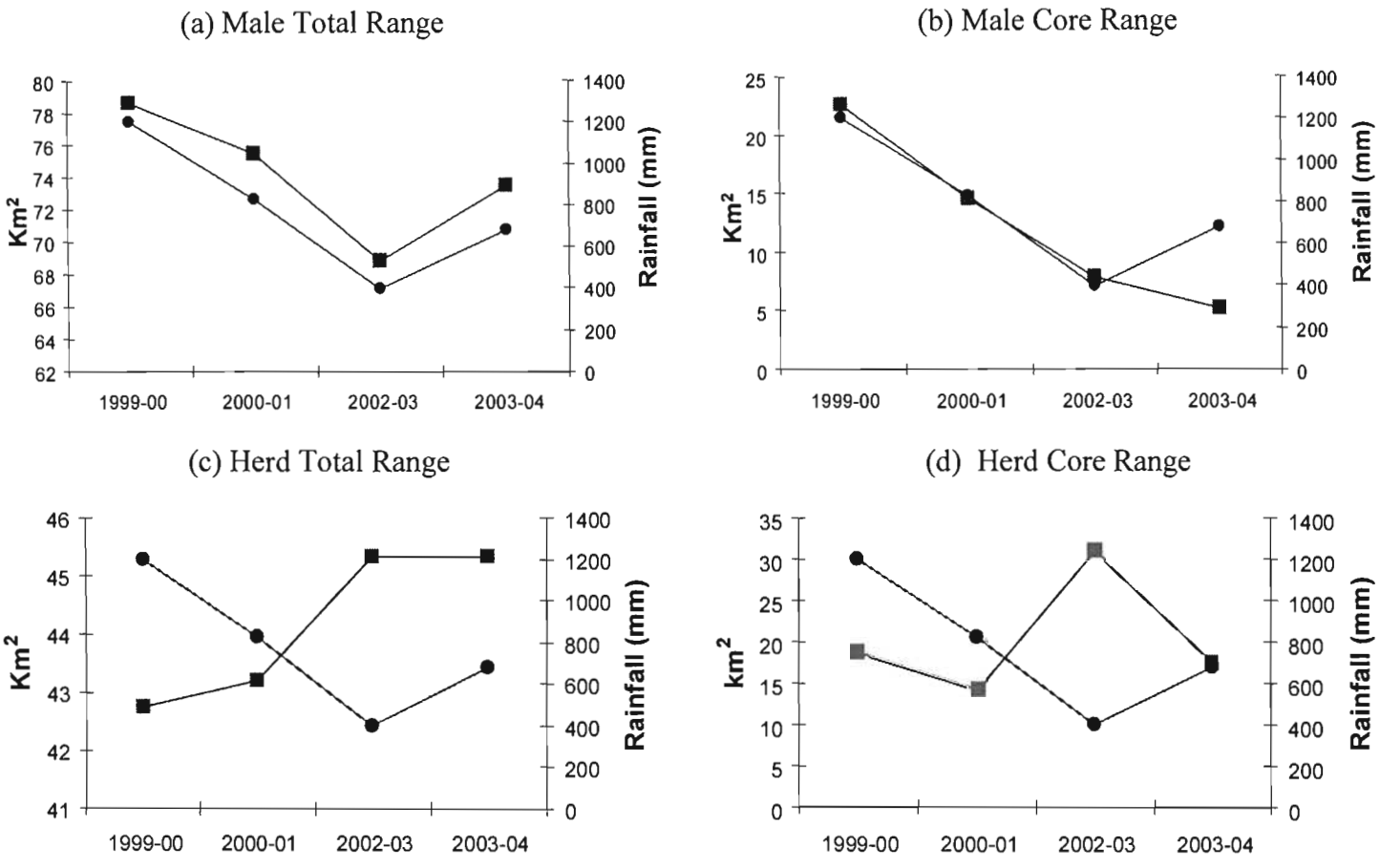


Figure 5. The effect of annual rainfall = ● on the total and core ranges = ■ of male and female elephants in PGR.

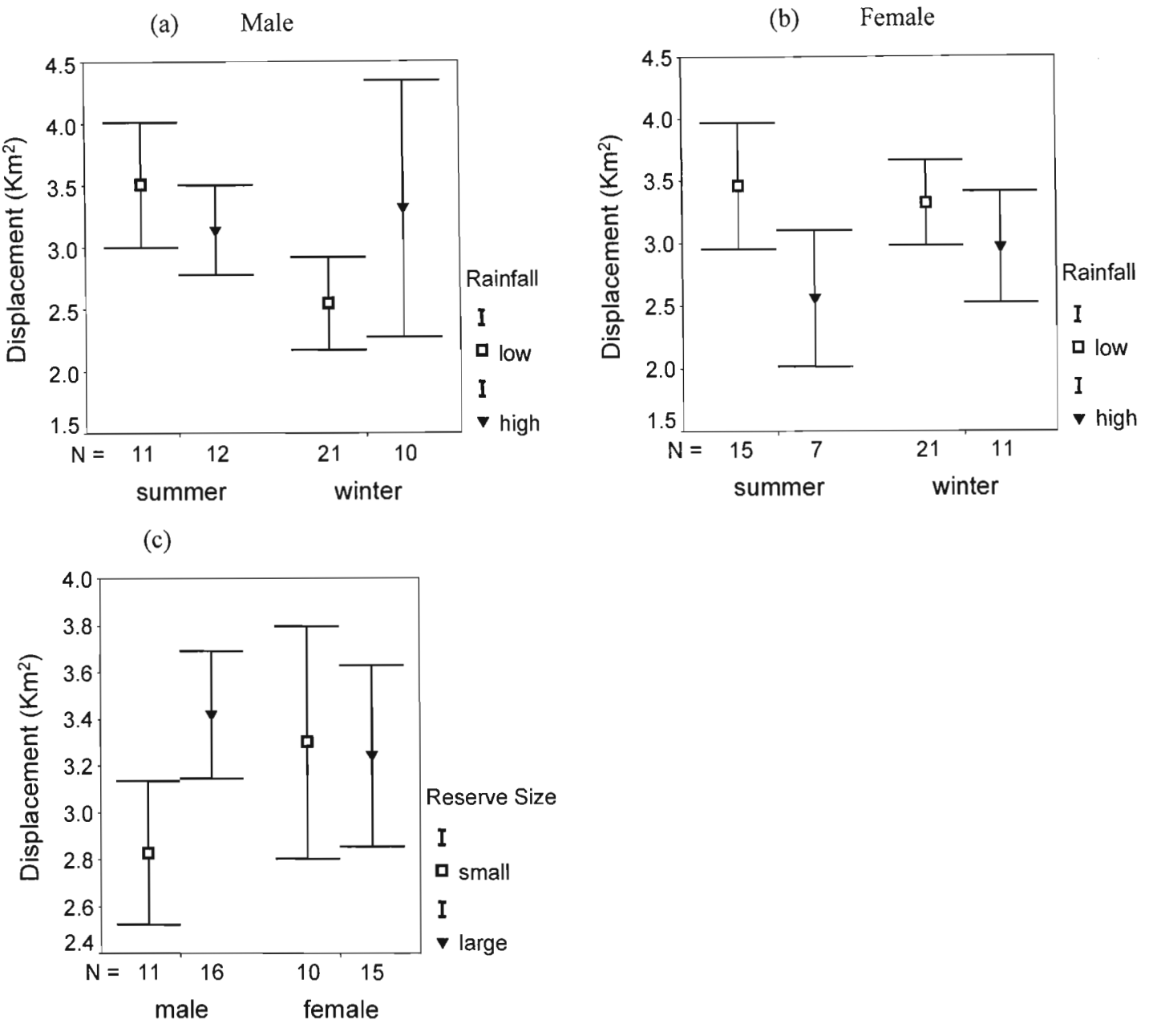


Figure 6. The influence of season and reserve size, on the 24hr displacement distance of male and female elephants in all five reserves (Data are mean ± 95% CI).

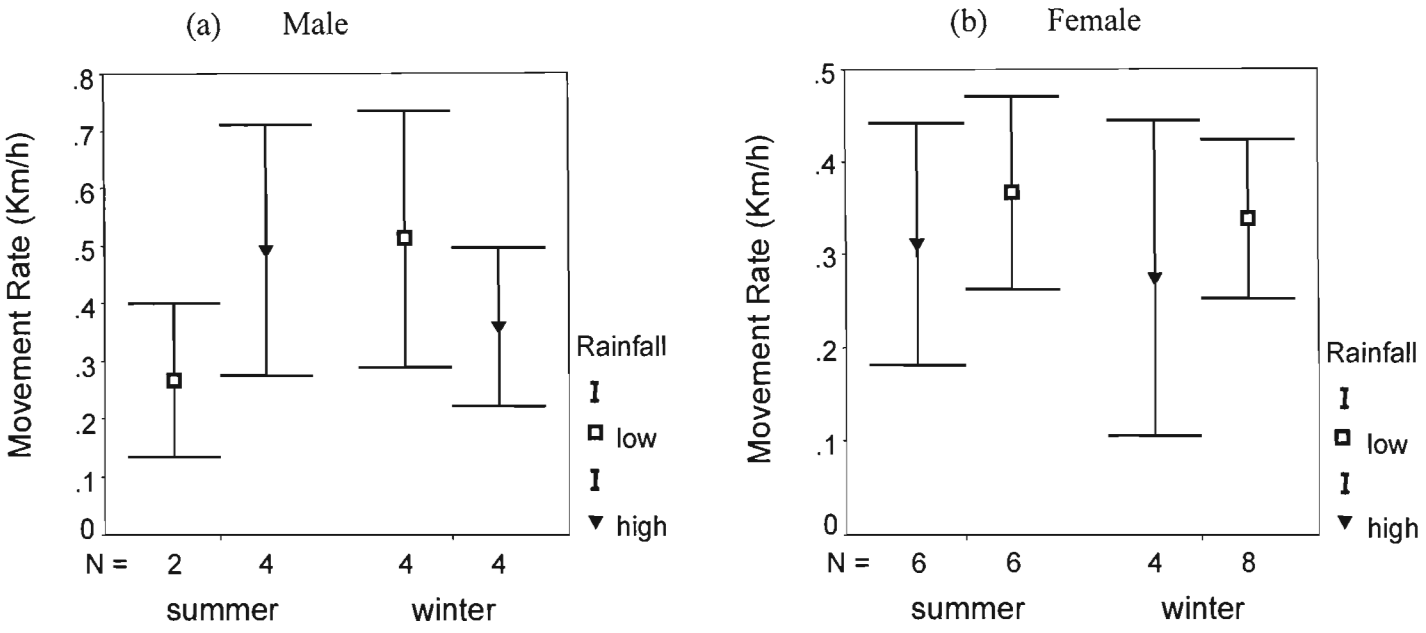


Figure 7. The effect of rainfall on movement rates of male and female elephants during the two distinct climactic seasons, winter and summer in all five reserves, low rainfall (<680 mm); high rainfall (> 680 mm) (Data are mean ± 95% CI).

Discussion

Biomass and Rainfall

Rainfall and primary productivity in the savanna ecosystem are positively correlated (Prins & Loth, 1988; Coe et al., 1976). This relationship has been used to predict carrying capacities (Coe et al., 1976; East 1984) and to investigate ungulate dynamics (Owen-Smith, 1990; Marshal et al., 2005). Similarly in this study, biomass availability and vegetation quality was positively related to monthly rainfall in PGR and PNP with the drought of 2002-03 exhibiting a significant reduction in the available biomass when compared with 2004. The minimum average temperature was also lower during the drought year and it is likely that this could suppress plant growth further, based on studies in temperate regions showing that temperature is an important factor in the onset of phenological cycles (White et al., 1997).

Home Range

Elephants of both sexes respond to variations in forage quality and availability by expanding their annual, summer and winter ranges in years with above average rainfall. This relationship was repeated for the core ranges and is consistent with the theory that abiotic factors dictate broad scale distribution of ungulates (Boyce et al., 2003; Redfern et al., 2003; Post & Stenseth, 1999). Seasonal range use by elephant has been described as a function of surface water availability (Osborn, 2003; Stokke & Du Toit, 2002; Thouless, 1995; Owen-Smith, 1992; Western & Lindsay, 1984). In this study water distribution was factored out and the results indicate a positive relationship between rainfall, forage quality and ranging behaviour. Research on the roe deer and ground squirrel suggests that smaller, relatively selective species reduce their range size as the quality of forage increases (Hubbs & Boonstra, 1998; Tufto et al., 1996). In contrast, larger species that live on abundant low quality forage (e.g. moose and white tailed deer) increase ranging as food availability improves (Henriksen et al., 2003; Mysterud et al., 2001a).

Both sexes exhibited a trend for reduced range size during the winter season in the larger reserves. However, total annual rainfall had a much greater influence on ranging behaviour than season alone, with male elephants exhibiting the strongest relationship. This is because total annual rainfall and productivity are directly related, whilst temporally distinguished seasons are associated with variable forage quality (Prins & Loth, 1988). During low rainfall years and winter seasons, elephants are likely to forage in habitats that maintain a relatively high abundance of non-woody biomass, such as river lines and thickets in low lying areas (Viljoen, 1989; Ottichilo, 1986). This is in accordance with the hypothesis that large herbivores can compress their winter ranges due to a tolerance of abundant low quality forage (Mysterud et al., 2001a). Despite the demands of group living, which can negatively impact the foraging efficiency of individuals (Fritz & De Garine-Wichatitsky, 1996), female elephants in the large reserves concentrated

their ranges to a similar extent as males in winters of below average rainfall. The changing dietary composition of male and female elephants may also play a role in their seasonal range expansion and contraction. During the summer, elephants have been observed to forage mainly on grass, however their approach switches to browsing in the winter period when the grasses loses nutritional value (Owen-Smith, 1992). Grass resources are generally widespread and homogenous whilst browsing opportunities are often discrete and patchily distributed, especially during the dry season. This adaptation in foraging behaviour may well affect the seasonal ranging patterns of the elephant.

In PGR the females exhibited consistently larger winter ranges despite fluctuating rainfall. This may be a function of restricted range size, seasonal habitat selection and the large number of elephants in the herd (Shannon et al., in press). There is also evidence of females expanding their ranges in other herbivores species such as roe deer. Females with fawns have larger home ranges due to the costs of lactation and also feed away from the young to prevent location by predators (Tufto et al., 1996). In elephants, it is probable that higher mass specific energy requirements, group living and the costs of reproduction require females to feed on higher quality food sources than males (Stokke & du Toit, 2000). In reserves of limited size such as PGR, it is unlikely that females can respond to a reduction in resource availability in the same manner as males. These differences were further highlighted, with male annual ranges (95% and 50%) being closely correlated with rainfall (Fig. 5), whilst the females showed no such relationship.

The reproductive strategies of male elephants are likely to be a major driver in the seasonal variation of range size. The majority of males enter musth and search for oestrous females during the summer months (Moss & Poole, 1983; Poole, 1989; Owen-Smith, 1992). When forage availability becomes limited, they reduce their expansive ranges to target remaining food resources. Females are likely to be driven by energy demands and the protection of the family group as year round priorities and therefore expand and compress their ranges on the basis of forage availability and quality.

Displacement

The daily range of herbivorous mammals is believed to scale with a value of ¼ body mass (Carbone et al., 2005). Despite their marked body size dimorphism (Poole, 1994; Owen-Smith, 1992) the elephants in this study showed no significant difference between the sexes in 24-hour displacement. This may be an artefact of the relatively small size of the reserves used in this study. Seasonal variation was noted, with females increasing their 24-hour displacement distance in summers with above average rainfall, as the abundance of forage enables family groups to exploit larger ranges..

Males responded at the seasonal level, exhibiting lower displacement in winter when they focus their foraging and do not range as widely. The males also exhibited significant interactions between season and rainfall with reduced displacement during dry winters when food quality and availability is at its lowest, possibly concentrating on distinct habitat patches. During wetter years male winter displacement increased as food availability was greater and it was optimal to move over significantly larger day ranges to target wider foraging opportunities. Females did not respond in the same manner, possibly due to their requirement for higher quality forage at a range of height classes (Stokke & du Toit, 2000) and the feeding limitations imposed by weaned calves (Owen-Smith, 1992; Stokke & du Toit, 2000). In general, female reproductive investment is high with lactation costs increasing the energy demands of some ungulate species by up to 150% during peak lactation (Blanchard, 2005).

Rate of Movement

Males had higher movement rates throughout the study period compared to females. This is probably due to their greater size and reproductive strategies, which involve moving across comparatively large areas in search of receptive females (Hall-Martin, 1987; Slotow & van Dyk, 2004). In summers with high rainfall, the males moved at a greater rate than in summers with below average rainfall. This could be due to improved food quality and availability, enabling males to range widely in search of oestrous females. Movement rate was reduced in summers with lower rainfall. This could be due to reduced forage quality requiring more time spent feeding in one locality. In moose, a decrease in food availability leads to a more general feeding approach, greater bite diameters of targeted saplings and longer feeding bouts (Vivas & Saether, 1987). Dry winter periods were associated with high movement rates as males moved through their limited ranges searching for remaining foraging opportunities. The seasonal movement rates of large herbivores have rarely been studied. However, a study on bobcats in Central Mississippi showed that during winter when food became scarce their movement rates increased (Chamberlain et al., 2003). Whilst it is difficult to draw direct comparisons between studies on carnivores and herbivores, it is interesting to note that this response to food availability has been previously recorded. We suggest that search time increases during resource scarcity and elephants can improve forage efficiency by moving at greater rates.

Female movement rates in small reserves were significantly higher than those in larger reserves. This may be linked to reduced foraging opportunities, larger group size and increased disturbance (e.g. tourism and hunting). Elephants in Addo Elephant National Park (100 km^2) had movement rates similar to those found in the small reserves of this study, with means of 0.49-0.54 km/h (Whitehouse & Schoeman, 2003). These values compare to average movement rates of 0.35 km/h for four collared female elephants in Tarangire

National Park, Tanzania throughout a 5 month (summer) study period (Galanti et al., 2000). In the larger reserves of this study, females exhibited movement rates averaging 0.25 km/h. Forage availability and habitat patch size may play a role in the reduced movement rate of females in larger reserves.

Temporal Scales

Temporal response to resource availability appears to occur at different scales (annual, seasonal, daily, hour) for males whilst females only exhibit significant variation at the seasonal and yearly level when rainfall is above average. Males are more adaptable to fluctuations over time and adapt their ranging behaviour according to access to females and forage availability. Females show significant variation in years with good rainfall and consequent abundant forage. The group dynamic and higher relative energy demands of female elephants appears to constrain their response to fluctuations in resource quality and availability.

Conclusions

Male and female elephants have markedly distinct ranging behaviours which are likely to be the result of their physiology, morphology and sociality. Both sexes exhibit larger ranges in the wetter years and seasons due to the abundance of available forage. However, when resources are scarce males adapt their home ranges, displacement and movement rates with greater flexibility than females. This is likely due to their size, independent nature and greater digestive efficiency, compared to the females who live in established family groups and have higher relative energy demands.

Adult males have expansive ranges that far exceed their energetic needs and it is likely that social and reproductive factors play a significant role in the establishment of these ranges (Whitehouse & Schoeman, 2003; Slotow & van Dyk, 2004). Females appear to have an alternate strategy which centres on satisfying energy demands and protecting the family group. The female response to variation in productivity is less flexible due to decision-making at a group scale and the elevated specific energy requirements. Females will maintain similar movement rates and displacement distances throughout the year as they search for optimal foraging opportunities. This is critical during resource scarcity as juvenile elephants are the most susceptible to loss of condition and death during drought periods (Dudley et al., 2001; Moss, 2001). Males are much more adaptive and can focus their ranges in relatively small areas that provide an abundance of low quality forage (Chapter 5 details further the foraging differences between males and female elephants).

Understanding how large herbivores respond to temporal and spatial heterogeneity is important for designing ecological research programs and for effective management, as large herbivores are a major component of terrestrial ecosystems. (Gross et al., 1995; Boyce et al., 2003; Fryxell et al., 2004; Gordon et al., 2004) Elephants are a prime example as they have the ability to alter habitat structure and have been linked to negative impacts when densities are elevated (Cumming et al., 1997; Lombard et al., 2001; Wiseman et al., 2004). During periods of resource scarcity elephants focus their foraging in smaller areas and this may accentuate impacts on woody vegetation at a localised scale (Slotow & van Dyk, 2004). Males in particular, due to their size and independent nature may have a greater impact during these periods than the more selective females and their family groups. Large sexually dimorphic herbivores such as the elephant may well need to be considered as acting as two different species with regard to their spatial ecology and thus their ecological roles and consequent impacts on vegetation will be different.

CHAPTER 4

THE CONSEQEUNCES OF BODY SIZE DIMORPHISM: ARE AFRICAN ELEPHANTS SEXUALLY SEGREGATED AT THE HABITAT SCALE?

Abstract

Sexual segregation is pronounced in dimorphic ungulates and is believed to have two distinct components: social segregation and habitat segregation. We investigated whether elephant exhibit marked habitat segregation on the basis of sex. Two main hypotheses have been proposed to explain habitat segregation. The forage hypothesis, which states that, due to large body size and allometric scaling, males can tolerate lower quality forage and are less specific in regard to their habitat utilisation, whilst females have greater mass specific energy requirements and target higher quality habitats. The predation hypothesis predicts that females will use 'safe' habitats in preference to those offering high nutritional return, whilst males invest heavily in growth and will take greater risks in order to secure nutritional gain. To test these hypotheses we recorded the locations of 12 family groups and 16 individual males in three distinct populations, Pongola Game Reserve (PGR), Phinda Private Game Reserve (PPGR) and Pilanesberg National Park (PNP), over a 2.5 year period. Preference ratios were calculated using the proportion of sightings divided by the proportion of area for each vegetation type. A Kendall's coefficient of concordance was used to analyse the data for each reserve, firstly within sex to see whether their habitat preferences exhibit concordance and then between the sexes. Female habitat preferences showed significant concordance across all the reserves and females also exhibited concordance in their summer foraging preferences. Their weakest association with habitat and foraging preference was during the winter period and this may be related to resource scarcity. Males exhibited significant concordance in their habitat preferences in PNP and PPGR but not in PGR. They had their weakest associations in the summer months and this may be linked to avoidance of other bulls in musth and forage abundance. There were no significant differences in habitat preference between males and females and it is likely that individual preferences vary as much as those between the sexes. Habitat utilisation does not appear to be driving sexual segregation in elephants and it is postulated instead, that social factors, reproductive strategies and foraging behaviour at the patch and plant scale play a more important role.

Introduction

Sexual segregation is a common consequence of dimorphism in large ungulates and it results in males and females living apart outside of the breeding season (Beier, 1987; Ruckstuhl, 1998; Conradt, 1998b, Barboza & Bower, 2000). This aspect of animal behaviour, which has also been recorded in primates, cetaceans and a number of bird species is not just an interesting biological phenomenon but has important

implications for the management and conservation of dimorphic species (Ruckstuhl & Neuhaus, 2000, Conradt et al. 2000, Bowyer 2004). This is because sexual segregation has a direct influence on spatial use, reproductive performance and survival (Owen-Smith; 1993; Conradt et al. 2000; Mysterud, 2000). As a result, extensive research into sexual segregation has taken place over the past 10 years. Despite this, the underlying mechanisms remain poorly understood. (Ruckstuhl, 1998; Kie & Bowyer, 1999; Conradt, 1999; Ruckstuhl & Neuhaus 2000; 2002; Bowyer, 2004). It also appears likely that the causes may vary depending upon the ecological conditions that the animal is exposed to as well as the different spatial and temporal scales at which they are studied (Conradt, 1998a; Conradt et al. 2000; Bonenfant et al. 2004).

Sexual segregation has been split into two broad categories, differential habitat utilisation by the two sexes (habitat segregation) or seperation into same sex groups within the same habitat (Social segregation) (Bon & Campan, 1996; Bonenfant et al. 2004; Perez-Barberia et al. 2005). Initially Social segregation was believed to be a result of habitat segregation, however recent studies have demonstrated that segregation can occur within homogeneous habitats due to social factors or differing activity patterns (Ruckstuhl, 1998; Conradt, 1999; Ruckstuhl & Kokko, 2002). Social segregation and habitat segregation need to be treated as two separate variables and not as a bi-product of one another (Conradt, 1999). In this chapter we deal with sexual segregation solely at the habitat scale.

Habitat segregation has been observed in a number of large herbivores including the red deer (*Cervus elaphus*) (Conradt, 1999; Bonenfant et al. 2004), alpine ibex (*Capra ibex ibex*) (Bon et al. 2001) and feral soay sheep (*Ovis aries*) (Conradt, 1999). Outside of the mating season, these animals separate into same sex groups, use different areas of their range and effectively exist as two distinct 'ecological species' (Demment, 1983; Ginnett & Demment, 1997). Elucidating the factors responsible for this segregation is important for understanding how herbivores are spatially and temporally distributed, how their resources are partitioned and the resulting influence on habitat structure and ecosystem function (Bowyer, 2004).

There are four main hypotheses that have been put forward to explain sexual segregation; these include the forage selection hypothesis, the reproductive hypothesis, the social preference hypothesis and the activity budget hypothesis (Ruckstuhl & Neuhaus, 2000; Perez-Barberia et al. 2005). Out of these four, the forage selection hypothesis and the reproductive hypothesis are the most likely to result in actual habitat segregation, whilst social factors and differing activity budgets will lead to separate groups forming in the same habitat.

The key assumption of the forage selection hypothesis is that body size has a significant influence on the energy requirements of an individual due to the allometric scaling of metabolic rate ($W^{0.75}$) (Mysterud, 1998; Ruckstuhl & Neuhaus, 2000; Stokke & du Toit, 2000). This results in larger individuals having reduced energy requirements per kg body mass (Demment, 1983; Demment & Van Soest, 1985). This relationship is coupled with an isometric scaling of gut size resulting in greater capacity and increased retention time proportional to body size (Demment & Van Soest, 1985; McNaughton & Georgiadis, 1986; Owen-Smith, 1992). This enables larger bodied herbivores to tolerate diets of lower quality since they can derive greater nutritional benefit from fibrous food as it spends greater time in the gut being digested. It is therefore theorised that large herbivores should concentrate their foraging approach on lower quality food which is abundant in the environment rather than searching out high quality food sources which are rarer (Stokke and du Toit, 2000).

The reproductive strategy hypothesis relates to the predation risks faced by females and males, and states that larger males are less likely to be targeted by predators compared to females and their offspring (Ruckstuhl & Neuhaus, 2000; Corti & Shackleton, 2002). Therefore males will select habitats primarily on the basis of foraging opportunities in order to maximize growth and reproductive potential (Owen-Smith, 1993). This has in fact been documented for Asian elephants, with males taking greater risks than females when crop raiding (Sukumar & Gadgil, 1988). Whilst the parental commitment of males usually ends once mating is completed, females invest disproportionately more energy and time into reproduction (Clutton-Brock & Harvey, 1978; Krebs & Davies, 1993). This alternative strategy and greater parental investment coupled with increased risk of predation results in females selecting habitats that are firstly safe, with forage quality and availability being a secondary consideration according to the hypothesis (Corti & Shackleton, 2002).

These two hypotheses have significantly different outcomes for females, with the forage hypothesis predicting that they will select higher quality habitats of greater nutritional quality, whilst the reproductive strategy hypothesis predicts that females will select sub-optimal habitats on the basis that they provide sanctuary from predators (Ruckstuhl & Neuhaus, 2000). However, a trade off may well be established where forage opportunities can over ride the predation risk.

The frequency of sexual segregation has been shown to increase with greater body size dimorphism (Mysterud, 2000). Therefore elephants should provide an ideal study animal due to their pronounced body size dimorphism, with adult males weighing up to 6000 kg, twice the weight of an adult female (Owen-Smith, 1992; Poole, 1994). In this chapter, we explore whether female and male elephant exhibit

pronounced sexual segregation at the habitat scale throughout the year and more specifically during the two distinct climatic seasons (wet and dry) whilst in Chapter 5 we focus on the spatial scale of the plant and the role of foraging behaviour in sexual segregation. The main aim of this chapter is to establish whether differential habitat use could cause sexual segregation in the African elephant. Data will be examined across three distinct populations to compare and account for regional variation.

A number of predictions were tested: (1) male elephants will occupy habitats less selectively than females since they can tolerate lower quality of forage. This is due to their larger body size which is predicted to enable them to have greater digestive efficency and tolerate a substantial intake of fibrous food stuff (Demment, 1983; Demment & Van Soest, 1985). Male elephants will focus on satisfying their energy demands through foraging on abundant low quality forage whilst females are predicted to be more selective and target higher quality habitats (Ruckstuhl & Neuhaus, 2000). Females have reduced gut efficency and increased energy demands per kg mass, due to their smaller body size and significant investment in reproduction. (2) Male elephants will exhibit less sensitivity to risk (predation) and will prioritise habitat selection on nutritional return. This is because male elephants range independently and are not restricted by the social constraints that are found in family groups. Males are predicted to pursue a strategy of maximizing intake in order to divert energy into growth and therefore greater reproductive success (McElligott et al. 2001). Females are expected to be sensitive to risk due to the susceptibility of their offspring, which represent a significant time and energy investment and are therefore predicted to take priority over nutritional return (Corti & Shackleton, 2002). (3) Habitat segregation between individuals and groups of the same sex will not be significantly different.

Methods

Study Sites

The Pongola Game Reserve (PGR) was established in 1993 and is situated in Northern Zululand with a total extent of 82 km^2 (27°54′ -27°35′ S; 32°01′-31°86′ E). The climate is hot and arid with an annual rainfall of 400-700 mm. The vegetation falls into three of Acocks (1988) veld types: Zululand Thornveld, Lowveld and Arid Lowveld. Seven vegetation or habitat types were recognized (Fig. 1a). PGR has three distinct elephant groups, a small orphan group (n=7), three adult males and a large herd (n=38) (elephant population size as of October 2004). The herd utilise only the eastern section of the reserve (40 km^2) due as they do not cross the railway line that effectively bisects the reserve in two. The males and orphan group range across the whole reserve.

Phinda Private Game Reserve (PPGR) is 180 km^2 in extent (27°92′ -27°68′ S; 32°44′-32°20′ E). The reserve has a diverse range of habitat types from the endemic sand forest through to the sweet lowveld bushveld, Natal low bushveld and the coastal bushveld of the savanna biome (Low & Rebelo, 1996). Nine distinct habitats were distinguished for the purpose of this chapter (Fig.1b). The reserve has an average rainfall of approximately 750 mm (averaged over a 10 year period) with a maximum temperature of 35°C and a minimum of approximately 10°C. There is one river that runs through the southern section of the reserve and 6 dams that are fed with water from boreholes during the wet season. The total elephant population in 2004 was 75, comprising 18 adult males and 21 adult females in five family groups.

Pilansberg National Park (PNP) is a 500 km^2 reserve situated in the North West province of South Africa. It was established in 1979 and is approximately circular in shape (25°8′ -25°22′ S; 26°57′-27°13′ E). It occupies the crater of an extinct volcano and as such has hilly savanna relief. Acocks (1988) distinguishes the vegetation types as sour bushveld. Seven broad habitat types were used in this analysis (Fig. 1c). The average yearly rainfall is 630 mm, which mainly falls in the summer (November-April) (Slotow & Van Dyk, 2001). The total population in early 2004 was 158 comprising 34 adult males and 124 females and juveniles in 16 family groups.

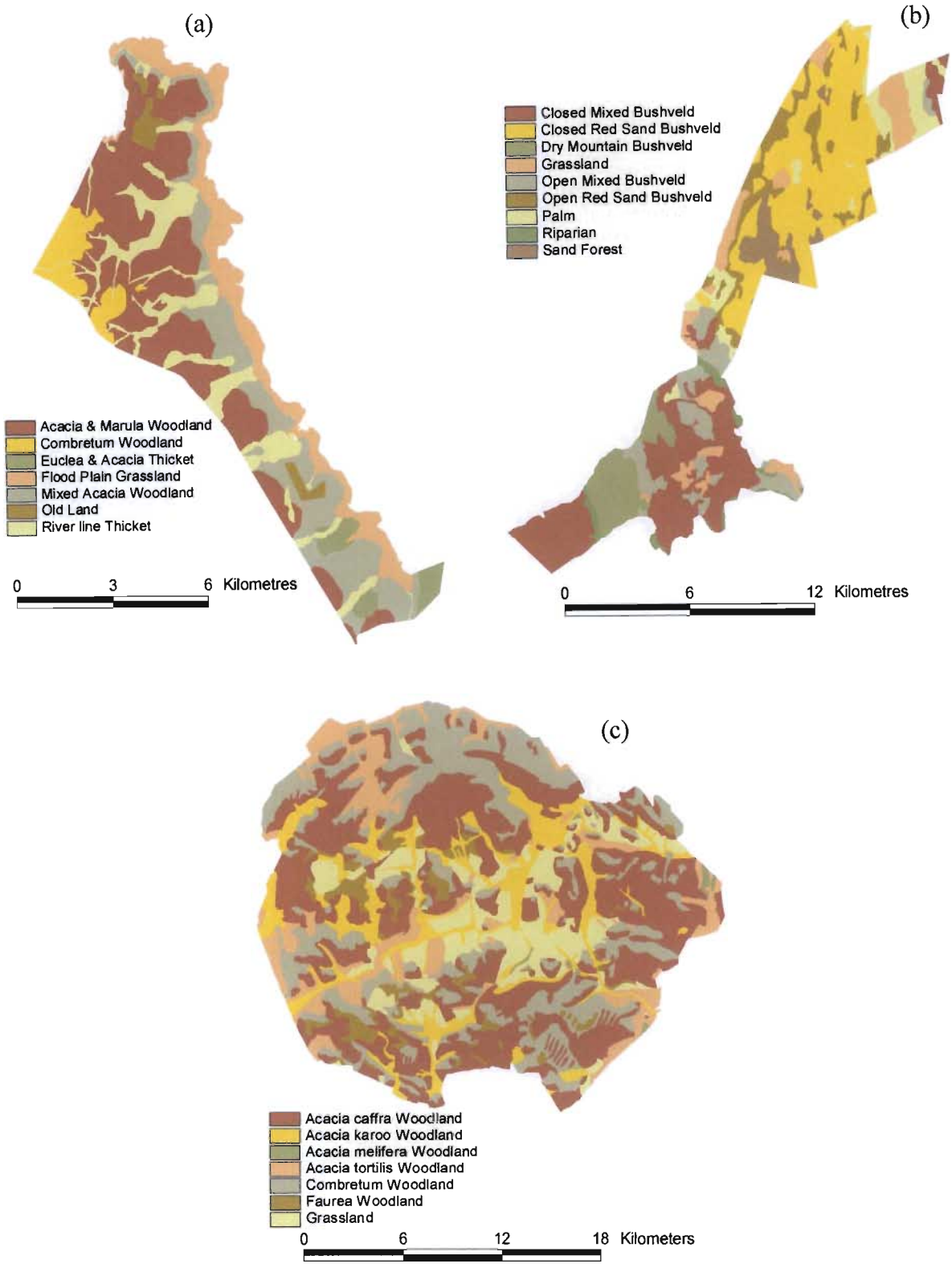


Figure 1. Habitat maps of the (a) Pongola Game Reserve, (b) Phinda Private Game Reserve and (c) Pilanesberg National Park.

Location Data

The data used in this analysis were collected over a 3 year period, from 2002 to 2005. The elephants were located using either radio telemetry or by traditional methods (following dung and tracks). On sighting an elephant, a GPS position of the observer was taken, along with date, time, habitat type and behavioural observations. The elephant's precise location was then calculated by estimating the distance and bearing from the observer to the individual elephant or the centre of the group. The elephants were then followed at a discrete distance until they moved out of sight, or the observation period ended. During this time, location points were taken at approximately 20-minute intervals. Satellite GPS collars and GPS/GSM collars automatically recorded positional data throughout the day at pre-determined times.

Habitat Mapping

Geographically referenced habitat maps were developed for each of the reserves. The habitat map of PGR was produced using satellite images, aerial photos and vegetation transect data. The transect data, collected at 47 different sites throughout the reserve provided information on the vegetation composition within different areas. Seven broad habitat types were derived from these data using a TWINSPAN analysis (Fig. 1a). The borders of the major habitats were digitised in ArcView® 3.2 from the aerial photos and satellite images using physiognomic features. The maps were then assessed for reliability using a GPS to record the actual positions of vegetation boundaries, river lines and other physical features of the landscape.

The habitat map of PPGR was developed by Hunter (1998). The map was created by first mapping the boundaries and major features of the reserve, including water points, roads and buildings. From this basic outline, the vegetation was surveyed in different areas of the reserve and a GPS used to delineate the boundaries of distinct vegetation types. The classification of the original vegetation types was done according to the species present, the overall habitat structure and a broad substrate classification. Aerial photos of the region were also used to distinguish habitat types and their boundaries. As with the other reserves, the vegetation map was checked for reliability using ground surveys. Nine habitat types were distinguished and all of these were used in the analysis (Fig. 1b).

The habitat map in PNP was created using an extensive ground surveying technique, which involved separating the reserve into distinct 250 m^2 blocks. Each of these blocks was then assigned a vegetation type on the basis of a previous analysis. A GPS was used to map distinct features of the reserve including the boundaries, roads and drainage lines, this enabled the vegetation blocks within the reserve to be spatially referenced. The map was checked for reliability using further field surveys. For the analysis in

this chapter, similar vegetation types were combined on the basis of shared attributes to create distinct physiognomic habitat types in the same way that had been done for PGR. These habitats were classified not just on the basis of vegetation composition but also terrain, aspect and slope. Contour maps and additional data from Moolman (unpublished data) were utilised for this aspect of the mapping. The final habitat map of PNP consisted of 9 broad types (Fig. 1c).

Statistical Analysis

Data were used from 12 female groups (PGR = 2, PPGR = 3 and PNP = 7) and 16 adult males (PGR = 3, PPGR = 7 and PNP = 6). These were selected on the basis that accurate location data were available for a minimum of 100 days throughout the study period. Microsoft Access was used to filter the data and select one location point for each individual/group per day. This ensured independence of the data and prevented errors associated with auto correlation (Slade et al. 1988; de Solla et al. 1999; Ramsey & Usner, 2003). The data were then separated further on the basis of season (summer and winter) and three time periods, 5:00-10:00, 10:00-15:00 and 15:00-20:00. Behavioural codes were also used to filter locations when foraging was observed so that an analysis could be carried out focusing on foraging preferences as well as overall habitat utilisation.

These positional data were imported into ArcView® 3.2 ensuring that each location was geographically referenced and in the correct format for spatial analysis. Using the Geo-Processing Wizard in ArcView® 3.2 each location point was assigned a habitat type in accordance with the reserve habitat maps (Fig 1). These data were then exported to Excel and the number of locations within each habitat type was determined. The X-tools extension in ArcView® 3.2 was used to calculate the area of each habitat within the reserve. Preference ratios were calculated for different habitat types as the proportion of locations in a particular habitat type divided by the proportional area of that habitat type i.e. (number of locations in a specified habitat / the total number of locations) / (the area of the specified habitat type / the total area).

If habitats were utilised in direct proportion to their occurrence then a preference ratio of 1 would be expected, whilst ratios below 1 suggested an avoided habitat and values above 1 indicated a preference. Two of the habitats (*Protea caffra* woodland and Tambothi) in PNP were removed from the analysis due to their limited size, (less than 1% of the area) and because there were no elephant sightings within them. The preference ratios were calculated for the entire data set (both seasons combined), separately for summer and winter and for the three daily time periods, in order to explore whether there was a temporal aspect to habitat segregation. This analysis was repeated for each female group and the individual males. Chi-Squared tests were used to ascertain whether male and female elephants were exhibiting habitat

preference and avoidance throughout the two seasons or using the available habitats at random. The mean preference ratios of both male and female elephants were used for this analysis.

A Kendall's coefficient of concordance test (Siegel & Castellan, 1988) was used to assess the preference ranking of each sex in the three different reserves. This non-parametric analysis tests the hypothesis that several related samples are from the same population. In this case, the related samples were the habitat preferences of the elephants and their ranking. The test returns a result of between 0 (no agreement) and 1 (total agreement). The data were initially tested for one sex at a time, females versus females and males, versus males to ascertain whether individuals of the same sex were ranking habitats in a significantly concorded manner. The male and female data were then combined and the analysis repeated, the theory being that intra-sexual and inter-sexual differences in habitat ranking could be compared from the two sets of results. If males and females were found to exhibit significant concordance in their preference of habitats then we could conclude that segregation is not being driven at the habitat scale. Similarly, the variation exhibited within one sex could be compared with the variation between sexes, and thus enable us to elucidate whether variation in habitat selection was based on the preferences of individuals, or whether it was driven by sex differences.

The data for the female groups in PGR were analysed using the Kendall's tau b test, as a sample size of two required the use of a bivariate correlation. The remaining data were analysed using the Kendall's coefficient of concordance due to sample sizes greater than three. The Kendall's tau-b test was also used to establish whether the mean preference ratios for the sexes, within a particular reserve, were significantly correlated. This allowed the actual preference values to be compared as well as the ranks that were calculated using the Kendall's coefficent of concordance. The results from these analyses were plotted with one standard error, to account for variation within the male and female data sets.

The foraging preference data were tested using the same methods, as this allowed an analysis of a key behaviour within the broad category of habitat selection. Whilst habitats may not be segregated on the basis of broad utilisation (all behaviours), there may well be sex driven differences with regard to feeding preferences. The females' data were tested first using the Kendall's coefficent of concordance to establish whether female groups in the same reserve ranked habitats in a similar manner with regard to their foraging behaviour. Once the sexes were analysed individually, the data were combined and the analysis re-run to determine if males and females were segregating on the basis of their foraging preferences (i.e. habitats that they selected for foraging). These data were presented in the same way as for the habitat

utilisation analysis that is detailed above. The data were analysed separately for each reserve due to the differences in habitat types.

Results

Elephant Habitat Preferences and Rankings

In order to use the Kendall's method to determine the decision making process and ranking of habitats by male and female elephants, it was necessary to establish whether habitats were being used at random or preferences and avoidances occured. The chi-squared test confirmed that both male and female elephants exhibited pronounced habitat selection throughout the year (Table 1.) The same result was repeated across the three data sets, with only the summer result for PGR males proving the exception. However, this result is in agreement with the 2000 -2001 PGR habitat utilisation analysis detailed in Chapter 2. The ranking of habitats by males and females (Fig. 2) indicates a strong relationship and preference for certain habitats, whilst others appear to be favoured by some individuals and rejected by others.

Habitat Utilisation in PGR

There was a strong correlation (Kendall's tau b) in habitat preferences for the two female groups throughout the year (Fig. 2 & Table 2). The summer season exhibited the strongest relationship with both groups ranking the seven habitats in the same order, (Kendall's tau b = 1.00, P = 0.00, N = 7). The winter association had a weaker correlation but was still significant (Kendall's tau b = 0.71, P = 0.02, N = 7). There was also a correlation between the temporal utilisation of habitats throughout the day, except in the third period (15:00 – 20:00). The three males in PGR did not exhibit concordance in the use of their habitats during the different seasons (Fig. 2 & Table 2). They had low Kendell's W values in both the summer and winter period. The three daily time periods are also non-significant (Table 2).

The combination of the male and female data indicate a significant concordance in the ranking of habitats, (Table. 2). The summer season in PGR showed no concordance across male and female habitat selection (Table 2). The temporal use of habitats throughout the year was correlated for females and males, suggesting similar patterns in use at the 5 hr scale (Table 2). The means of the male and female data were plotted with one standard error to show the male and female habitat use in the two seasons, using the actual preference ratios (Fig 3a & b). Males used all seven habitats during the summer, whilst the females only used five, thus creating a significant difference in habitat use (Kendall's tau b = -0.05, P = 0.88, N = 7). The winter utilisation showed a closer correlation between the two sexes but remains non-significant (Kendall's tau b = 0.43, P = 0.18, N = 7). The *Combretum* woodland was removed from the analysis as the herd do not access this habitat due to it occurring solely on the western side of the railway line. The

summer remained non-significant for the analysis of the means (Kendall's tau b = 0.28, P = 0.44, N = 6) but the mean winter habitat preferences for the two sexes were significantly correlated (Kendall's tau b = 0.73, P = 0.04, N = 6).

Habitat Utilisation in PPGR

The females in PPGR showed a strong statistical concordance with regard to habitat preferences during the summer months, this weakened during winter and the result was non-significant (Fig. 2 & Table 2). The three family groups also exhibited concordance during the three time periods (Table 2). The males showed concordance in their habitat preferences through all the different analyses and all the daily time periods (Fig. 2 & Table 2). The combined data indicates concordance in habitat choices by males and females (Table 2). The mean preference ratios for both sexes exhibited a similar pattern throughout the year (Fig. 3c & d). The largest discrepancy was in the winter period when males target the ORSB to a much greater extent than the females. The mean habitat preferences of males and females were significantly correlated in the summer (Kendall's tau b = 0.611, P = 0.02, N = 10) but not in winter (Kendall's tau b = 0.44, P = 0.1, N = 10).

Habitat Utilisation in PNP

The females and males both exhibited significant concordance in their habitat preferences across all analyses (Fig. 2 & Table 2). The combined data showed significant concordance in habitat preferences across male and female elephants in PNP, across all analyses (Table 2). The mean habitat preferences of female and male elephants was correlated in the summer season (Kendall's tau b = 0.015, P = 0.78, N = 13), whilst winter is non-significant (Kendall's tau b = 0.43, P = 0.18, N = 13). The use of *A. melifera* woodland by the females may well account for a significant level of variation (whilst males completely avoid the habitat).

Feeding Preferences

The data were further analysed to establish whether different habitats were used for foraging by the two sexes (Fig. 4). Female groups in all three reserves exhibited strong statistical concordance with regard to feeding preference during the summer months, whereas during the winter the concordance was much weaker, with non-significant results for both PGR and PPGR (Fig. 4 & Table.3). The males exhibited the opposite relationship, with weaker concordance during the summer months, including non-significant results for PGR and stronger concordance in the winter (Fig. 4 & Table 3).

The three time periods showed varied results for both sexes, but all of them were statistically significant, except for the males in PGR during the second time period (10:00 -15:00) (Kendall's W = 0.50, P = 0.18, N = 7). The males in PPGR exhibited concordance throughout all of the time periods. However, the Kendall's values were below 0.5 for each result and this suggests a substantial variation in preference between individual elephants. PNP showed a consistently (W = >0.6) high concordance throughout the day as did the female groups in all three of the reserves.

Male and female seasonal foraging preferences showed concordance throughout the data set except for one non-significant result the PGR summer data (Table 3). Despite the concordance there was a high level of variation with Kendall's values ranging from 0.42 – 0.68 (Table 3). Male and female elephants in PNP showed the highest concordance in foraging preference. The three time periods were significantly concorded throughout all of the data sets, suggesting a similar pattern of temporal use throughout the day for both males and females. The means were calculated and the values plotted for each sex in all three reserves and a Kendall's tau b correlation was used to test whether there was a significant relationship between mean habitat preference for females and males (Fig. 5).

In summary females and males exhibited concordance across their results and are therefore not selecting habitats significantly differently from each other. However, there were distinct patterns exhibited by each sex throughout the three data sets. The females had their weakest concordance values throughout the winter periods for both habitat and foraging preferences, whilst the males showed the opposite relationship with their weakest concordance values occurring in the summer period.

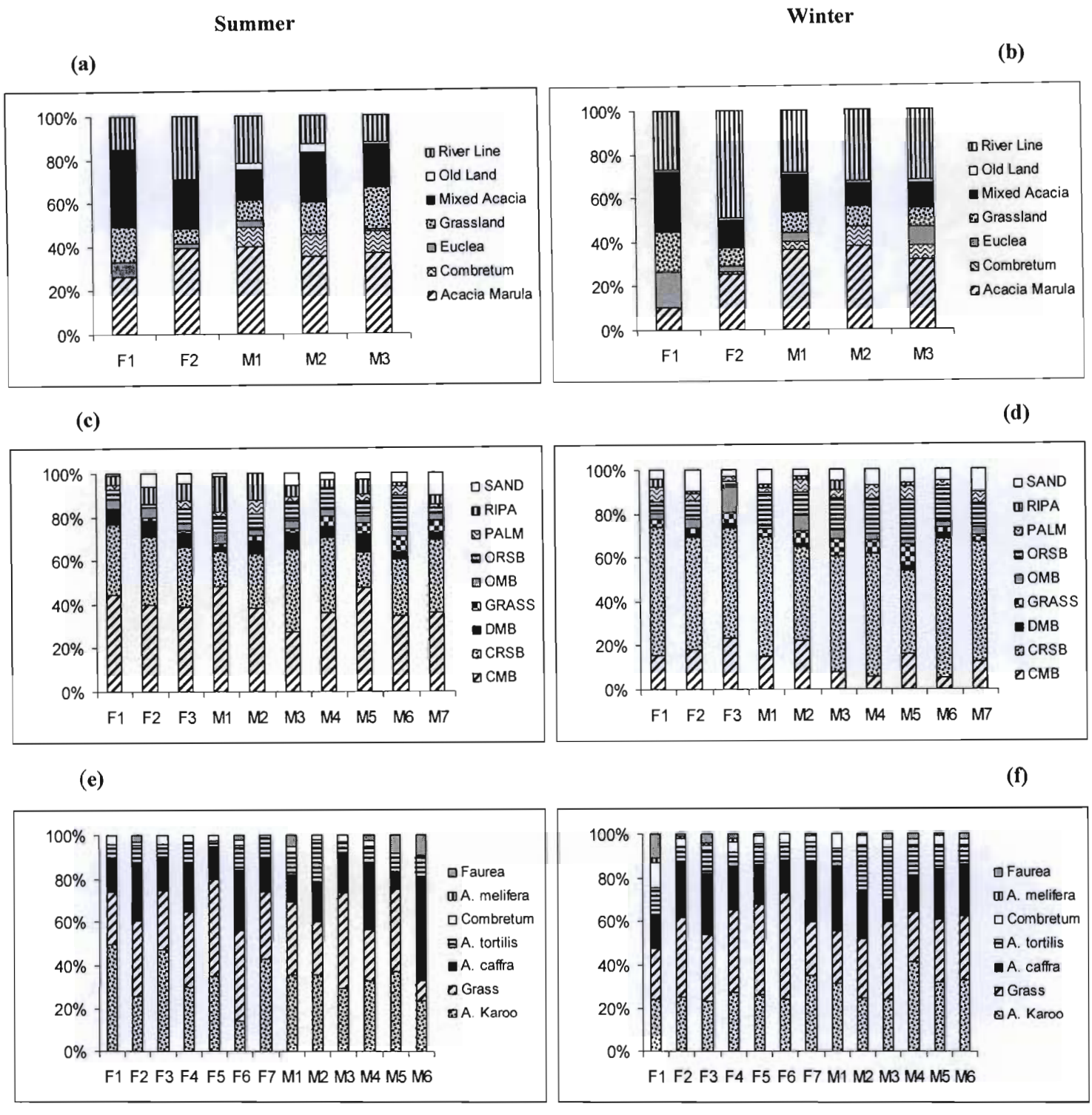


Figure 2. The ranking of habitat types by male and female elephants during the summer and winter seasons, in the (a & b) PGR, (c & d) PPGR and (e & f) PNP. (F = females M = males). Refer to Figure 1 for habitat types.

Table 1. Results of a chi-squared test showing that males and females are utilising habitats in a non-random manner. Mean preference ratios for males and females in PGR, PPGR and PNP were used in the analysis.

	PGR		PPGR		PNP	
	X^2_6	P- Value	X^2_8	P- Value	X^2_6	P- Value
Summer Female	21.34	<0.005	27.54	<0.005	106.23	<0.001
Winter Female	72.7	<0.001	31.61	<0.001	80.01	<0.001
Summer Male	3.40	>0.75	17.94	<0.025	79.11	<0.001
Winter Male	23.13	<0.001	39.53	<0.001	71.53	<0.001

PGR female groups n = 2 and males n = 3 PPGR female groups n = 3 and males n = 7, PNP female groups n = 7 and males = 6

Table 2. The results of a Kendall's coefficient of concordance analysis (P <0.05 indicates concordance) to establish whether female and male groups exhibit concordance in their habitat preferences.

	PGR		PPGR		PNP	
	Kendall's W	P- Value	Kendall's W	P- Value	Kendall's W	P- Value
Female Total	0.78	0.02	0.80	0.01	0.68	0.00
Female Summer	1.00	0.00	0.84	0.01	0.94	0.00
Female Winter	0.71	0.02	0.58	0.08	0.54	0.00
Female Time 1	0.62	0.05	0.81	0.01	0.61	0.00
Female Time 2	0.62	0.05	0.81	0.01	0.53	0.01
Female Time 3	0.59	0.07	0.60	0.03	0.87	0.00
Male Total	0.63	0.08	0.70	0.00	0.95	0.00
Male Summer	0.49	0.18	0.60	0.00	0.73	0.00
Male Winter	0.56	0.12	0.67	0.00	0.91	0.00
Male Time 1	0.60	0.10	0.54	0.00	0.84	0.00
Male Time 2	0.57	0.12	0.47	0.00	0.86	0.00
Male Time 3	0.68	0.06	0.63	0.00	0.80	0.00
Male & Female Total	0.50	0.02	0.65	0.00	0.72	0.00
Male & Female Summer	0.20	0.43	0.63	0.00	0.81	0.00
Male & Female Winter	0.52	0.02	0.58	0.00	0.60	0.00
Male & Female Time 1	0.46	0.03	0.49	0.00	0.63	0.00
Male & Female Time 2	0.58	0.01	0.47	0.00	0.56	0.00
Male & Female Time 3	0.64	0.00	0.61	0.00	0.82	0.00

PGR female groups n = 2 and males n = 3, PPGR female groups n = 3 and males n = 7, PNP female groups n = 7 and males = 6

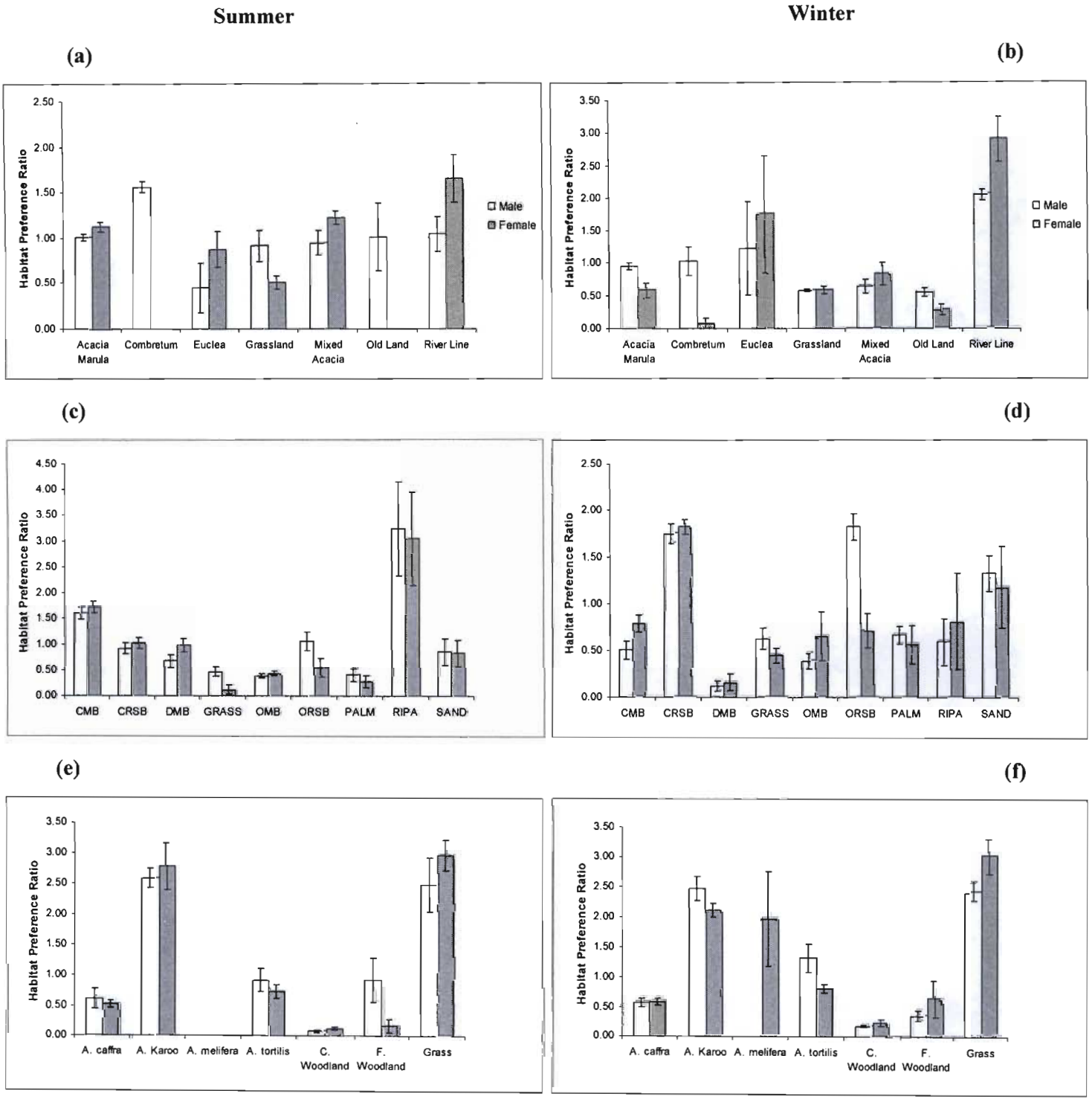


Figure 3. Comparing habitat utilisation of male and female elephants using the mean preference ratios for both summer and winter in (a & b) PGR, (c & d) PPGR and (e & f) PNP (Data are mean ±1 standard error).

Table 3. The results of a Kendall's coefficient of concordance analysis (P <0.05 indicates concordance) to establish whether female and male groups exhibit concordance in their foraging behaviour.

	PGR		**PPGR**		**PNP**	
	Kendall's W	P- Value	Kendall's W	P- Value	Kendall's W	P- Value
Female Total	0.52	0.10	0.76	0.02	0.62	0.00
Female Summer	0.80	0.01	0.90	0.01	0.79	0.00
Female Winter	0.29	0.29	0.35	0.40	0.49	0.00
Male Total	0.65	0.07	0.52	0.00	0.85	0.00
Male Summer	0.48	0.20	0.38	0.01	0.57	0.01
Male Winter	0.73	0.04	0.63	0.00	0.88	0.00
Male & Female Total	0.43	0.05	0.52	0.00	0.68	0.00
Male & Female Summer	0.07	0.91	0.49	0.00	0.64	0.00
Male & Female Winter	0.54	0.01	0.43	0.00	0.63	0.00

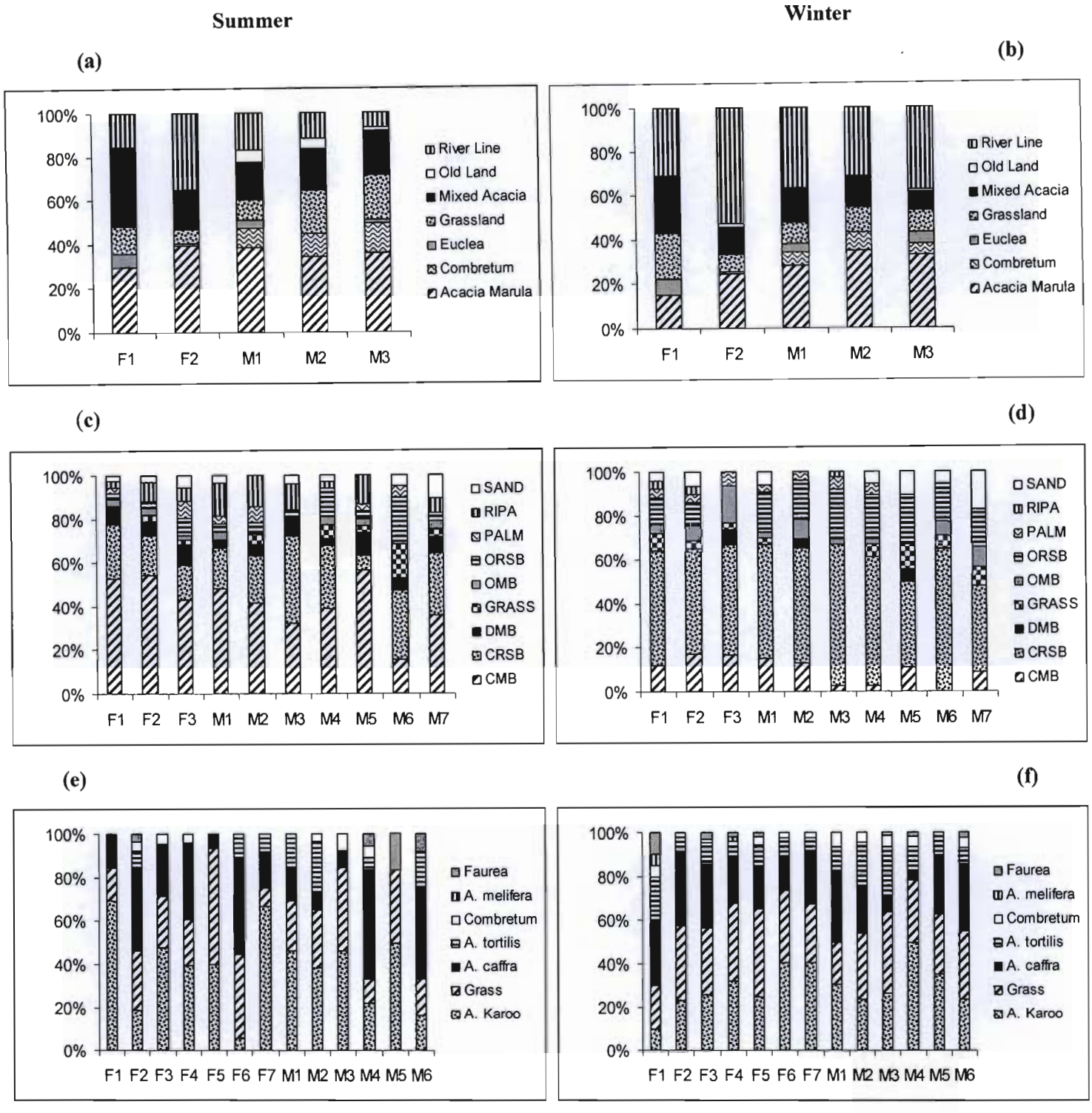


Figure 4. The ranking of habitat types by male and female elephants on the basis of forage preference during the summer and winter seasons, in the (a & b) PGR, (c & d) PPGR and (e & f) PNP. (F = individual females M = individual males). Refer to Figure 1 for habitat types.

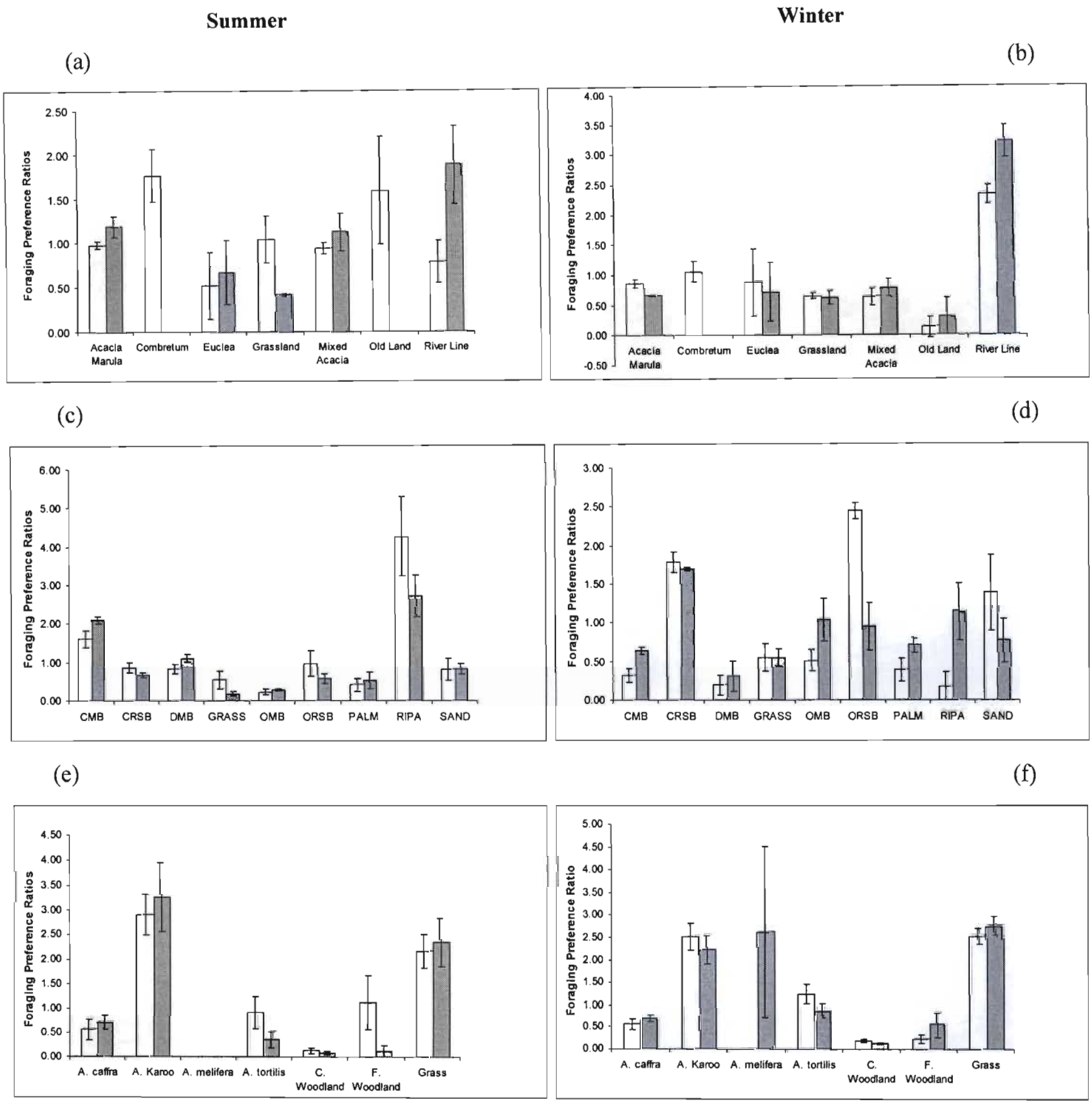


Figure 5. Comparing habitat utilisation of male □ and female ▩ elephants using the forage preference ratios for both summer and winter in (a & b) PGR, (c & d) PPGR and (e & f) PNP (Data are mean ±1 standard error).

Discussion

Male and female elephants exhibit distinct habitat preferences and do not use their available range in a random manner. This is in agreement with the findings of Chapter 2 and previous studies on elephant (Viljoen, 1989; Babassa, 2000). However, the analyses in this chapter suggest that sexual segregation of elephants is not being driven at the habitat scale. This is because males and females appear to be responding in a similar manner with regard to their habitat preferences, throughout the reserves, and on the basis of both season and time. In fact the variation in habitat selection is as broad between the sexes as it is within groups and individuals of the same sex. Stokke and du Toit (2002) investigated habitat segregation of elephants in the Chobe National Park (referred to as Chobe from here on), Botswana and found that the proximity of water rather than vegetation quality had the most significant effect in determining habitat preference. This was because females and offspring had higher rates of water turn over and lower mobility compared to males. In this study, access to water is factored out of the analysis due to the relatively small size of the reserves (<500 km^2) and the abundance of permanent water points. This may be a contributory factor in explaining why habitat segregation did not occur.

The reproductive strategy hypothesis suggests that females should choose 'safer' habitats as their offspring are vunerable to predation. Natural predation of elephants in the three study sites chosen for this research is almost non-existent and even in large open systems, the predation of elephant is minimal and opportunistic (Ruggiero, 1991). However, predator response has evolved over millions of years and it is likely that there will be a perceived risk whether predators are present or not (Ruckstuhl & Neuhaus, 2000). Human predation must also be considered as it has been a very significant factor in the mortality of elephants over the past 500 years. Therefore elephants in the small reserves are expected to show similar fear responses and risk aversion behaviour as elephants in larger more open systems. Despite this, female elephants are utilising habitats in a similar approach to males and there is no indication of avoidance due to 'predation risk'. Female elephants do however get disturbed and stressed with greater frequency than male elephants leading them to seek out dense habitat for safety (personal observation). However, this appears to be a fairly short-term response and feeding will resume within the previous habitat once the threat has passed. Male elephants have been recorded to exhibit greater risk tolerance in order to maximize nutritional return (Sukumar & Gadgil, 1988. This is often the reason that the majority of crop raiding is perpetrated by male elephants (Hoare, 1999). This behaviour appears to be opportunistic however and varies from one individual to another.

Habitat segregation has been exhibited in a number of dimorphic species, including bighorn sheep (*Ovis canadensis*) (Ruckstuhl, 1998), red deer (*Cervus elaphus*) (Conradt, 1999), and soay sheep (*Ovis aries*) (Bonenfant et al. 2004), however these species are smaller and more selective than the elephant and they are likely to target particular patches and species within habitats. The majority of these animals are also temperate ruminants that live in relatively simple systems and they maximize nutritional intake by selecting higher quality grazing. The elephant represents a very large generalist herbivore with the ability to digest significant quantities of fibrous forage and is therefore able to feed in a wide range of habitats. The diversity of biomes and habitats where the African elephant is found is further evidence to its generalist approach and adaptability (Owen-Smith, 1992, Spinage, 1994). Therefore, despite body size differences, females and males will be able to utilise most habitats for foraging as they can target a wide range of forage species from grass to browse (Owen-Smith, 1992). The results from this study indicate that the forage selection hypothesis does not influence the segregation of elephant at the habitat scale. More likely, the feeding approach at the patch and plant scale may provide the catalyst for segregation on the base of resource use (Stokke, 1999; Stokke & du Toit, 2000). Similar results were found for the giraffe which despite being a ruminant, is also classified as a mega-herbivore. Male and female giraffes were found to use similar habitats but exhibited significant differences in their use of forage resources at the patch and plant level (Ginnet & Demment, 1997). This highlights the importance of investigating different spatial and temporal scales in studies on sexual segregation (Conradt, 2000; Bonenfant et al. 2004). Chapter 5 confirms the importance of foraging behaviour in the sexual segregation of elephants, with males exhibiting a significantly different foraging approach to females. These differences include males targeting larger trees, ingesting greater quantities of low quality forage, having feeding bouts of longer duration and exhibiting more destructive feeding behaviour.

Both sexes demonstrated interesting seasonal patterns of variation in the concordance of habitat and foraging preferences. The female groups exhibited the greatest variation (i.e. lowest Kendall's values) in cocncordance during the winter periods, whilst in summer the values were much greater. This may well be a function of resource abundance which enables family groups to forage in close proximity to each other. Such aggregations serve a social purpose, as female groups exhibit a complex societal structure which is often reaffirmed when resources permit and groups can interact (Wittemyer et al. 2005). In PGR for example, the summer period accounted for 64% of the recorded associations between the two female groups. In winter however, resource scarcity may force family groups to segregate in an attempt to reduce potential competition. The group dynamics of impala have been shown to reduce individual foraging efficiency and cause significant intraspecific competition (Fritz & Whichatitsky, 1996). This may also be

a factor that influences the association of female elephants during the winter season or drought periods (Wittemyer et al. 2005).

Males show the opposite relationship to females. During winter they exhibited high values of concordance for both habitat and foraging preferences. This could be associated to their large size and independent nature which allows them to target abundant low quality forage with little if any competitive exclusion. Whereas in the summer males have their lowest values of concordance, suggesting higher levels of variation in habitat preferences from one elephant to the next. This may be explained by the presence of musth males which have heightened levels of testosterone and display aggressive behaviour towards would be competitors (Poole, 1989 Slotow et al. 2000). Musth most commonly occurs during the summer when resources are abundant (Poole, 1994; Owen-Smith, 1992). Males in musth are avoided by other males and this tends to indicate that reproductive strategies play a significant role in habitat preferences and selection during the summer period. This was also postulated as a reason for segregation in a study on elephant habitat use in Chobe National Park (Stokke & du Toit, 2002).

Conclusions

Elephants exhibit distinct patterns of habitat utilisation; however the differences that occur are as pronounced for individuals of the same sex as they are when males and females are compared. This is confirmed across all three reserves, despite their diversity in vegetation, size differences, populations and history. Large generalist herbivores such as the elephant are able to target a wide diversity of habitats and food sources within the African savanna and it is unlikely that the pronounced segregation observed in elephant is being driven at the habitat level by the foraging selection hypothesis. Instead, the actual foraging approach adopted by males and females is expected to be significantly different at the patch and plant level where decisions on how to feed and for how long occur. Male elephants may show greater tolerance to disturbance than females and therefore use more 'risky' habitats but this has been difficult to assess and is generally an occasional event rather than a distinct strategy. Threat perception also varies greatly from one elephant group to the next, being rarely the result of natural predation events and it is concluded that the reproductive strategy hypothesis is not causing segregation in elephants. The results in this study are in accordance with those from the Chobe study, where habitat segregation was found to be driven by access to surface water and avoidance of musth males, and not vegetation quality and abundance. It therefore appears that social factors and reproductive strategies are more likely to be driving observed habitat segregation than resource quality and abundance. However, habitat selection by the sexes is unlikely to be the mechanism by which elephants are segregated.

CHAPTER 5

FORAGING BEHAVIOUR AND SEXUAL SEGREGATION IN THE AFRICAN ELEPHANT: THE INFLUENCE OF BODY SIZE DIMORPHISM

Abstract

Sexual dimorphism in elephant is pronounced and in this study we test the prediction that size differences and sociality are significant enough to segregate the sexes on the basis of foraging strategies alone. Two distinct theories are tested: the scramble competition hypothesis (SCH) and the forage selection hypothesis (FSH). Body size has a significant influence on the foraging strategies of herbivores due to the differential scaling coefficients of metabolism and gut size. Larger individuals can therefore tolerate greater quantities of fibrous vegetation, whilst having lower mass specific energy requirements. Comprehensive behavioural and location data from the Pongola Game Reserve and the Phinda Private Game Reserve in South Africa were collected over a 2.5 year period and analysed using sex as the independent variable. Adult females adopted a much more selective foraging approach as predicted by the body size hypothesis and the increased demands of reproductive investment (lactation and pregnancy). The SCH was rejected as a cause of sexual segregation due to the relative abundance of low quality forage and the fact that feeding heights were similar for males and females in both reserves despite marked size disparity. Males targeted larger trees (average height, 4.7 m compared to 3.8 m for females), displaying significantly more destructive behaviour (31% of observations, 11% for females) and ingesting greater quantities of lower quality forage during each feeding bout. The independent ranging behaviour of adult males enables them to have longer foraging bouts as they experience fewer social constraints than females. The difference in foraging strategies of the two sexes is sufficient to cause social and habitat segregation as postulated by the FSH. Sexual dimorphism and the associated behavioural differences have important implications for the management and conservation of elephant and other dimorphic species as the sexes act as different "ecological" species based on forage selection.

Introduction

Body size influences the foraging behaviour of mammalian herbivores in three distinct ways. Firstly, metabolic rate scales with a coefficient of approximately 0.75 as body size increases (Clutton-Brock & Harvey, 1978; Owen-Smith, 1992; Mysterud; 1998). This results in larger animals requiring less energy per kg of mass due to greater muscular efficiency and reduced heat loss. Secondly, larger body size is coupled with a directly proportional increase in gut capacity (Demment, 1983; Demment & Van Soest, 1985). Increased gut size enables larger quantities of forage to be retained for longer periods and thus more complete digestion is achieved, as cell wall digestion is positively correlated with retention time

(Van Soest, 1996; Clauss et al., 2003). Finally, forage quality varies dramatically across a range of scales in terrestrial biomes, from the different plant parts and chemical constituents (e.g. tannins) to the diversity of different species at the habitat and landscape scale (Demment, 1983; Seagle & McNaughton, 1992; Skarpe et al., 2000). Therefore, unlike mammalian carnivores where protein availability and energetic return per kg is relatively constant, herbivores often need to make a complex series of decisions in order to maximize nutritional intake (Senft et al., 1987; Choat & Clements, 1998). This is dependent on body size and the scale of habitat resolution.

The relationship between decreasing metabolic rate, increased gut size and longer retention time, enables large herbivores to consume and digest greater quantities of abundant lower quality forage (Demment & Van Soest, 1985; Mysterud, 1998; Clauss et al., 2003). Large herbivores are therefore more likely to trade off quality against quantity as the benefits of abundance outweigh the costs of searching for forage opportunities of high nutritional return that are generally rare in the environment (McNaughton & Georgiadis, 1986). In contrast, smaller herbivores which have greater relative energetic demands and reduced gut efficiency will forage selectively for higher quality food sources (Demment & Van Soest, 1985). Therefore, as the body size of herbivores increases, the relationship between the organism and the environment changes, especially with regard to the scale of resolution (Demment, 1983). This relationship is evident across herbivores of different sizes and is also believed to play a significant role in species that exhibit pronounced sexual dimorphism (Owen-Smith, 1992; Stokke & du Toit, 2000).

Sexual dimorphism in ungulate species is believed to result from two contrasting reproductive strategies. Males gain an advantage by having a larger body size, enabling them to dominate smaller males and achieve greater mating success (Poole, 1989; McElligott et al., 2001). The reproductive investment for the male ends after successful copulation and is only limited by the availability of females in oestrus (Clutton-Brock & Harvey, 1978; Krebs & Davies, 1993). Females exhibit much higher levels of investment in reproduction and select mates on the basis of size and fitness (McElligott et al., 2001). They are limited by the number of offspring they can produce (Clutton-Brock & Harvey, 1978; Le Blanc, 2001), subsequently no significant advantage is gained from larger body size. Tusk size is another indication of this differing investment, with adult males having on average tusks seven times larger than females by the time they reach 50 years (Poole, 1994). These tusks provide secondary characteristics for a male to exhibit his strength and fitness to a female or to be used when fighting with other males (Spinage, 1994). This has also been documented in the red deer, where a 30 year data set indicated that larger antler size was directly related to reproductive success in males (Kruuk et al., 2002).

In addition to smaller body size, female ungulates experience elevated energy demands during pregnancy and lactation, with peak lactation costs increasing the energy requirements of an individual by as much as 150% (Dunbar et al., 2002; Blanchard, 2005). This is especially pronounced in elephant as an adult female is often in a state of pregnancy, lactation or both. This is energetically expensive, especially considering that the gestation period is 22 months and the subsequent weaning of the calf takes approximately 2 years (Spinage, 1994). This considerable investment of energy into reproduction results in female elephants attaining their full height around 20-25 years old whilst males continue to divert energy into growth throughout their lives (Poole, 1994). Up until their mid-teens, male and female elephants have similar body sizes and comparable energy demands but after this age they begin to exhibit pronounced dimorphism and behavioural differences (Poole, 1994; Lee & Moss, 1995).

Sociality in elephants is also strongly dependent on sex, with adult females and their offspring remaining together in tightly bonded groups (Moss & Poole, 1983; McComb et al., 2001; Charif et al., 2005). This complex and highly developed sociality is believed to have developed in response to predation pressure (Wittemyer et al., 2005). Young males are forced out of the family group between the ages of 10-15 and either establish bachelor groups or range independently. The social ties between male elephants is much weaker than the ones between related females and as such they make decisions on an individual basis as opposed to the group decisions made in elephant herds (Barnes, 1979; Poole, 1994; Spinage, 1994; Rands et al., 2003).

As with other large ungulates, elephants are sexually segregated for the majority of the year, with males and females only associating for the purpose of reproduction (Poole, 1994). The forage selection hypothesis (FSH) is one of the main theories put forward to explain sexual segregation in dimorphic species (Ruckstuhl & Neuhaus, 2000). It is based on the premise that differences in body size, energy budgets and efficiency of digestion result in distinct feeding strategies for both females and males (Ruckhustal, 1998). Females are predicted to be more selective in their foraging approach due to their higher relative energy demands and reduced digestive efficiency, whilst males consume greater quantities of fibrous, low quality forage (Ruckstuhl & Neuhaus, 2000). These feeding differences are predicted to result in both spatial and temporal segregation (Ginnet & Demment, 1999; Ruckstuhl & Neuhaus, 2000). A second theory which we tested in this study is the scramble competition hypothesis, (SCH) which suggests that when resource availability is low, females out compete and therefore displace larger males (Clutton-Brock et al., 1987; Ruckstuhl & Neuhaus, 2000). Females are predicted to be superior competitors due to allometric relationships and lower absolute metabolic requirements resulting in them

being able to exploit and tolerate lower plant biomass than males. In browsing animals this scramble competition is believed to be expressed as differences in feeding height (du Toit, 1990).

The role of the FSH in sexual segregation of elephant has previously been investigated by Stokke & du Toit (2000), a study which was carried out during the dry season in the Chobe National Park using vegetation sampling methods to assess the foraging behaviour of elephants after they had fed at a particular location. In this study we use direct observations of elephant feeding bouts in both the summer and winter seasons. The data were collected from two populations where repeat sightings of known individuals were possible. The objectives were (1) to test both the forage selection hypothesis and scramble competition hypothesis as explanations for sexual segregation in elephants. (2) To quantify the differences in foraging approach between males and females. (3) To establish what influence age and sociality have on the foraging behaviour of elephants. (4) To compare our findings with those of Stokke & du Toit (2000).

Methods

Study Site

The Pongola Game Reserve (PGR) is 82km^2 in extent and situated in Northern Zululand, South Africa (27°54′ -27°35′ S; 32°01′-31°86′ E) on the western shoreline of the Jozini Dam. The climate is hot and arid with an annual average rainfall of 650 mm and a range of 350-1000mm. The vegetation falls into three of Acocks (1988) veld types: Zululand Thornveld, Lowveld and Arid Lowveld. Seven vegetation or habitat types are recognized. PGR has three distinct elephant groups, a herd of 38 individuals consisting of two closely associated families, a small orphan group totalling 7 individuals and 4 adult males The youngest male in PGR was approximately 17 years old, whilst the other three were all older than 32. There were 13 adult females (12 yrs +) in the herd and a further 4 in the small orphan family group, all of which were used in the analyses. The four males and the orphan group range across the whole reserve, whilst the herd only utilised the eastern section of the reserve (40 km^2) between the lakeshore and the railway line that bisects the reserve from the southern border to the northwest fence line.

Phinda Private Game Reserve (PPGR) is situated in southern Maputaland and covers an area of 180 km^2 (27°92′ -27°68′ S; 32°44′-32°20′ E). The reserve has a diverse range of habitats, from the endemic sand forest to the sweet lowveld bushveld, Natal low bushveld and the coastal bushveld of the savanna biome (Low & Rebelo, 1996). The reserve has a ten-year average rainfall of approximately 750 mm and maximum temperatures of 35°C during the summer months. The minimum temperature experienced in winter is approximately 10°C. There is one river that runs through the southern section of the reserve and

6 dams which are fed with water from boreholes during the wet season. PPGR has a total population of 80 individuals, consisting of 5 family groups with 21 adult females and 19 adult males. Only 4 of these males were above 30 years of age.

Data Collection

Data were collected during a 2.5 year study period (January 2003- July 2005) in both PGR and PPGR. The two populations were selected for this study because of reserve access, stable herd structure and habituation to research vehicles. After the elephants had been located using telemetry or traditional tracking methods, positional and demographic data were collected. The position of the observer was recorded with a global positioning system (GPS) and corrected for the group or individual by calculating the distance and the bearing to the elephant(s). Notes were made regarding the group behaviour and site details were recorded regarding the weather and habitat type.

Once a sufficient period had passed for the elephants to settle down (the time taken for the observer and vehicle to be ignored), behavioural observations were carried out. Adult elephants were selected at random and as soon as they initiated a foraging bout (feeding on a distinct woody plant >0.5m in height), the exact time was recorded and the numbers of mouthfuls were counted. A mouthful was distinguished as each time the trunk delivered food into the mouth. The parts of the tree that were targeted during the feeding bout were recorded, along with the species name. Once the elephant moved from the particular tree, the time was noted down. After the foraging bout ended, the tree height and feeding height were measured and values for the total biomass removed and biomass utilised was estimated. This was done by appraising the canopy as a whole prior to the bout and estimating how much of the canopy was remaining. This was further broken down by assessing the amount of the canopy that was ingested by the elephant compared to that left lying on the ground or in the tree. The feeding bout was then classified on a five-point scale depending upon the intensity of feeding and the amount of biomass removed (Table 1). Where possible, the reason for the cessation of the feeding bout was also stated. This included five broad categories: (1) feeding close by on a separate tree, (2) displaced by another elephant, (3) social interactions and demands of group or (4) walking away from feeding site and (5) other.

Table 1. The five-point classification of foraging behaviours

Foraging Behaviour	Description
1: Very Selective	1-4 small mouthfuls, short time spent at the tree (<1min), impact negligible
2: Selective	5-10 mouthfuls, small branches and leaves, 1-3 min, <10% of canopy removed
3: Moderate	>10 mouthfuls, removal of some medium branches, 3-5 min duration
4: Intensive	>10 large mouthfuls, breaking of large branches, >5 min duration
5: Destructive	Removal of more than 50% of canopy, tree pushed over or debarked

The elephant would be sampled again if it moved to a second tree within close and observable range. If not, a second individual was selected until the group or individual moved out of sight. Data were discarded if it was felt that an individual curtailed a foraging bout due to interference from the observer or another human source or the bout was less than 15 seconds in duration, as this was considered too short a period for an actual foraging event.

Statistical Analysis

The data were separated into male and female categories with only adult animals (>15 years old for males and females with calves) included in the analysis. Analyses were carried out separately for the two reserves. The PGR data set was the most comprehensive of the two with a total of 394 feeding bouts (female n= 218 and male n= 176) whilst the PPGR data set consisted of 102 feeding bouts (female n=34 male n=68). The data were imported into the SPSS statistical package and analysed using ANOVA to establish whether there was significant variation in the length of feeding bouts, the heights of trees targeted and the mean feeding height. Sex was used as the independent variable to establish whether there were significant differences in the foraging behaviour of male and female elephants. To test the relationship between age and foraging behaviour, the average feeding time was plotted against age. Due to the small sample sizes, the data were pooled for individuals of the same age and sex. A regression was then used to test the relationship. Both reserves and sexes were combined for the analysis. The data were then separated into respective sexes and a line of best fit plotted, the R^2 value was calculated from these plots.

Two-way ANOVAs enabled us to investigate the influence of season on tree height and feeding bout length. ANOVA was also used to explore the feeding rates of both sexes in the two reserves. Patterns of feeding behaviour for male and female elephants were tested with a G-test to establish whether the intensity of feeding bouts varied between the sexes. The data for each reserve were compared to investigate if the sexes had similar approaches in different reserves. Plant parts fed upon, canopy

utilisation and the reasons for the end of the feeding bouts were compared for females and males using a G-test in order to establish whether the foraging approach differed significantly between the two sexes.

The destructive feeding bouts were examined in more detail as they often lead to the removal of a tree and as such have a significant impact on the ecosystem. They also are important in evaluating whether males are more destructive than females in their foraging approach. A number of different methods were used by the elephants including debarking, uprooting and stem breaking. The heights of the trees and the lengths of destructive feeding bouts were explored for both sexes using an ANOVA. All of the data sets were also analysed according to the winter and summer seasons, since they have a significant role in the ranging behaviour of elephant, biomass availability and plant phenology.

Results

Length of feeding bout

The duration of feeding bouts in PGR was significantly different between the sexes ($F_{1,392} = 29.90$, $P<0.01$), with the males having a mean feeding time of 426 seconds compared to 174 seconds for the females (Fig. 1). There were no significant seasonal differences in forage bout length for either the males or females ($F_{1,390} = 1.20$, $P >0.25$). Data for females in PPGR were similar to that in PGR with an average feeding bout length of 168 seconds. The feeding bouts of male elephants in PPGR were not significantly different from the females, with a mean of 228 seconds (3.8 min) ($F_{1,100} = 1.11$, $P >0.25$). This value was significantly different to that of the males in PGR ($F_{1,242} = 6.818$, $P = 0.01$).

Data for the young adult male in PGR were also analysed separately. The average feeding bout length was 228 seconds compared to 475 seconds for the three older males. The mean values for each of the adult males were 366 seconds, 468 seconds and 558 seconds. Data for the young male in PGR were significantly different from the adult males ($F_{1,169} = 5.26$, $P <0.025$) but non-significant when compared with the result for the PPGR males with ($F_{1,104} = 0.00$, $P >0.95$). The lengths of feeding bouts were analysed using age as the dependent variable, a logistic regression returned a significant result ($F_{1,14} = 26.90$, $P <0.01$ $R^2 = 0.66$). Male elephants ($F_{1,9} = 48.25$, $P <0.001$ $R^2 = 0.84$) exhibit significantly longer feeding bouts than females ($F_{1,9} = 18.50$, $P <0.005$ $R^2 = 0.66$) after the age of 18 years, this coincides with rapid growth in male body size whilst the female puts energy into reproduction and lactation (Fig. 2).

Tree height and feeding height

In PGR, male elephants selected significantly larger trees than females ($F_{1,392} = 15.45$, $P <0.001$) (Fig. 3). In PPGR, there was no significant difference between males and females ($F_{1,100} = 0.24$, $P >0.5$) (Fig. 3).

However, there was a significant difference in the height of trees selected by females in PGR compared to females in PPGR ($F_{1,250} = 6.44$, $P < 0.025$) but no significant difference in the selection of tree heights by males in PGR compared to those in PPGR ($F_{1,242} = 1.50$, $P > 0.2$). The interaction term of reserve and sex was not significant, indicating no overall difference in the pattern of behaviour across the two reserves ($F_{1,492} = 4.258$, $P > 0.3$).

Male elephants in PGR fed on average at a greater height, with a mean and median of 2 m as opposed to 1.8 m for females. The range of feed heights was slightly larger for males 0- 5.5 m, whilst for females it was 0 -5.2 m. An ANOVA comparing the two sexes exhibited a strong trend, but it was slightly above the 5% threshold of significance ($F_{1,390} = 3.28$, $P = 0.07$). In PPGR, both male and female elephants had a mean feeding height of 2.2 m. The median for males was 2.3 m and 2.45 m for females. The range of feeding heights were similar with values of 0- 4.75 m for males and 0- 4.5 m for females ($F_{1,100} = 0.00$, $P > 0.9$).

Feeding intensity

Male elephants exhibited more destructive feeding behaviour than females, with 31% of total feeding bouts (PGR and PPGR combined) being categorised as destructive compared to 11% for the females (Fig. 4a). A G-test showed that there was a significant difference between the intensities of feeding across all 5 categories between the herd females and males of PGR ($\chi^2_4 = 65.54$ $P < 0.001$). A significant result was also obtained when comparing the orphan females in PGR with males ($\chi^2_4 = 49.91$ $P < 0.001$). However when the two female groups were compared the result was non-significant ($\chi^2_4 = 4.498$ $P > 0.25$). On comparing the results for PPGR, the males and females exhibited no significant difference from one another in terms of their feeding bout classifications ($\chi^2_4 = 4.92$ $P > 0.25$). Both the PGR herd and orphan group did not show significant differences to the feeding behaviour of the females in PPGR. The males of PGR were significantly different to both the females and males in PPGR ($\chi^2_4 = 47.45$ $P < 0.001$ $\chi^2_4 = 52.77$ $P < 0.001$ respectively).

The trees targeted by males during destructive feeding bouts in PGR were significantly larger, 4.8m compared with 3.6m for females ($F_{1,89} = 6.79$, $P < 0.05$). There was a significant relationship between the season and the height of trees selected during destructive feeding bouts for both sexes ($F_{1,87} = 11.29$, $P = 0.01$) with the trees targeted in summer being significantly larger than those selected during the winter months (Fig. 4b). There were insufficient data from PPGR to carry out the same analyses. Feeding rates were also analysed. In PGR, the males had a mean of 3.1 mouthfuls/min compared to 4.1 mouthfuls/min for the females. The results from PPGR were slightly higher for both sexes, with males having a mean of

3.3 mouthfuls/min and females 4.3 mouthfuls/min. Females had significantly higher bite rates than males ($F_{1,482} = 12.82$, $P < 0.01$) (Fig. 5).

Tree parts targeted during feeding bouts

During the feeding bouts, males and females in PGR targeted different parts of the tree (Fig.6). Males fed on the roots of trees to a greater extent than females. They also fed on medium sized branches with greater frequency. Females selected leaves, flowers and fruit in greater proportion than males. Both sexes devoted the majority of their feeding bouts to feeding on a combination of leaves and small branches. The parts of the tree eaten during each of the feeding bouts were significantly different between males and both females in the large herd ($\chi^2_8 = 54.29$ $P < 0.001$) and females in the smaller orphan family group ($\chi^2_8 = 48.26$ $P < 0.001$). There was no significant difference in the selection of plant parts between adult females from the herd and the orphan family group ($\chi^2_8 = 12.94$ $P > 0.1$), indicating a similar foraging approach. The PPGR data exhibited less variation with no significant difference in the selection of tree parts by males or females ($\chi^2_8 = 2.55$ $P > 0.9$). There was no significant difference between the orphan family group in PGR and female data from PPGR ($\chi^2_8 = 2.55$ $P > 0.9$). The PPGR males had significantly different preferences when compared with those of the males in PGR, suggesting that they have different foraging approaches ($\chi^2_8 = 27.31$ $P < 0.001$).

Species Use

Females in both reserves exhibited a greater diversity of tree species in their diets than the males. In PGR, males selected an average of 14 species/100 feeding bouts whilst females selected 17 species/100 feeding bouts. In PPGR, these values were much higher with 28 species/100 feeding bouts for males and 40 species/100 feeding bouts for females. In PGR, *Acacia nigrescens* was the most commonly selected species, occurring in over 20% of foraging bouts for both sexes. Seventy percent of recorded male and female feeding bouts consisted of only 6 species in PGR with males in PGR exhibiting selection of *A. nigrescenes, A. tortilis, A. nilotica, Dichrostachys cinerea, Sclerocarya birrea and Grewia flava.* Females showed a preference for the same four *Acacia* species and *Dichrostachys cinerea* but in addition they also selected *A. leuderitzii* and *Grewia villosa.*

Tree utilisation

The percentage of the canopy, roots and or bark removed was recorded for all feeding bouts (Fig. 7). In PGR females utilised only 1-5% of the available biomass in 70% of their feeding bouts, compared to just over 40% in males. Male elephants utilised greater amounts of biomass per tree with a mean of 12%

utilisation compared to 8% for the females ($G^2_6 = 28.96$ $P<0.001$). In PPGR, the mean percentage utilisation for males was 8.5 and 5 for females but the result was not significant ($G^2_4 = 3.12$ $P>0.5$).

Feeding bout cessation

The primary reason for the end of a feeding bout for both males (57%) and females (45%) was to move and feed on another tree close by (Fig. 8). Females were also strongly affected by social dynamics, resulting in 40% of their feeding bouts ending whilst male elephants had a much higher proportion of feeding bouts ending with them walking away from the feeding site. Overall the differences were highly significant ($G^2_4 = 28.59$ $P<0.001$). There were insufficient data available from PPGR for this analysis.

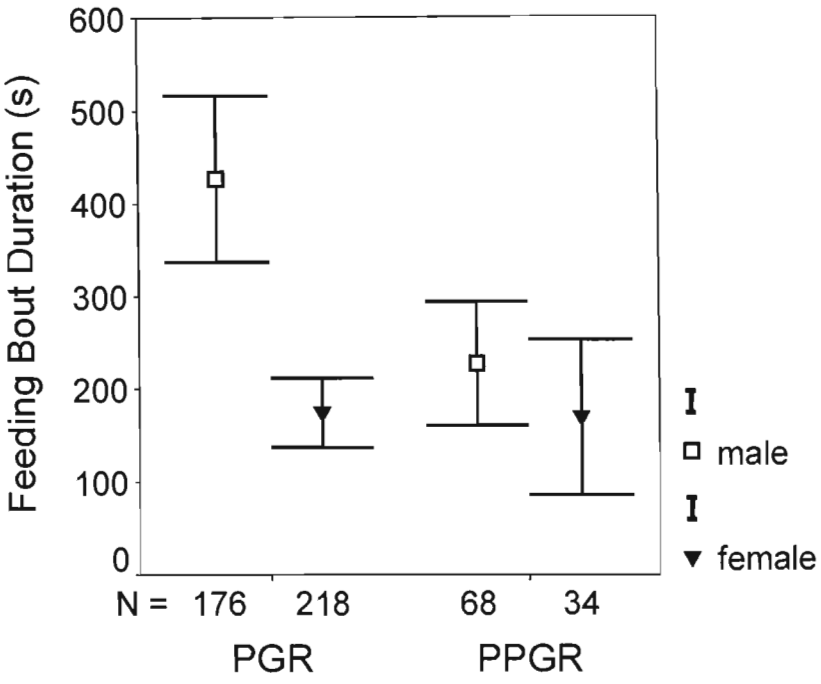


Figure 1. The mean feeding bout duration of male and female elephants in PGR and PPGR. Males in PGR are feeding on average, significantly longer than females whilst no significant difference is evident for PPGR (Data are mean 95% ± CI and N = the number of focal samples).

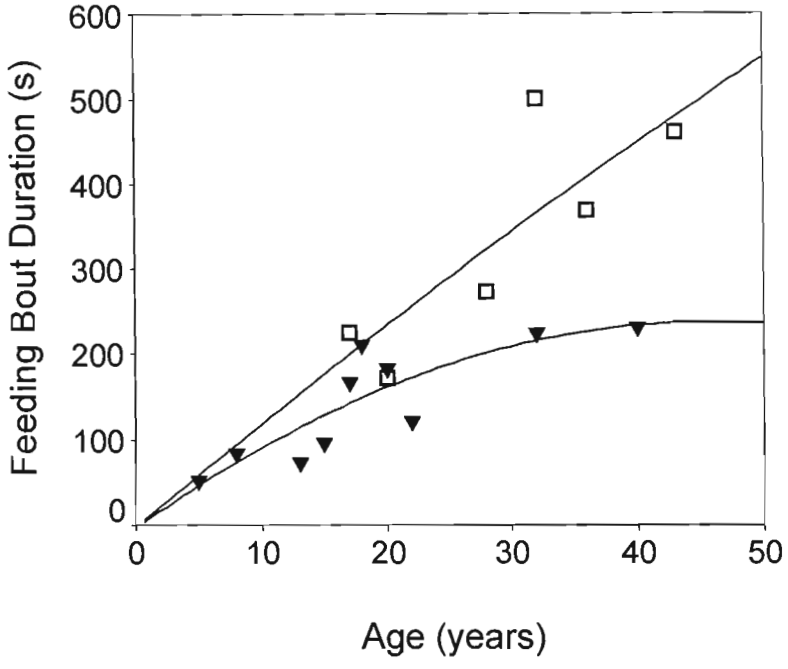


Figure 2. The effect of age on feeding bout length for both male □ and female elephant ▼

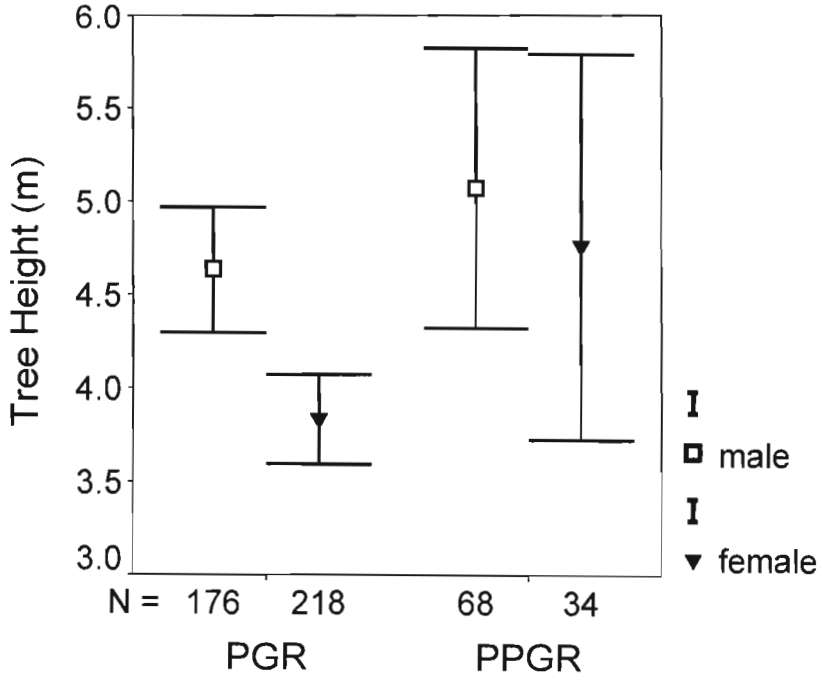


Figure 3. Tree heights selected by male and female elephants in PGR and PPGR. Males are selecting taller trees on average in both reserves; however the PPGR result is not significant. (Data are mean ± 95% CI and N = the number of focal samples).

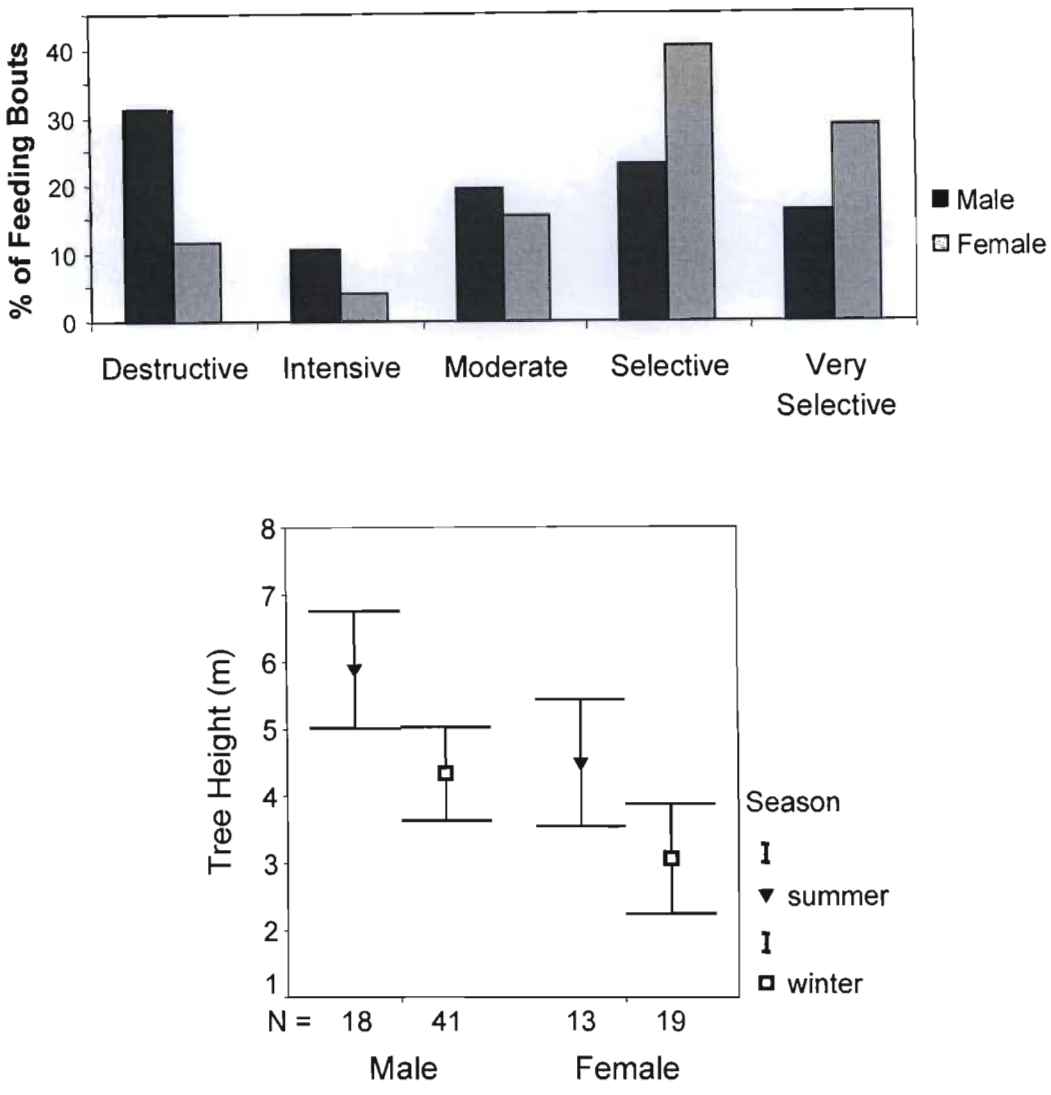


Figure 4. Comparing the intensity of feeding behaviour exhibited by male and female elephant (a) The relative proportions of feeding bouts classified into five different categories of foraging intensity (PGR and PPGR data combined). (b) The relationship between season, sex and the height of trees targeted during destructive feeding bouts in PGR (Data are mean ± 95% CI).

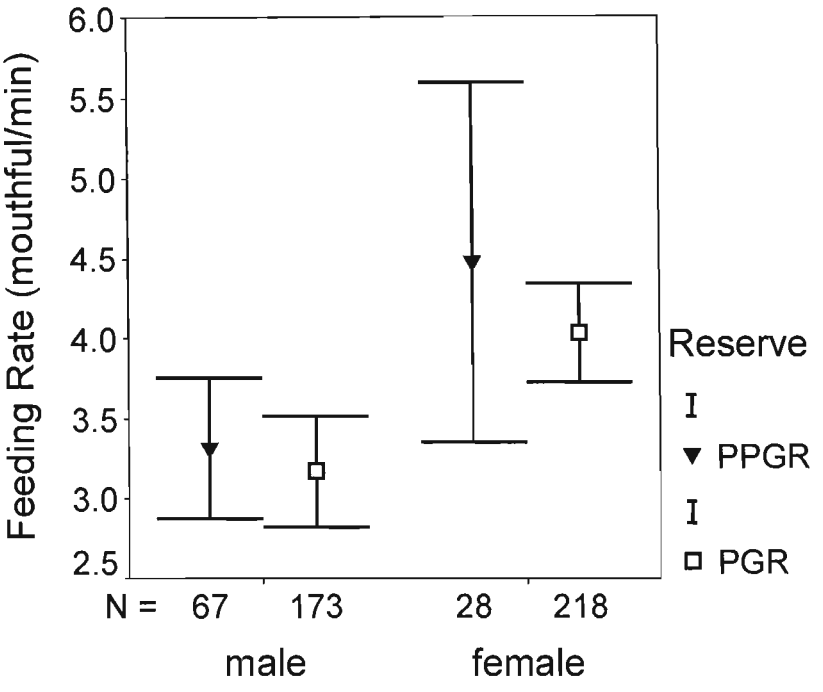


Figure 5. The feeding rates (mouthfuls/min) of male and female elephants in PGR and PPGR (Data are mean ± 95% CI).

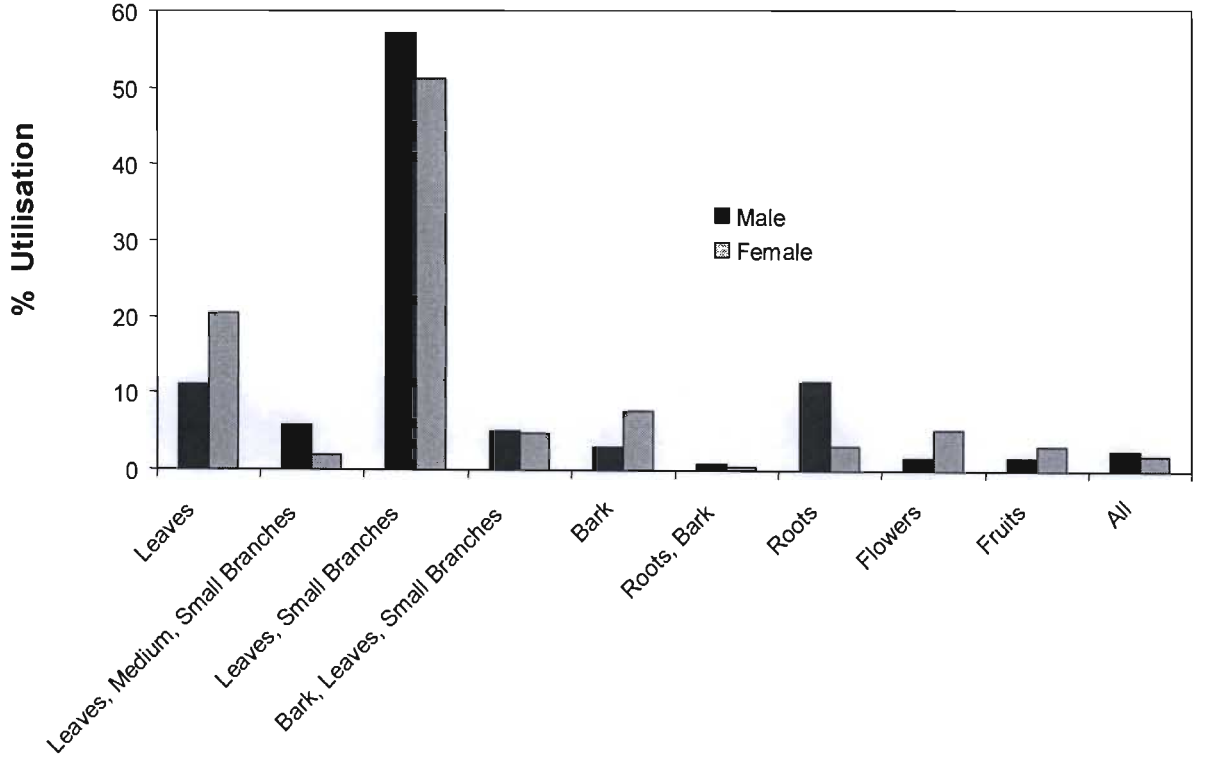


Figure 6. The proportion of tree parts targeted by elephants during all of the feeding bouts recorded in both PGR and PPGR.

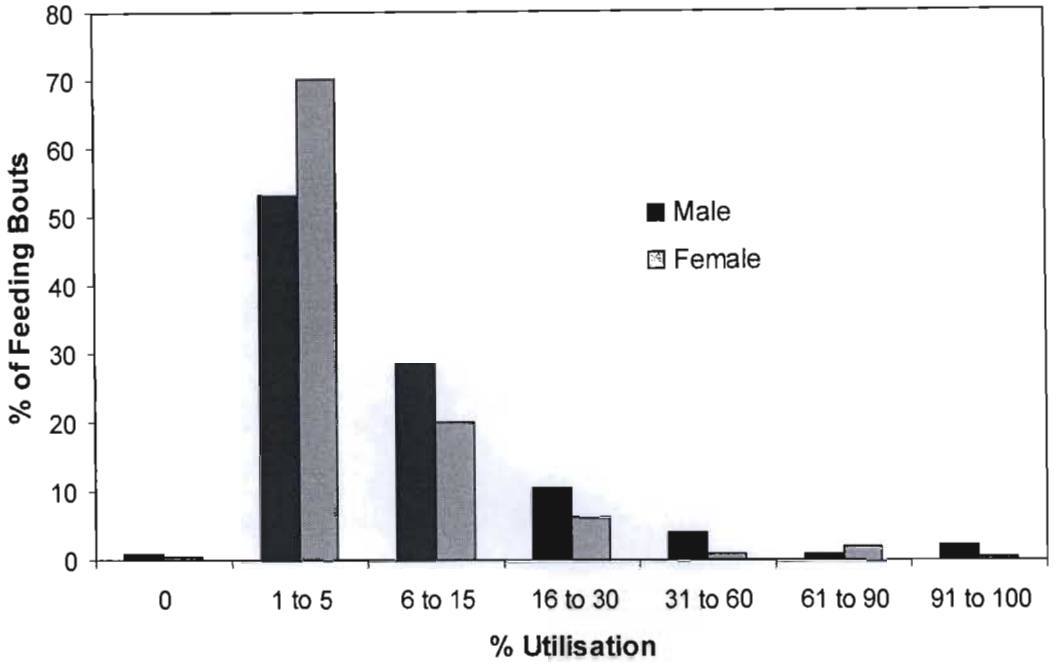


Figure 7. The proportion of available biomass utilised by male and female elephants in both PGR and PPGR.

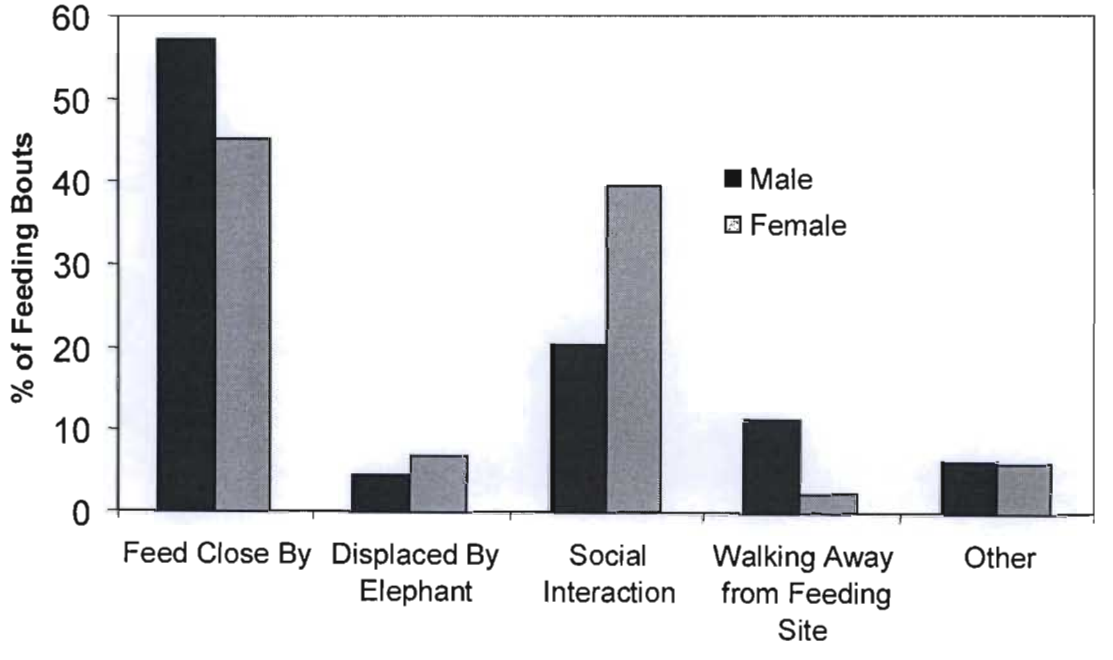


Figure 8. The proportions of male and female feeding bouts that end due to five broad behavioural categories.

Discussion

The length of feeding bouts were significantly shorter for females than males in PGR and this concurs with the results from the study in Chobe National Park where male foraging bouts averaged 540 seconds compared to 216 seconds for the females (Stokke & du Toit, 2000). Shorter feeding bouts indicate a more selective foraging approach (Stokke & du Toit, 2000). In PPGR, the feeding bout lengths of males and females were not significantly different, despite the mean feeding bout length being greater for males than females. Two reasons for this are the limited sample size and the number of young males in PPGR. Whilst three out of the four males in PGR were over the age of 32 and therefore fully grown and independent in nature (75% of the feeding bouts), only 3 of the 20 males sampled in PPGR were above the age of 30 (only 15% of feeding bouts).

The young male in PGR (approximately 17 years old) had a very similar mean feeding bout length when compared to the data for the males in PPGR (average age of 25 years). This is consistent with the body size hypothesis, as a 20 year old male elephant is approximately half the weight of a full grown adult (Laws et al., 1975). This disparity in body size is likely to have a significant influence on foraging behaviour when comparing fully grown adult males to young adult males, due to the scaling of allometric relationships such as metabolism and gut size (Demment & Van Soest, 1985; Owen-Smith, 1992; Stokke & du Toit, 2000). Feeding bouts of males and females are of relatively similar length until they reach approximately 20 years of age (Fig. 2). This may explain the similarity between males and females in PPGR. After 20 years of age there is a divergence in behaviour, with males continuing to increase their feeding bout length as they get older, whilst the feeding duration of the females levels off at 228 seconds. The male response is directly correlated to increasing body size and greater digestive efficiency (Demment, 1983, Demment & Van Soest, 1985), whilst the females begin to invest heavily in reproduction (Moss & Poole, 1983; Poole, 1994; Lee & Moss, 1995) and therefore have greater relative energy demands and social restrictions. This requires a more selective foraging approach, with higher quality food resources being targeted (Beier, 1987; Stokke & du Toit, 2000). The relationship between feeding bout duration and age match closely with the correlations of body mass and age, for both sexes (Laws et al., 1975; Lee & Moss, 1995).

It is also noteworthy that the elephant population in PPGR was established using orphans from Kruger National Park. Sociological impacts associated with removing these young elephants from stable herd structures are therefore likely to occur (Slotow et al., 2000; Slotow & van Dyk, 2001; Garai et al., 2004). In PPGR young male elephants (15 years+) were observed quite often to follow the female groups at discrete distances (H. Druce personal communication). The majority of the feeding bouts recorded for

males were taken in close proximity to females. It is evident that the PPGR males' feeding bout duration falls below the line of best fit (Fig 2.). These negative residuals may well be as a direct result of the association between the two sexes, which constrains the foraging behaviour of the males.

Male body size was also observed to influence the feeding behaviour of bighorn sheep with adults spending less time on actual feeding and more on ruminating when compared to sub-adult. (Pelletier & Festa-Bianchet, 2004). The greater kudu (*Tragelaphus strepsiceros*) also exhibited distinct differences in foraging behaviour linked to body size, with sub adult males feeding for approximately 10% more time than adults (Owen-Smith, 1998). In sexually dimorphic ungulates it is likely that the mass specific energy requirements are higher for young males than for fully grown adults, which could ultimately lead to segregation between age groups as well as sex (Ruckstuhl, 1998).

Trees targeted by males in PGR were significantly larger than the ones selected by females and this may be explained by the larger body size and greater reach of males (Owen-Smith, 1992). The mean feeding heights of males (2m) and females (1.8m) in PGR were very similar and do not reflect the size differences between the two sexes. In PPGR the average height was the same for both sexes (2.2m). It is therefore unlikely that the SCH plays a significant role in the segregation of the sexes, otherwise resource partitioning would be marked, with males feeding higher in the canopy due to competition from females (du Toit, 1990; Stokke & du Toit, 2000). Male elephants did push over more trees (see % destructive feeding bouts fig. 4a) than females in both of the reserves and this would have reduced the average feeding height to some extent. Stokke & du Toit (2000) also found that females fed at similar average heights to males (1.25m compared with 1.5m). Due to the relative abundance of low quality forage it is in fact unlikely that the SCH is a significant factor in the sexual segregation of large herbivores throughout the savanna ecosystem, even during the dry season (Ginnett & Demmentt, 1999; Ruckstuhl & Neuhaus, 2000; Stokke & du Toit, 2000). In this study and those of Guy (1976) and Stokke & du Toit (2000), it was noted that the majority of foraging bouts occurred at <2m, which is well within the reach of many smaller browsers and well below an elephant's maximum reach (du Toit, 1990) suggesting that neither intra or inter specific competition has a significant role to play in the development of elephant foraging strategies.

Females rarely displayed destructive behaviour and when it did occur, it was mainly debarking. This finding is consistent with that of Guy (1976) in Zimbabwe, where males accounted for 80% of the trees pushed over. Male elephants in PGR were also more likely to push trees over in the winter season when, possibly because of reduced feeding opportunities, roots were targeted as a ready source of nutrition through the dry winter season (Owen-Smith, 1992). Male elephants are using their size advantage in this

regard and a similar result was found in Guy's (1976) study where all the tree pushing events occurred during winter. In PGR both sexes targeted larger trees in destructive foraging bouts during the summer. This may be an artefact of habitat selection, with the larger trees occurring in the north of the reserve on shallow well drained soils. These habitats were avoided during the winter periods (Shannon et al., in press). The feeding approach of the females and males differed in both study areas but more significantly in PGR, with over 50% of the female feeding bouts being classified as selective or very selective. This fits well with the body size hypothesis, whilst males which are larger and more independent in nature, spent more time on each foraging bout with 43% ending up as destructive.

Female elephants exhibited a wider diet selection than males in both reserves, yet in PGR only six species accounted for 70% of the feeding bouts of both sexes. This may be a result of the relatively simple vegetation structure of the savanna in PGR. The disparity in female and male feeding approaches was also evident with regard to the tree parts targeted during foraging bouts. Females were much more likely to select the small branches, leaves fruits and flowers which are likely to contain the least fibre and highest nutritional return (McNaughton & Georgiadis, 1986). Males selected larger branches more commonly than females and often uprooted trees to target the roots. This required the extra size and body mass to push over the trees. The males fed in a manner consistent with the predictions that they would ingest a greater quantity of fibre and lower quality forage than the females. Bite rates were significantly different between the two sexes, with females taking more bites per min than males, probably in response to smaller selective mouthfuls (Stokke & du Toit, 2000). In order to meet higher relative energy demands, females process mouthfuls quicker than males. This has been shown in bighorn sheep (Ruckstuhl et al., 2003) and in a study by Murray & Brown (1993) which compared the bite rates of three different sized herbivores in the African savanna. Ruckstuhl et al., (2003) also showed that lactating females had a higher bite rates than both adult males and non-lactating females indicating that bite rate is related to energy demand.

Male elephants exploited more of the available biomass per tree than females. Considering the longer feeding bouts and larger size of the males, this is expected and validates the theory that males tolerate greater quantities of fibrous forage than females. Females were more likely to end their feeding bout due to the social constraints of group living compared to males who were more likely to move on and feed upon another tree or walk away from the feeding site. This exhibits the more independent nature of the male elephants compared to females who are operating under the constraints of group living (Fritz & De Garine-Wichatitsky, 1996). The social nature of elephants is highly developed and the matriarch has a strong influence on the behaviour of the group as a whole (McComb et al., 2001), although it has been

demonstrated that democratic decisions are more effective for the group than individual decisions, even if they are the most experienced (Conradt & Roper, 2003). Despite this, there are distinct costs associated with group living, including competition (Fritz & De Garine-Wichatitsky, 1996) and synchronisation of behaviour (Rands et al., 2003). Male elephants do not undergo such pressure and this is reflected in their independent ranging, longer feeding bouts and more destructive foraging behaviour. The data presented here highlight the significant differences in the foraging behaviour of male and female elephants, which are pronounced enough to drive sexual segregation. Our findings are consistent with those of Stokke & du Toit (2000).

Conclusion

Elephants are one of the most sexually dimorphic terrestrial species and the size difference coupled with social behaviour has a distinct influence on their respective foraging strategies. Females are smaller, have a high reproductive input and live in permanent groups with close social bonding. This results in a feeding approach that maximizes nutritional intake through selective foraging bouts of short duration targeting the highest quality plant parts. Feeding rate is high and the tree impact much less severe than when compared to adult males. Male elephants are able to feed in-situ for longer as they do not experience the same social constraints of group living as females. They are more likely to utilise lower quality forage to meet their energy demands by bulk feeding, in contrast to the females who experience the limitations of group living, greater relative energy demands and reduced digestive efficiency due to smaller body size. The male approach might in fact be a time minimizing strategy which allows them to concentrate on other activities including reproduction and ranging. Vegetation impacts, such as tree pushing are much more likely to be driven by males than females, with trees commonly targeted both as a feeding strategy and for social reasons (e.g. displacement behaviour). This study therefore finds little evidence to suggest that the SCH is operating with regard to the segregation of elephant but it is highly probable that the FSH could lead to pronounced sexual segregation, due to the disparity in foraging approach and duration. This study has implications for other sexually dimorphic herbivores and clearly indicates that the sexes of such species can be markedly different with regard to foraging behaviour and habitat utilisation. Both management and conservation efforts must take this into account in order to prevent over-simplification of ecological systems. Population structure in large dimorphic herbivores is likely to be as important as population size with regard to effective management.

CHAPTER 6

SEXUAL DIMORPHISM AND ACTIVITY BUDGETS OF THE AFRICAN ELEPHANT

Abstract

Sexually dimorphic ungulates exhibit pronounced segregation on the basis of sex. The activity budget hypothesis is one of four main theories proposed to explain segregation between the sexes. Females, due to their smaller size are predicted to be less efficient at digesting forage and therefore will need to feed for longer to satisfy their energetic and nutritional demands. This will lead to differing activity budgets between the males and females, which in turn makes synchrony of behaviour difficult, finally resulting in temporal and/or spatial segregation. Sexual segregation is pronounced in elephant, with females and their young forming defined herds whilst adult males range independently or in loosely associated groups. We tested the hypothesis that this segregation is due to different activity budgets. Three distinct populations of elephant were studied over a 3 year period (2002-2005). Group behavioural codes were assigned to each location point taken during the study. Behavioural observations were made throughout the daytime period with a minimum interval of 10 minutes. Individual 15 minute focal samples, of male and female elephant were also recorded. Synchrony of behaviour was studied using four broad behaviours, drinking, resting, walking and feeding. Neither activity synchrony nor feeding time varied significantly between the sexes and it is unlikely that activity budgets are the main factor involved in the sexual segregation of elephant. In fact the behavioural patterns were remarkably similar and it is likely that environmental factors influence synchrony more than body size. Due to the broad foraging approach exhibited by male and female elephants coupled with their substantial energy demands, increasing feeding time is only one method by which nutritional return can be increased. Such diverse methods, coupled with hind gut fermentation and a generalist foraging approach are likely to explain the similarity in the proportion of time that males and females spent feeding. The activity budget hypothesis was therefore rejected as the causal mechanism in sexual segregation of elephants.

Introduction

Sexual dimorphism is a common feature of many ungulate species, with males being much larger than females (Jarman, 1983; Stokke & du Toit, 2000; McElligott et al., 2001). This body dimorphism is believed to have evolved due to competition for females in polygynous breeding systems (Clutton-Brock & Harvey, 1978; Owen-Smith, 1992). Such breeding systems are commonly observed in ungulates with larger males being conferred an advantage as they are able to out compete smaller individuals and achieve greater mating success (Pérez-Barbería & Gordon, 1998). Females are not exposed to the same selection pressure and therefore direct energy into reproduction rather than growth (Le Blanc et al., 2001). There

also appears to be a positive relationship between weight, polygyny and sexual dimorphism in ungulates. In ruminants for example, species above 90 kg are all polygynous whilst those below 20-30 kg are monogamous and exhibit little if any sexual dimorphism (Loison et al, 1999).

Species that are sexually dimorphic are generally segregated into male and female groups outside of the breeding season (Michelena et al., 2004; Yearsley & Perez-Barberia, 2005), with segregation being more pronounced in species that exhibit greater levels of dimorphism in body size (Mysterud 2000). The cause of sexual segregation has been the subject of much debate over the past decade (Main et al., 1996). Understanding this aspect of spatial ecology is important in managing species and gaining greater understanding as to the evolution of sociality, reproductive strategies and optimal behaviour (Pérez-Barbería et al., 2005).

Four broad hypotheses have been put forward to explain sexual segregation (Main et. al. 1996; Ruckstuhl & Neuhaus, 2000; Pérez-Barbería et al., 2005). (1) The predation risk hypothesis: females and their offspring are at greater risk of predation than males and will therefore utilise habitats which provide greater protection and safety. Males are more likely to select habitats on the basis of forage availability as they invest heavily in body growth (Corti & Shackleton, 2002). (2) The forage selection hypothesis: diet and habitat selection vary between the two sexes as a result of differing energy requirements and foraging efficiency. (3) The social factors hypothesis: groups of the same sex are formed on the basis of shared behaviour and social affinity (Bon & Campan, 1996). For example, young males often prefer to group together and practice their sparring. This behaviour establishes dominance hierarchies that will be important when they compete for females (Ruckstuhl & Neuhaus, 2000; Le Pendu et al., 2000). (4) The activity budget hypothesis: the most recent hypothesis to be put forward (Ruckhustuhl, 1998), it states that body size dimorphism leads to different behavioural activity budgets due to females having higher relative energy requirements, lower digestive efficiency and greater selectivity when feeding than males (Demment & van Soest, 1985; Stokke & du Toit, 2000). This is likely to result in females foraging for longer and the two sexes ultimately segregating over space and time. These differences can lead to sexual segregation but not necessarily habitat segregation (Conradt, 1998b; Ruckstuhl & Neuhaus, 2000). Synchronising behaviour is also likely to be an energetically expensive strategy when taking into account different energy requirements and activity budgets. Therefore mixed groups are likely to segregate whilst single sex groups are able to synchronise behaviours and maintain group cohesion (Conradt, 1998; Ruckstuhl, 1999; Ruckhstuhl & Neuhaus, 2001; Ruckstuhl & Kokko, 2002). For example, drinking is an important behaviour for a large water dependent animal such as the elephant and therefore water points are visited on average once per day (Owen-Smith, 1992). These water points are discrete and involve an

animal making a conscious decision to move towards them. Therefore a significant variation in drinking time may segregate the two sexes on a temporal and spatial basis.

The first three hypotheses have received most of the research focus, whilst activity budgets have received significantly less attention (Ruckstuhl & Kokko, 2002; Michelena et al., 2004). However, the four hypotheses are not mutually exclusive and sexual segregation may result from a combination (Neuhaus & Ruckstuhl, 2004). The majority of studies have concentrated on temperate species of ungulate including the big horn sheep (Ruckstuhl, 1998; Ruckstuhl, 1999; Le Blanc et al., 2001; Mooring et al., 2003), ibex (Ruckstuhl & Neuhaus, 2001), mule deer (Bower & Kie, 2004), red deer (Conradt, 1998; Conradt, 1999) and merino sheep (Michelena et al., 2004). In this study we investigate the influence of sexual dimorphism on both the activity budgets and behavioural synchrony of the African elephant. Elephants provide an interesting study animal due to their pronounced body size dimorphism, with adult males weighing twice (6000 kg) as much as adult females (3000 kg) (Poole, 1994) and their distinct sexual segregation.

Sexual segregation is a well documented aspect of elephant ecology (Laws et al., 1975; Owen-Smith, 1992) but the reasons for it have rarely been investigated. Stokke and du Toit (2000) carried out the only study and found strong evidence supporting the forage selection hypothesis. However behavioural aspects were not addressed in their study due to the complex nature of studying animals in a large system such as the Chobe National Park (Stokke and du Toit, 2000). Our data were collected from three distinct and well documented elephant populations in South Africa. The closed nature of the reserves and their relatively small size aided behavioural data collection. The hypotheses tested in this study are: (1) Females are more selective in their foraging habits than males and will spend a greater amount of time feeding during a given period: (2) The onset of a particular behaviour is likely to be asynchronous between the two sexes due to differing activity budgets: (3) Males are segregated from females due to the energetic cost of maintaining group cohesion with asynchronous behaviour and different activity budgets.

The objectives of this study were to: (1) Establish whether adult male and female elephants exhibit different activity budgets (2) and to determine seasonal differences in activity of male and female elephants. (3) To investigate whether males feed for proportionally less time than females. (4) Determine whether elephant behaviour is sexually asynchronous with regard to timing and duration. (5) Establish whether patterns are repeated across the three elephant populations.

Methods

Study Sites

The Pongola Game Reserve (PGR) is situated in Northern Zululand with a total extent of 82km^2 (27°54′ - 27°35′ S; 32°01′-31°86′ E). The climate is hot and arid with an annual rainfall of 400-700mm per annum. The vegetation falls into three of Acocks (1988) veld types; Zululand Thornveld, Lowveld and Arid Lowveld. Seven vegetation or habitat types are recognized (Shannon et al., In Press). The reserve's eastern boundary is defined by the Jozini dam, which provides a plentiful water source. In addition to the dam there are a number of pumped water points throughout the west of the reserve. PGR has three distinct elephant groups, a large herd of 38 which only utilises the east of the reserve (40 km^2), a small orphan group of 7 and three adult males (elephant population size as of October 2004). The males and orphan group range across the whole reserve.

Pilansberg National Park (PNP) is situated in the North West province of South Africa and is 500 km^2 in extent (25°8′ -25°22′ S; 26°57′-27°13′ E). It is made up of the crater of an extinct volcano and as such is roughly circular with hilly relief. The average yearly rainfall is 630 mm and mainly falls in summer (November-April) (Slotow & Van Dyk, 2001). Acocks (1988) recognises the vegetation as sour bushveld. Pumped water points are distributed throughout the reserve and one large central dam. During the period of 1979-1998, 58 male and 37 female elephants were introduced. 14 of the males were culled and 15 further elephants died between 1979 and 2001 (Slotow & Van Dyk, 2001). In 1998 six adult males were introduced from Kruger National Park. The total population in early 2004 was 158 (this comprised 34 adult males and 124 females and juveniles in 16 family groups).

Phinda Private Game Reserve (PPGR) is situated in northern KwaZulu-Natal and is180 km^2 in extent (27°92′ -27°68′ S; 32°44′-32°20′ E). The reserve has an average rainfall of approximately 750 mm (averaged over a 10 year period), with a maximum temperature of 35°C and a minimum of approximately 10°C. There are a diverse range of habitats from the endemic sand forest to the sweet lowveld bushveld, Natal low bushveld and the coastal bushveld of the savanna biome (Low & Rebelo, 1996). There is one river that runs through the southern section of the reserve and 6 dams that are fed with water from boreholes during the wet season (Druce et al., unpublished). Twenty four males and 34 females were introduced during 1992-1994. In 2003 37 elephants were translocated and 3 adult males were introduced from Kruger. The total elephant population in 2004 was 75, comprising 18 adult males and 21 adult females in five family groups.

Data Collection

Two methods were employed to collect the behavioural data. The first involved coding the dominant behaviour of individuals and groups of elephants observed at discreet points in time, with at least 10 minute intervals between repeat sightings. The elephants were located using either traditional tracking methods or radio telemetry. On sighting the elephant(s), a GPS (global positioning system) was used to record the exact position of the observer. The distance and bearing to the middle of the elephant group or to the individual was then recorded so as to correct the co-ordinates. A behavioural code was assigned, depending upon the activity which was being engaged in by the majority of the individual elephants present. Behaviours could be recorded instantaneously and elephants that subsequently moved out of sight did not invalidate the previous data as each sighting was independent of the next. These data were collected throughout the three reserves between 6am and 6pm.

The second method involved fixed length focal observations that concentrated on an individual adult elephant. Once an elephant was selected, it was observed for 15 minutes and its behaviour recorded every minute using the same behavioural codes as the first method. The position of the animal and ID code were recorded along with the date and the starting time of the focal. If the elephant moved out of sight, it was recorded (more than 5 observations out of sight and the data were discarded) i.e. a minimum of 10 behaviours contributed to any specific focal observation.

Statistical Analysis

The group activity data (i.e. data point for one individual male or a family group) were initially compared on the basis of sex and season. The sightings and behavioural codes of each female group or individual male elephant were filtered into one of the six, two-hour time intervals, from 6:00-18:00. The proportions of the four main behaviours (feeding (F), resting/standing (R), walking (W) and drinking (D) were calculated for each group or individual elephant by dividing the number of occurrences of a particular behaviour by the total number of sightings within that time period. The remaining codes were grouped together under the category of other. These data were then compiled across all the reserves and averaged using sex and season as the independent variables. The seasons were defined using annual rainfall data (see method in Chapter 3). A daily activity budget for male and female elephants in both the summer and winter season was generated as initial qualitative analysis to describe the broad trends of male and female activity budgets throughout the three study sites (Fig. 1).

ANOVA was then used to analyse the proportions of time, that individual males and female groups spent engaging in the four main behaviours, across the six different time categories. This enabled us to test

whether males and females were exhibiting synchrony in their behavioural patterns throughout the day. The data were normalised using the arcsin square root transformation (Kolmogorov-Smirnov test $P>0.05$). Each of the four main behaviours were analysed using a separate ANOVA, with the proportion of time for individual males or female groups being used as a separate data point in the analysis. The reserves were combined in the ANOVA and entered as an independent variable to establish if significant differences in behaviour occurred across the three study sites. If this was the case then the data from each reserve was analysed separately and presented accordingly. The coefficient of variance was also calculated for each of the behaviours per individual. This enabled us to measure the level of variation in activity synchrony between the two sexes.

The 15 minute focal samples were used to examine the proportion of time that each sex devoted to feeding, in both summer and winter seasons and across the three reserves. The initial analysis was done by calculating the proportion of feeding observations for all of the 15 minute focal samples. This was completed for each of the three reserves. The data were then classified according to sex, season and reserve. The data could not be normalised and therefore a Kruskal-Wallis test was used to test for the effects of reserve, season and sex on the proportion of time spent feeding.

The second stage of the analysis involved using the mean proportion of time spent feeding for individual male and female elephants which had been repeat sampled throughout the study period. Only elephants which had three or more 15 minute observations were analysed. Due to the small sample size of the PPGR dataset, only focal data from PGR and PNP were used in this stage of the analysis. The average proportion of time spent feeding was calculated for each individual using the results from their focal samples. These data were normalised using the arcsin square root transformation and an ANOVA was used to test for differences in the mean proportion of time spent feeding by individual male and female elephants. This method enabled variation to be accounted for on the basis of individual elephants rather than compiling all the data and only distinguishing sex and season as in the previous analysis. The coefficient of variance was also calculated and an ANOVA was used to test whether significantly different levels of feeding variation were exhibited by males and females during their 15 minute observations.

Results

Activity budgets

The qualitative analysis of activity budgets shows similar patterns for both sexes throughout the year (Fig. 1). Both males and females display a pattern of reduced feeding and increased time spent resting towards the middle of the day. Seasonal differences are evident for both sexes with more time spent resting during the summer period, especially in the middle of the day. The proportion of time spent walking is relatively consistent throughout the day for males and females in winter. This is in contrast to the summer period when walking rates peak in the early morning and late afternoon. Midday periods in summer are associated with the highest incidence of other behaviour, such as mud bathing, dust bathing and interacting.

Drinking Synchrony

There was a significant difference in drinking times between individual males and females (Fig. 2a). The data were pooled across the three reserves as the ANOVA showed there was no significant reserve effect ($F_{2,120} = 0.315$, $P > 0.5$). Males exhibited much higher levels of drinking in the morning, whilst females preferred from the midday onwards with a peak in the late afternoon. Males also spend more than females at water points (Fig. 2). Drinking by individuals was significantly different for males and females ($F_{1,120} = 9.543$, $P < 0.01$ and across the time of day ($F_{5,120} = 5.692$, $P < 0.001$). Males and females had a very similar level of variation throughout the day, except during the 6-8am time period when females exhibited very high variation with a coefficient of 227%. During the rest of the day, males averaged 75% with a range of 51-92% and females 71% with a range of 53-94%. This indicates a similar level of variation in drinking behaviour for both sexes across all three of the reserves.

Resting Synchrony

No reserve effect was noted ($F_{2,126} = 0.430$, $P > 0.5$) and the data were pooled for analysis of sex and time effects. There were no significant differences in resting patterns for male and female elephants ($F_{1,126} = 2.010$, $P > 0.1$ The proportion of resting increased, until the middle of the day after which levels dropped again (Fig. 2b). The proportion of time spent resting was significantly different for the time categories, with low levels of resting in the early morning and late afternoon, compared to midday when resting was at its highest ($F_{5,126} = 6.202$, $P < 0.001$). Males exhibited a relatively consistent level of variation throughout the day with an average coefficient of variance of 64% and a range of 54-77%. The females exhibited very low variation during the 10-12am time period with a coefficient of variance of 28% compared to a daily average of 69% and a range of 28-95%.

Walking Synchrony

The proportion of time spent walking was significantly different among reserves ($F_{2,126}$=9.999, P <0.001), therefore the walking data were examined separately for the three reserves. Both PNP ($F_{1,54}$=5.029, P <0.05) and PPGR ($F_{1,54}$=6.118, P <0.05) exhibited significant differences between the sexes, in contrast to PGR ($F_{1,18}$=0.476, P >0.25). In PPGR the females tended to spend more time walking, while in PNP the males spent more time walking. The PGR data exhibited similar patterns for males and females throughout the day. Females exhibited the least variation from one time period to the next with an average coefficient of variance of 47% and a range of 33-56%. Males had an average of 54% with a range of 30-85%. The lowest variation occurred between 8-10am and the highest between 12:00-14:00. The combined data show distinct patterns over the 12 hour period (Fig. 2c).

Feeding Synchrony

The feeding data were pooled as no reserve effect was detected ($F_{1,54}$ = 6.118, P <0.05). Males and females showed the greatest proportion of feeding per unit time between 6-8am, followed by a reduction until early afternoon, when the proportion of feeding increased once again (Fig. 2d). The relationship was matched for both sexes and there was no significant difference in five out of the six time periods ($F_{1,126}$ = 1.244, P >0.25). However, the 16:00-18:00 time period did show a marked difference between the sexes with males continuing to feed at a relatively high proportion of unit time whilst females exhibited a reduced feeding rate. There was a significant relationship between time ($F_{1,54}$ = 6.118, P <0.05) and the proportion feeding. Feeding had the lowest level of variation from one time period to the next out of all four of the behaviours and for both sexes. Males had an average coefficient of variation of 22% and a range of 16-35% compared to the females who had an average of 18% with a range of 14-27%.

Analysis of Focal Data

There was no significant difference between the sexes in the proportion of time spent feeding (χ^2=2.014, d.f. 1, P >0.1) (Fig. 3) with means of 42% and 45% for females and males respectively when all the time budget data were pooled. The data were analysed per reserve, to assess whether significant differences in the time spent feeding occurred within the three datasets. All three of the reserves returned a non-significant result (PNP: χ^2_1 = 3.78, P = 0.052 PPGR: χ^2_1 = 1.43, P >0.7 & PGR: χ^2_1 =1.03, P >0.3). PNP was only marginally above the threshold of significance; but there were no clear differences between the two sexes (Fig. 4). There was no seasonal difference in the proportion of time spent feeding by males and females (Summer: χ^2_1= 3.005, P >0.05, winter χ^2_1 = 0.082, P >0.5).

Further analysis was carried out by calculating the time budgets for individual male and female elephants in PNP and PGR (PPGR excluded due to limited data). There was no sex difference when the datasets were analysed together ($F_{1,46} = 1.702$, $P > 0.1$). However, there was a significant reserve effect ($F_{1,46} = 4.677$, $P < 0.05$), so separate analysis was carried out. The data from PGR were non significant ($F_{1,14} = 0.89$, $P > 0.75$) but PNP returned a significant result ($F_{1,32} = 4.164$, $P = 0.05$) with males devoting greater proportions of their time budgets to feeding. (Fig. 5). The levels of variation within the data sets were also compared. There was no significant reserve effect when comparing the coefficient of variation ($F_{1,48} = 0.848$, $P > 0.25$) but there was a significant difference between the sexes ($F_{1,48} = 5.136$, $P < 0.05$) with females showing a greater coefficient of variation than males (Fig. 6).

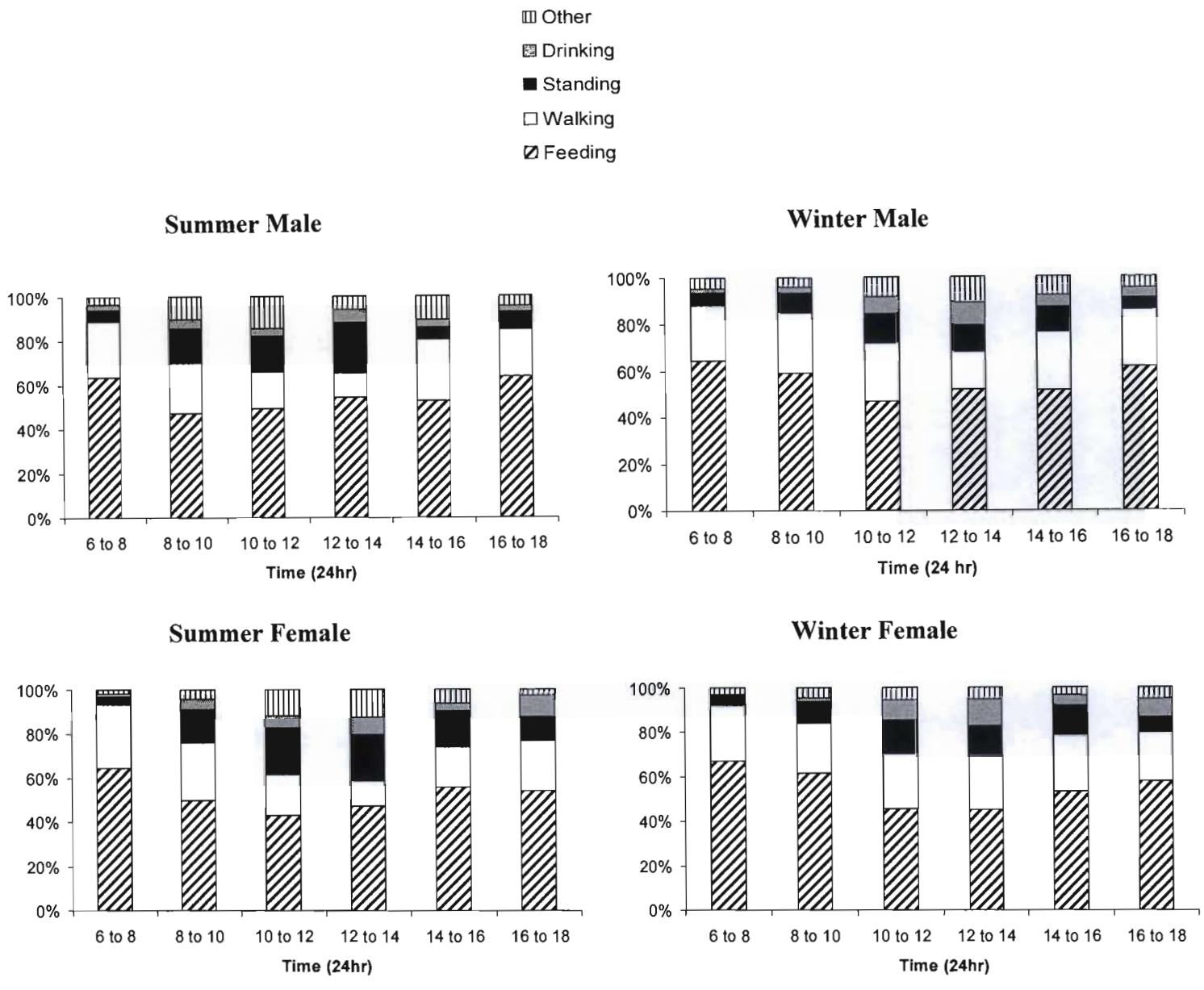


Figure 1. The seasonal activity budgets for male and female elephants, from 6am until 6pm. The results are calculated by averaging the activity budgets for the 18 males and 9 female groups across all the three reserves.

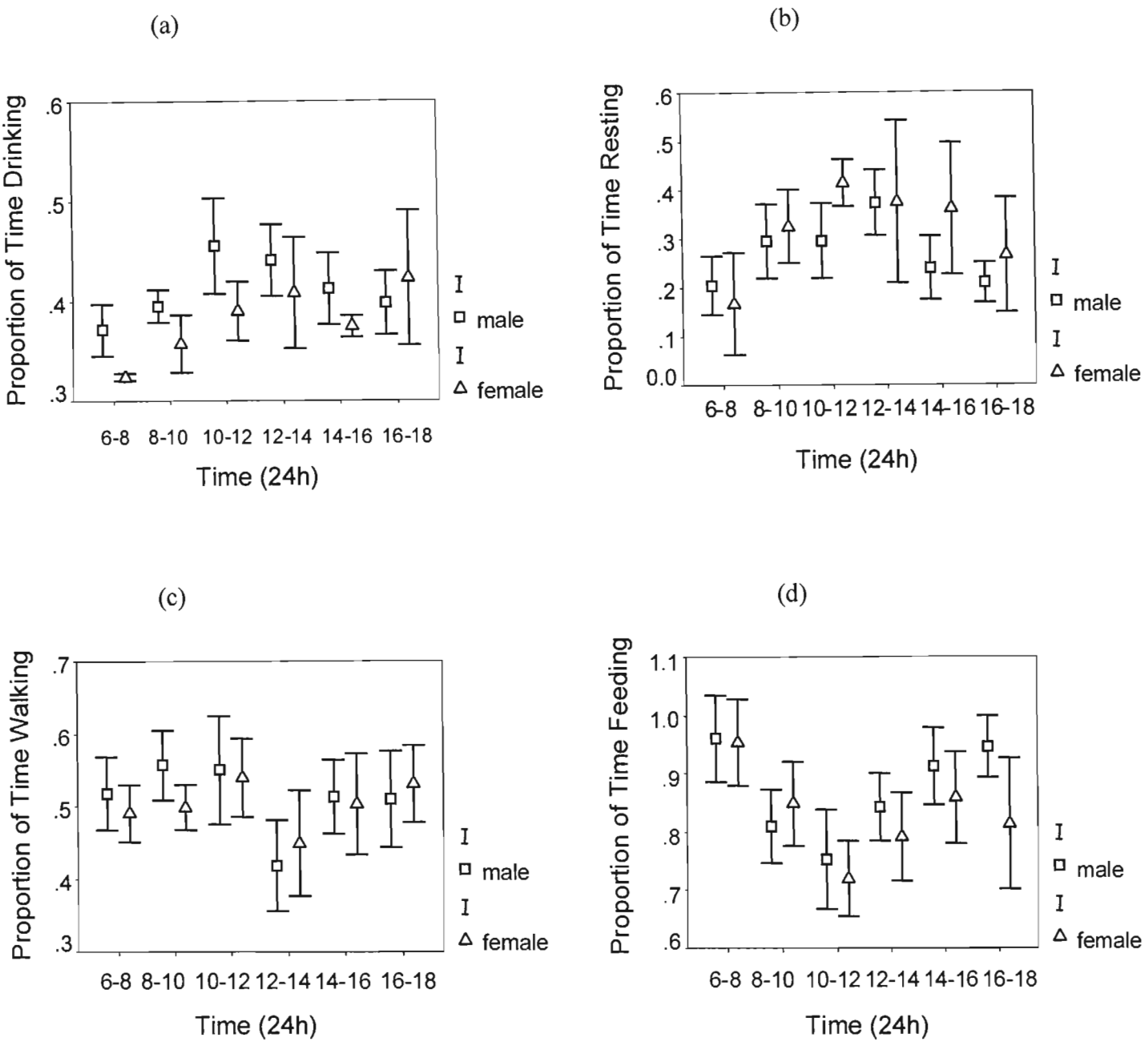


Figure 2. The relative proportions (data were arcsin square root transformed) of time spent drinking (a), resting (b), walking (c) and feeding (d) by both female and male elephants between the hours of 6am and 6pm. Both sexes are exhibiting similar activity patterns throughout the day, indicating a statistically significant level of synchrony (Data are mean ± 95% CI and N= 18 male and 9 female).

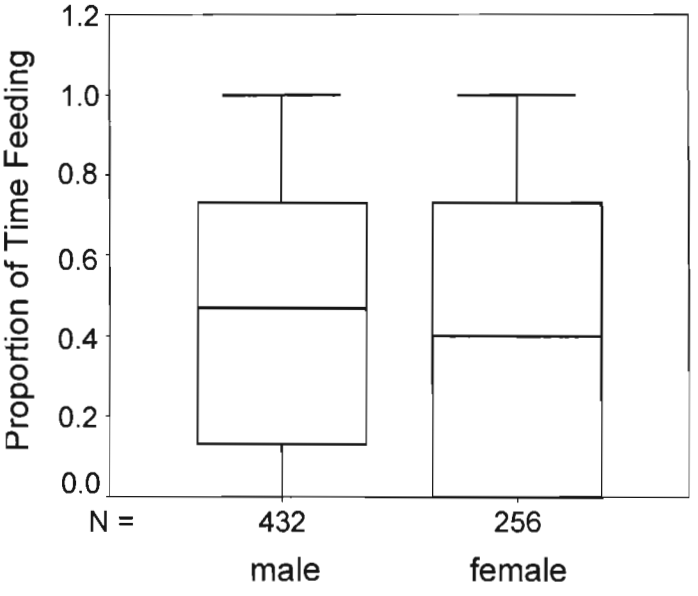


Figure 3. Proportion of time that males and females spent feeding from the analysis of all the 15 minute behavioural observations (Data are presented as Box and Whisker plots N = number of 15 minute focal observations for each sex).

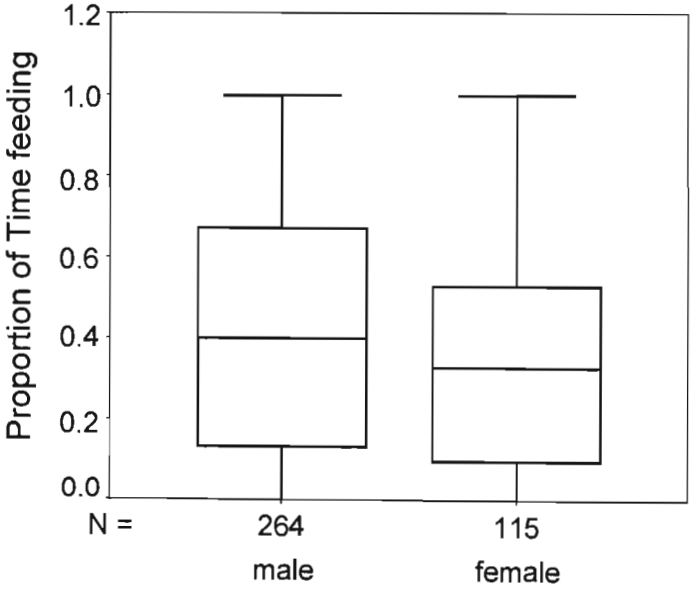


Figure 4. The proportions of time spent feeding by male and female elephants in PNP (Data are presented as Box and Whisker plots, N = number of 15 minute focal observations for each sex).

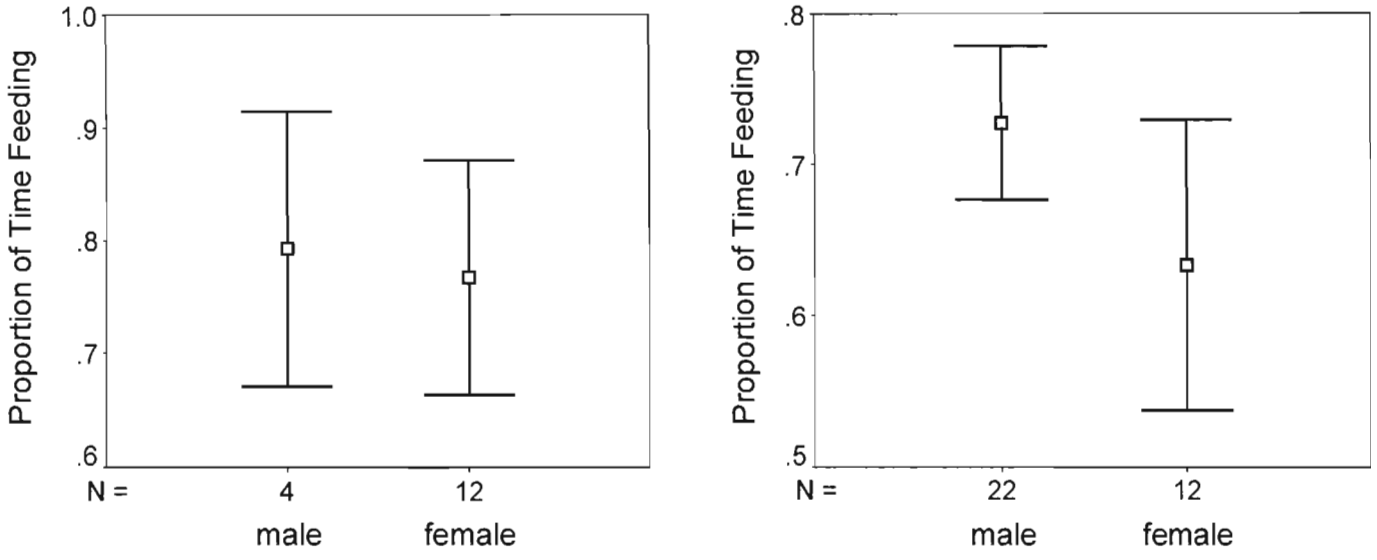


Figure 5. The proportion of time individual males and females feed for during the 15min focal observations in (a) PGR and (b) PNP (Data are mean ± 95% CI, N = number of male and female elephants used in the analysis).

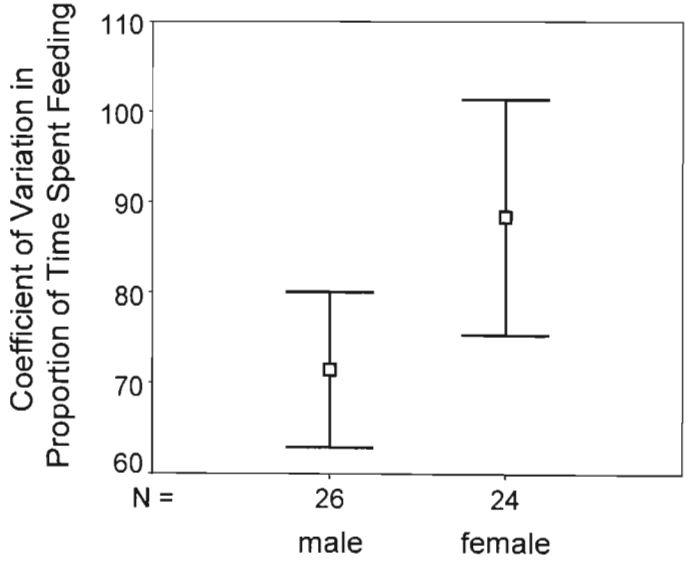


Figure 6. The coefficient of variation for the proportion of time spent feeding during the 15 minute focal observations for both males and females (Data are mean ± 95% CI, N = number of male and female elephants used in the analysis).

Discussion

Seasonal Activity Budgets

There were no observable differences in the seasonal activity budgets of male and female elephants. Both sexes exhibited distinct spikes in feeding activity during the early morning and late afternoon, whilst the middle of the day was correlated to the lowest proportion of time spent feeding. This pattern is likely to be a response to increasing temperature, with the daily maximum (between midday and 14:00) corresponding to the lowest activity period of the day. Similar activity patterns have been noted before in elephant (Owen-Smith, 1992) and other African herbivores including white rhino (Owen-Smith, 1992), giraffe, kudu and impala (Owen-Smith, 1998; du Toit & Yetman, 2005) and blesbok and wildebeest (Twine, 2002). Seasonal differences such as the reduction in the proportion of time spent resting in the middle of the day during winter are apparent in our data set, but they occur for both male and female elephants. A temperature effect is likely to play a causal role in these patterns, with the elephants not experiencing the same thermoregulatory constraints in the winter as in the summer period.

Although both small and large African herbivores reduce their activity levels during the hottest period of the day, larger bodied animals appear to be affected by this inactivity to a greater extent, as body size is positively correlated with feeding time (Owen-Smith, 1992; du Toit & Yetman, 2005). Small herbivores are therefore able to adapt and feed in the cooler early morning or late afternoon, whilst larger herbivores are less flexible and may lose out on foraging opportunities during very hot days (du Toit & Yetman, 2005). The similarities observed in the seasonal activity budgets of male and female elephants may suggest that environmental factors outweigh the influence of body size and the associated physiological differences (Jeschke & Tollrain, 2005). In contrast to African herbivores, temperate species of increasing body size exhibit reduced activity time (Mysterud, 1998; Pelletier & Festa-Bianchet, 2004). This further indicates the role of environmental conditions in dictating the length of daily foraging time (Owen-Smith, 1998). In this study, males fed for approximately 55% of the 12 hour study period in summer and 56% in winter. Females had slightly lower values with 51% in summer and 55% in winter. These figures are similar to those from other studies which suggest that elephants feed for anywhere between 42-80% during daylight hours (Owen-Smith, 1992).

Feeding Budgets

The analysis using all of the15 minute behavioural observations as separate data points, indicated that there was no sex difference in the proportion of time spent feeding across the three reserves. This was in agreement with the results from the location data although the mean values were lower (42% females and 45% males), but this may be attributed to the continued, clear line of sight that is required for 15 minute

focal data collection. The proportion of feeding may therefore be underrepresented, especially when it takes place in dense vegetation. However, any sampling difficulties applied to both males and females and the data can be compared with confidence. The data were then pooled and averaged for each elephant. This data also confirmed that there was no significant difference between the sexes with regard to the time spent feeding. PNP did exhibit a sex difference when analysed alone, with males feeding for significantly longer periods than females. This result concurs with other research on the activity budgets of African herbivores, where increasing body size is associated with an increase in the proportion of daily time spent feeding (du Toit & Yetman, 2005). This has been shown between species and is believed to be due to the physical differences in forage (e.g. spinescence) and the added handling time compared to that of temperate species (Cooper & Owen-Smith, 1986; du Toit & Yetman, 2005). The marked size disparity between male and female elephants is probably significant enough for such effects to be observed within the species. Females exhibited more variation in their feeding behaviour than males, indicating that females are less consistent in their foraging approach. This may be an indication of group decision making which involves one or two dominant individuals in each group (McComb et al., 2001; Couzin et al., 2005). Males are less socially constrained and therefore may feed with a more constant approach.

Behavioural Synchrony

Despite females and males exhibiting very similar seasonal activity patterns, the scale is rather broad and significant differences may not be evident. The activity synchronisation of individual male elephants and family groups were investigated to establish whether a preference for particular behaviours at certain times could lead to spatial and temporal segregation between the two sexes. Synchronising activity may prove costly if an individual has to miss out on engaging in a profitable behaviour due to the preference of the rest of the group. It is therefore believed to be a significant factor in sexual segregation (Conradt, 1998b; Ruckstuhl, 1999; Conradt & Roper, 2000; Ruckstuhl & Neuhaus, 2001).

The daily drinking patterns were different for the two sexes, with males spending a greater proportion of time drinking, in five of the six time periods. This result makes biological sense as male elephants require greater quantities of water than females and are generally less sensitive to being in open areas around water points (Spinage, 1994). Although the result is significant, drinking only accounted for an average 6% of the 12 hour study period (data for both sexes pooled). It is unlikely that asynchrony of a behaviour with such short duration is driving sexual segregation. This is further evident when considering that strong group cohesion in big horn sheep is exhibited when behavioural synchrony is greater than 80% and still allows for substantial variation from one individual to the next (Ruckstuhl, 1999). However, this study was carried out in small enclosed reserves with abundant water supplies, which reduces the priority

of locating adequate drinking water. In larger more open systems with spatially heterogeneous water points, drinking synchrony may become more pronounced and result in sexual segregation. This potentially large behavioural effect of providing artificial water needs to be further investigated because of the ecological consequences.

The proportion of resting increased with the time of day, peaking during the 12:00-14:00 time period. This behaviour is to be expected as it reflects the influence of increasing temperature on activities such as feeding and walking. Thermoregulatory constraints appear to influence males and females to similar extents, despite the body size differences. Males did however exhibit a greater level of variation during the hottest part of the day, whilst females showed a consistent response at this time across all three reserves, with a coefficient of variation of 28% compared to the mean of 68%. This is likely to be related to group dynamics and reduced decision making flexibility, associated with a group situation where the dominant female(s) make decisions (Mcomb et al., 2001; Couzin et al., 2005). Males on the other hand, can vary their behaviour with greater ease as they often move alone or in loosely bonded groups (Poole, 1994).

Overall the proportion of time spent walking remained relatively similar throughout the whole day except during the 12:00-14:00 period when both males and females exhibited a reduction in the proportion of walking. This is further evidence as to the thermoregulatory response that strongly influences the activity budgets of elephant. Looking at the reserves separately, PNP males attributed more time to walking than females, whilst in PPGR the females exhibited higher proportions of walking than males in five out of the six time periods. There was no sex effect in PGR. The vegetation types and extent of these reserves was very different, and due to the relatively large size of PNP, males may move greater distances to interact with females and their family groups. In PPGR, the females were sensitive to disturbance and maintain relatively high movement rates (H. Druce, Pers. comm.).

Males and females exhibited similar feeding preferences throughout the day, with the exception of the 16-18:00 time period when females reduced feeding rates and males maintained a relatively high proportion of feeding. The reduction in the proportion of feeding around midday fits the theory that activity rates are lowered in response to increasing temperature in both sexes. The average coefficients of variation were approximately 20% for males and females, indicating that for both sexes the proportion of time spent feeding does not vary greatly. This could be predicted on the basis that feeding is the dominant activity and time is a limiting factor when it comes to elephants meeting their sizeable energetic demands.

Although occasional significant behavioural differences between males and females appear in this analysis, it is evident that there is a high level of similarity in the duration and synchronisation of behaviour. This is all the more significant when considering that the data come from three distinct reserves, 18 males and 9 different family groups. For activity synchronisation to play a significant role in the segregation of elephant, it would have to be marked with clearly defined activity patterns. Yet instead, males and females follow a relatively similar activity budget throughout the day. However, synchronisation of behaviour is believed to be a significant factor in the sexual segregation of other herbivores, including big horn sheep (Ruckstuhl, 1999), ibex (Ruckstuhl & Neuhaus, 2001) and red deer (Conradt & Roper, 2000). In all of these temperate species, there is pronounced dimorphism and the females have been shown to feed for substantially longer than males.

The activity synchronisation theory is based on the fact that the proportion of time spent feeding differs between the two sexes, leading to asynchronous behavioural patterns (Conradt, 1998; Ruckstuhl, 1999). The majority of the research has been carried out on grazers that concentrate on food sources similar in physical structure and nutritional return. These herbivore species are generally only able to increase energy intake by faster bite rates, longer periods spent feeding and to a lesser extent, selection of higher quality habitats. Therefore sexually dimorphic ruminant grazers are likely to segregate because males will rest and ruminate for longer periods whilst females will continue to feed in order to satisfy higher relative energy requirements. Ultimately this will lead to spatial and temporal segregation, even in homogeneous environments, due to differing activity budgets and asynchronous behavioural patterns (Conradt, 1998; Ruckstuhl, 1998; Conradt & Roper, 2000; Ruckstuhl & Neuhaus, 2001; Ruckstuhl & Kokko, 2002). Elephants, on the other hand, are faced with a much wider diversity of resources due to their catholic diets, large size and tolerance to fibrous plant parts (Laws et al., 1975; Owen-Smith, 1992; Stokke & du Toit, 1999, 2000). Therefore, increasing the time spent feeding is only one of a number of methods that can be employed to increase energy intake. Elephants are also non-ruminants and spend most of their time foraging (feeding and moving) and are not limited by the need to feed selectively and spend time re-masticating ingesta as is the case for ruminants. Therefore males and females are influenced by similar temporal and environmental pressures. The synchronisation of behaviour does not appear to play a significant role in their segregation.

The activity budget theory was developed using research on temperate species and was based on the fact that females digest forage less efficiently and as a result feed for longer (Conradt, 1998; Ruckstuhl, 1998, Ruckstuhl & Neuhaus, 2000, 2002). Across our data sets, it appears that on average, male elephants are feeding for slightly longer than females. However, there is no clear evidence of a relationship which

would be a pre-cursor for the segregation of elephants on the basis of feeding. In bighorn sheep, males fed for 39% of the time and females 53% (Ruckstuhl, 1998). This is a difference that Ruckstuhl (1998) believes can lead to spatial and temporal segregation. However, the activity budget hypothesis has not proved to be a single unifying theory in sexual segregation for temperate ruminants. Mule deer (Bowyer & Kie, 2004), merino sheep (Michelena et al., 2004) and desert bighorn sheep (Mooring et al., 2003) did not exhibit significant differences in activity budgets or the synchrony of behaviour. It is therefore likely that if similar sized ruminants are not conforming to the same ecological theory, then the sexual segregation of elephant (large, hind gut fermenters) may also be driven by factors other than foraging time. For example, the discrepancy in drinking behaviour between male and female elephants appears relatively small and inconsequential in this study. However it may have much greater implications in large open systems with limited water availability. It is therefore conceivable that drinking may prove to be a more decisive factor in segregation of large water dependent herbivores than foraging time and this requires further investigation.

Conclusion

The activity synchrony of elephant was consistent for females and males throughout the three study sites and whilst seasonal effects were noted, they were similar for both of the sexes. The strong relationship between reduced activity (feeding and walking) around the middle of the day (12:00-14:00), indicates that environmental factors may play a greater role in dictating the diurnal activity patterns of elephants than body size and its associated physiological differences. The proportion of time spent feeding was not different between males and females and there is no indication that activity budgets would vary significantly enough to be a determining factor in driving sexual segregation. Female and male elephants feed and move throughout the day and it is likely that one or more of the other hypotheses (see introduction) will explain the pronounced sexual segregation that is observed in elephant.

CHAPTER 7
CONCLUSIONS

Why the African Elephant?

The broad aim of this study was to investigate the differences in the spatial and foraging ecology of a large sexually dimorphic herbivore. The African elephant was an ideal candidate, firstly it is a generalist feeder utilising hind gut fermentation as a method of microbial digestion (Owen-Smith, 1992), and this is in sharp contrast to the majority of research on sex differences in large herbivores which have focussed on temperate ruminants (Beier, 1987; Bon & Campan, 1996; Conradt, 1998a, 1998b, 1999; Ruckstuhl, 1998, 1999; Ruckstuhl & Neuhaus, 2001). Secondly, the megaherbivore status of the elephant and its significant role in ecosystem functioning and habitat structure neccesitates greater understanding with regard to their spatial and foraging ecology for effective management and conservation. This is especially relevant in the enclosed and spatially restricted populations of South Africa (Slotow & van Dyk, 2004). Thirdly, the elephant is one of the most sexually dimorphic species and therefore the resultant influence on spatial ecology and foraging behaviour should be marked, enabling hypotheses to be rigorously tested. Finally the elephant is a gregarious species, which forages in a clearly defined manner making quantifiable behavioural research possible.

There are a plethora of elephant related articles in the literature, however many of these have dealt with describing elephant behaviour, population dynamics and interactions with plants. Only a few studies have applied ecological theory to understanding elephant behaviour and its implications for management. This is due to the nature of their movements, extensive ranges and the difficulty and expense of collecting long term data sets on known individuals. In this study we applied the use of the latest technology (GPS and Satellite collars) in conjunction with intensive field data collected in five reserves to accurately record the movements and foraging behaviour of male and female elephants. This enabled hypotheses to be established and tested in a rigorous manner which would not be possible in an open system (e.g. Chobe National Park or the Serengeti). Prior to this study Stokke (1999) and Stokke & du Toit (2000, 2002) produced the only work to date on sexual differences in the foraging behaviour and habitat utilisation of the African elephant. Their research was focussed in a 3600 km^2 section of the Chobe National Park, Botswana, which is an extensive open system and as such has limitations with regard to behavioural research (Stokke & du Toit, 2000). Whereas the limited size of the reserves and their associated small elephant populations in this study, enabled repeat behavioural sampling to be carried out for known individuals. These data were then used to test theories of body size dimorphism and segregation.

It has often proved difficult to elucidate the effects of vegetation quality and abundance on ranging behaviour and habitat utilisation because of the high levels of water dependence demonstrated by elephants (Western, 1975; Owen-Smith, 1992; Stokke & du Toit, 2002). However, the reserves used in this research had abundant, evenly spaced water supplies, which led to the assumption that the availability of surface water was not limiting behavioural patterns. This allowed a unique insight into the movement behaviour and foraging decisions of male and female elephants on the basis of forage availability and quality.

Ranging Behaviour

Males and females responded to temporal and spatial heterogeneity at the annual and seasonal scale in a similar manner, by altering their range sizes. However, males exhibited greater flexibility and were able to adapt their ranging behaviour and movements at a variety of scales, whereas females only exhibited distinct ranging patterns at the seasonal scale. The correlation of male range size with rainfall was indicative of their response to environmental factors and their ability to focus ranging behaviour during resource scarcity and expand their ranges when food availability was abundant. This result all the more significant when considering that relationship held across all five reserves despite their different locations, size, land use history and herbivore populations.

Females were less responsive at the smaller scales due to their higher mass specific energy demands, social constraints of group living and their substantial investment in reproduction. These findings were in agreement with those from temperate studies where the males were found to be the more adaptive and less constrained of the two sexes (Corti & Shackleton, 2002). As with temperate ruminants, the reproductive strategies of male elephants have a significant role to play in their summer range use and association with other males. Whereas females have a year round strategy that focuses on protecting the family group, whilst maximizing nutritional return. Males are independent and are likely to take a riskier approach to ranging, foraging (Sukumar & Gadgil, 1988) and competing for females, if greater reproductive success or energetic gain results, however this can lead to greater mortality rates as recorded in the giraffe (Ginnet & Demment, 1997, 1999) and kudu (Owen-Smith, 1993). Both sexes exhibited pronounced habitat preference and avoidance which appears to be based on forage abundance and quality. This is especially pertinent in the winter season when low lying habitats which maintain foraging opportunities were targeted by both sexes (Shannon et al., in press). Removing surface water as a factor from our analyses revealed the strong role that vegetation availability plays in dictating the movements and foraging behaviour of elephants. This response is directly comparable with studies on other herbivore species (Mduma et al., 1999; Wilmhurst et al., 1999; Boyce et al., 2003) and despite their generalist

approach, elephants are making a series of decisions at different scales regarding their foraging and ranging behaviour. Heterogeneous use of habitats can lead to heterogeneous impacts on vegetation structure and this is particularly pertinent in the case of large male elephants that focus their ranging behaviour during the winter period in relatively defined ranges with limited daily displacement. This disparity in ranging behaviour between the sexes is as a direct consequence of body size dimorphism and is all the more evident in elephants due to their large size. Despite this, and the fact that they are hind gut fermneters, elephants are responding in a manner that has been predicted from studies carried out on temperate ruminants.

Foraging Behaviour

Male elephants meet their substantial energy demands with a significantly different approach than that pursued by females. Larger body size enables males to be less selective in their forage choice and more destructive in their behaviour. They ingest greater quantities of fibrous material as is evident from the size of branches targeted and the frequency with which this occurs. The smaller body size of females, coupled with their substantial reproductive investment requires them to feed with greater selectivity to meet their considerable mass specific energy demands. Females therefore, focus their foraging on the nutrient rich plant parts, target a greater variety of species and ingest a greater number of mouthfuls per unit time. These results give credence to the body size hypothesis and provide evidence as to the fact that feeding differences within species can be a result of physiological differences i.e. gut size. This has been a difficult aspect of sexual dimorphism to prove, due to the subtleties of foraging behaviour and food quality. However, the elephant provides an ideal test species due to the range of forage quality that is targeted and the methods by which this is done.

The body size relationship has been further strengthened by the similarity in feeding approach of young males and adult females. These individuals were of similar body size and both have relatively high energy requirements, due to the reproductive investment in females and growth in males. However, as body size dimorphism becomes more pronounced between the sexes, so too does foraging behaviour. This coincides with males leaving the family groups and ranging independently. Previously, the exclusion of young males from the family group was thought to be driven solely by the action of females (Moss & Poole, 1983; Owen-Smith, 1992) but it may also be as a result of differing foraging approaches and energy requirements.

Group living, coupled with the demands of young elephants also played a significant role in foraging behaviour, resulting in reduced feeding bout length and lost feeding opportunities for female elephants.

Whereas males feed independently and were only limited by their own energy demands. As with ranging behaviour this suggests that large sexually dimorphic males will exhibit greater flexibility with regard to their foraging approach and will be able to respond to resource scarcity with more ease than females. This has previously been highlighted during droughts, where young elephants and females experience greater mortality rates compared to males (Dudley et al., 2001; Moss, 2001).

The differences in foraging behaviour of male and female elephants are predicted to be significant enough to drive sexual segregation. This is due to the pronounced influence of body size dimorphism and distinct reproductive strategies. In fact, the variation in foraging approaches coupled with their physiological and morphological adaptations (e.g. male's larger gut size, lower metabolic rate and greater tolerance to fibre) would suggest that resources are likely to be partitioned to such an extent that competition between the sexes is of minor importance. This was evident in our study where males and females fed at similar heights, which would not be likely if females out-competed males, as suggested by the scramble competition hypothesis (Clutton-Brock & Guiness, 1987). Our findings concur with those of Stokke & du Toit (2000), suggesting that the behaviour of elephants in the confined reserves of this study is a reflection of natural behaviour and is not adversely affected by their restricted range. This is important for the application of these results to larger open systems which present much greater logistical barriers with regards to intensive large herbivore research.

Activity Budgets

Unlike a number of temperate ruminant species (e.g. big horn sheep, ibex, merino sheep and red deer), elephants did not exhibit significant differences in their activity budgets. In fact their patterns of behaviour were similar across the three distinct populations, with both sexes exhibiting similar responses across the seasons. Behavioural synchrony was also significantly correlated throughout the data, despite variation in drinking time, a result which was postulated to have a bigger effect on segregation in large open systems which have limited water supplies. This was highlighted in a study on elephant in the Chobe National Park (Stokke & du Toit, 2002). In temperate ruminants, many of which are grazers, increased feeding duration is often the only method by which to achieve greater nutritional intake rate and therefore foraging times are distinctly different between males and females. In elephant however, there are a diverse number of strategies that can be adopted to maximize energy intake, including selective browsing, bulk grazing in the summer period or by targeting particular plant parts and species. As such, it is unlikely that males and females will vary greatly in the time spent feeding, but more likely the foraging approach will vary. As for the synchronisation of behaviour this seems to be dictated by environmental factors (e.g. climate), which have been shown to have a significant influence on other large African

herbivores (Owen-Smith, 1998; du Toit & Yetman, 2005). It is also worth noting that the activity budget hypothesis was generated using temperate ruminants which have been shown to reduce their foraging time with increasing body size (Mysterud, 1998). African herbivores exhibit the opposite relationship, which is believed to be a result of complex plant architecture and spinescence (du Toit & Yetman, 2005). It is therefore likely that activity budgets in large African herbivores may well be influenced to a much greater extent by food quality, resource distribution and environmental factors than by differences between the sexes. This is especially pertinent in the elephant, due to its large size, hind gut fermentation and tolerance of low forage quality.

Habitat Segregation

Temperate ruminants have exhibited distinct patterns of habitat segregation on the basis of sex and it was initially anticipated that this would be evident in elephants, with males tolerating lower forage quality than females. Despite this, there was statistical concordance in the habitat preferences of males and females across all three reserves. Compared to ruminants the foraging approach of both male and female elephants is sufficiently broad that large physiognomic habitat types were not differentiated on the basis of sex. This suggests that the diversity at the habitat scale overrides any sex differences and as such is not causing segregation. It is more likely that the heterogeneous nature of the savanna ecosystem results in the formation of micro habitats, within the larger habitat types. These patches will exhibit significant variation in forage quantity and quality which males and females will respond to differently, unlike the broad nature of habitat selection.

Whilst competition between the sexes is not evident at the foraging scale, it may be a significant factor in the spatial separation of family groups during winter, as was exhibited by the lowest values of concordance in their habitat preferences. This may be as a direct result of competition for relatively high quality forage at a range of feeding heights. Males can exploit low quality forage and were unlikely to be affected in the same manner and this further indicates their flexibility to spatial and temporal heterogeneity, which is a result of body size and independent ranging behaviour. In summary, elephants exhibited pronounced ecological segregation on the basis of foraging behaviour, movements and sociality. The importance of testing different spatial scales was further highlighted in this study as elephants are not exhibiting habitat segregation like temperate ruminants but are instead resolving patch and plant scales (behaviour at the scale of the individual plant) with significant difference as shown in Chapter 5. It is interesting to surmise that generalists such as the elephant are more likely to exhibit segregation at the foraging scale, compared to temperate ruminants which appear to segregate on the basis of habitat differences.

Ecological Species

This study highlights that male and female elephants are behaving as ecologically distinct species due to their differences in body size and social organisation. These differences have been driven by sexual selection and the polygynous nature of their breeding system. Both sexes also exhibit marked resource partitioning on the basis of the disparity in their digestive efficiency and mass specific energy requirements, which results in them resolving their ranges and foraging opportunities at different scales. Despite this, the sexes do not exhibit variation in their habitat segregation or activity budgets, highlighting that although differences between individuals may only occur at particular spatial and temporal scales, it may still be sufficient to exceed the ecological variation commonly observed between two distinct species.

Implications for the Management and Conservation of African Elephants

Effective management of large herbivores and their ecosystems entails understanding the processes and interactions that occur between the species and its environment. This requires a scientific approach in both asking the questions and answering them. Sound ecological research is therefore of critical importance to conservation efforts as it provides direction and knowledge with which to make informed decisions. In this study I attempted to answer questions regarding the spatial ecology of the elephant which have direct relevance to their management. The differences observed in male and female elephants are pronounced and suggests that they need to be treated as separate ecological species on the basis of their vegetation impacts, resource requirements and responses to spatial and temporal heterogeneity. Male elephants have the potential to drive disproportionately large impacts in focussed areas due to their large size, limited daily displacement and sustained foraging bouts. Tree destruction is one of the major concerns regarding the management of elephants and this study highlights that male elephants are responsible for 80% of tree pushing events. The nature of vegetation use is driven by quality and abundance and will not be homogenous, during resource scarcity the ranging behaviour of male elephants has been shown to focus on relatively small areas and highly preferred habitats. This could lead to significant impacts but they will be spatially defined and not necessarily cause for concern. Female elephants by and large will adopt a more selective foraging approach and will require sufficient forage at the lower height classes for weaned calves. This presents the potential for resource competition both between elephants and other browsers during resource scarcity.

Elephants of both sexes are likely to exploit habitats in a similar manner due to their generalist foraging approach and therefore distinct differences in their foraging approach are only likely to be elucidated at the patch and plant scale (assessment on the basis of the individual plant). Knowledge of this behaviour

will aid in differentiating the impacts of female and male elephants and therefore enable sound management to be applied. Up until now, the management of elephant has been solely based on population size and the area of available range, little if any consideration is given to the population structure and the divergent effects of females and males which are acting as ecologically distinct species.

Future Work

This study has used sound ecological theory and principles to answer questions on the influence of sexual dimorphism in elephant. The elephant has been used as a test species rather than the main focus of the PhD, and further highlights the need to apply ecological theory rather than just answering specific descriptive questions about individual species, that are not in context of the bigger ecological picture. With regard to sexual differences in elephant, more work needs to be carried out on the limitations imposed by group living and the influence of young elephants on the foraging efficiency of adult females. This study also attempted to elucidate the influence of scale on behaviour and has produced some interesting and unexpected results, most notably the lack of habitat segregation that was observed between elephant. Future studies need to investigate the patch scale which is in between that of the habitat and the individual plant, to establish if significant differences occur in resolution at this scale. The determinants of patch distinction may well be different between male and female elephants due to their divergent strategies. On this basis large physiognomic habitats may actually be divided up into distinct micro habitats that will favour different foraging approaches by different sexes. The diet switching of elephants from grass to browse and the chemical analysis of the forage selected by females and males would also provide another scale of resolution with regard to the nutrients being selected for and the relative quality of their diets. Likewise, faecal analysis will provide further information with regard to the efficiency of digestion and diet selection.

Determining the competition within groups and between family groups may also allow greater understanding with regard to the association of herds during resource abundance and the resultant limitations on group size in the winter periods when resources are scarce. Female investment of resources and energy in reproduction is significant and therefore their strategy of protecting the herd is a priority, to what extent is this perceived to influence foraging behaviour? In essence, assessing the predation risk hypothesis for elephants. Finally, sexual dimorphism and the resultant segregation are common amongst many African large herbivores and it is therefore important to test theories on sex differences in a range of species, with particular focus on ruminants that can be directly compared to their temperate counterparts.

REFERENCES

Abouheif, E. & Fairbairn, D.J. (1997) A comparative analysis of allometry for sexual size dimorphism: Assessing Rensch's rule. *The American Naturalist*, **149,** 540-562.

Acocks, J.P.H. (1988) *Veld Types of South Africa.* Third Edition. Botanical Research Institute, Pretoria.

Alonzo, S.H. & Warner, R.R. (2000) Female choice, conflict between the sexes and the evolution of male alternative reproductive behaviours. *Evolutionary Ecology Research*, **2,** 149-170.

Amarasekare, P. & Nisbet, R.M. (2001) Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *The American Naturalist*, **158**, 572-584.

Babassa, D. (2000) Habitat selection by elephants in Bwindi Impenetrable National Park, south western Uganda. *African Journal of Ecology*, **38**, 116-122.

Ball, J.P., Danell, K. & Sunesson, P. (2000) Response of a herbivore community to increased food quality and quantity: an experiment with nitrogen fertilizer in a boreal forest. *Journal of Applied Ecology*, **37,** 247-255.

Barboza, P.S. & Bowyer, R.T. (2000) Sexual segregation in dimorphic deer: A new gastrocentric hypothesis. *Journal of Mammalogy*, **81,** 473-489.

Barnes, R.F.W. (1979) *Elephant ecology in Ruaha National Park, Tanzania.* PhD Thesis, Cambridge University UK.

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology Individuals, populations and communities, third edition.* Blackwell Sciences, Oxford.

Beier, P. (1987) Sex differences in quality of white-tailed deer diets. *Journal of Mammalogy*, **68,** 323-329.

Bell, R.H.V. (1971) A grazing ecosystem in the Serengeti. *Scientific American*, **225**, 86-93.

Bell, R.H.V. (1986) *Soil-plant herbivore interactions*. In: Bell R.H.V. & McShane-Caluzi, E. (eds) Conservation and wildlife management in Africa 109-130. US Peace Corps, Washington DC.

Belovsky, G.E. (1984) Herbivore optimal foraging: a comparative test of three models. *American Naturalist*, **124,** 97-115.

Belsky, A.J. (1984) Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania, *African Journal of Ecology*, **22,** 271-279.

Blanchard, P. (2005) On lactation and rumination in bighorn ewes *(Ovis Canadensis). Journal of Zoology, London*, **265,** 107-112.

Blanckenhorn, W.U. (2000) The evolution of body size: what keeps organisms small? *Quarterly Review of Biology*, **75,** 385-407.

Bleich, V.C., Bowyer, R.T. & Wehausen, J.D. (1997) Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs*, **134,** 1-50.

Bon, R. & Campan, R. (1996) Unexplained sexual segregation in polygamous ungulates: a defense of an ontogenetic approach. *Behavioral Processes*, **38**, 131-154.

Bon, R., Rideau, C. Villaret, J. & Joachim, J. (2001) Segregation is not only a matter of sex in Alpine ibex *Capra ibex ibex*. *Animal Behaviour,* **62,** 495-504.

Bond, W.J. & Lofell, D. (2001) Introduction of giraffe changes acacia distribution in a South African savanna. African Journal of Ecology, **39**, 286-294.

Bonenfant, C., Loe, E. L., Mysterud, A., Langvatn, R. Stenseth, N., Gaillard, J. & Klein, F. (2004) Multiple causes of sexual segregation in European red deer: enlightenments from varying breeding phenology at high and low altitude. *Proceedings of the Royal Society, London,* **271**, 883-892.

Bowyer, R.T. (2004) Sexual segregation in ruminants: Definitions, hypotheses and implications for conservation and management. *Journal of Mammalogy*, 85, 1039-1052.

Bowyer, R.T. & Kie, J.G. (2004) Effects of foraging activity on sexual segregation in mule deer. *Journal of Mammalogy*, **85**, 498-504.

Boyce, M.S., Mao, J.S., Merrill, E.H. & Fortin, D. (2003). Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* **4,** 421-431.

Branch, G.M. (1985) *Competition: Its role in ecology and evolution in intertidal communities*. In: Vrba, E.S., ed. Species and speciation. 97-104, Transvaal Museum Monograph No. 4. Transvaal Museusm

Brown J.S. (2000) Chapter 10. *Foraging ecology of animals in response to heterogeneous environments*. In: Hutchings J. & Stewart A. (eds) The ecological consequences of environmental heterogeneity 181-214.

Calder, W.A. (1984) *Size function and life history*. Cambridge, Harvard University Press.

Carbone, C., Collishaw, G., Isaac, N.J.B. & Rowcliffe, J.M. (2005) How far do animals go? Determinants of day range in mammals. *The American Naturalist*, **165,** 290-297.

Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215-244.

Chamberlin, M.J., Leopold, B.D. & Conner, L.M. (2003) Space use, movements and habitat selection of adult bobcats (*Lynx rufus)* in central Mississippi. *American Midland Naturalist*. **149**, 395-405.

Charif, R.A., Ramey, R.R., Langbauer, W.R., Payne, K.B., Martin, R.B. & Brown, L.M. (2005) Spatial relationships and matrilineal kinship in African savanna elephant (*Loxodonta Africana*) clans. *Behavioural Ecology and Sociobiology*, **57**, 327-338.

Chase, M. (2003) Ecology, population structure and movements of elephant populations in northern Botswana. *Unpublished Conservation International Report.*

Choat, J.H. & Clements, K.D. (1998). Vertebrate herbivores in marine and terrestrial environments: A nutritional ecology perspective. *Annual Review of Ecological Systematics*, **29,** 375-403.

Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C. Rossner, G.E. & Streich, W.J. (2003) The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut and adaptations of hindgut fermenters. *Oceologica*, **136**, 14-27.

Clutton-Brock, T.H. & Harvey, P.H. (1978) Mammals, resources and reproductive strategies. *Nature*, **273**, 191-195.

Clutton-Brock, T.H. & Guiness, F.E. (1987) Sexual segregation and density related changes in habitat use in male and female deer (*Cervus elephus*) . *Journal of Zoology, London*, **211**, 275-289.

Coe, M.J., Cumming, D.H. & Philipson, J. (1976) Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, **22**, 341-354.

Conradt, L. (1998a) Measuring the degree of sexual segregation in group-living animals. *Journal of Animal Ecology*, **67**, 217-226.

Conradt, L. (1998b) Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proceedings of the Royal Society of London, Series B-Biological Sciences*, **265**, 1359-1363.

Conradt, L. (1999) Social segregation is not a consequence of habitat segregation in red deer and feral soay sheep. *Animal Behaviour*, **57**, 1151-1157.

Conradt, L., Clutton-Brock, T.H. & Guiness, F.E. (2000) Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Animal Behaviour*, **59**, 1049-1060.

Conradt, L. & Roper, T. J. (2000) Activity synchrony and social cohesion: a fission fusion model. *Proceedings of the Royal Society of London, Series B*, **267**, 2213-2218.

Conradt, L. & Roper, T. J. (2003) Group decision-making in animals. *Nature*, **421**, 155-158.

Cooper, S. M. & Owen-Smith, N. (1986) Effects of plant spinescence on large mammalian herbivores. *Oecologia*, **68**, 446-455.

Corti, P.C. & Shackleton, D.M. (2002) Relationship between predation-risk factors and sexual segregation in Dall's sheep (*Ovis dalli dalli*). *Canadian Journal of Zoology*, **80**, 2108-2117.

Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. (2005) Effective leadership and decision making in animal groups on the move. Nature, **433**, 513-516.

Cumming, D.H. Fenton,M.B., Rautenbauch,I.L., Taylor,R.D., Cumming,G.S., Cumming,M.S., Dunlop,J.M., Ford,A.G., Hovorka,M.D., Johnston,D.S., Kalcounis,M., Mahlangu,Z. & Portfors,V.R. (1997) Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science*, **93**, 231-236.

Darwin, C. (1871) The *descent of man, and selection in relation to sex*. D. Appleton, New York.

De Boer, W.F., Ntumi, C.P., Correia, A.U., Mafuca, J.M. (2000) Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology*, **38**, 188-201.

De Solla, S.R, Bonduriansky, R..& Brooks, R.J. (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology* **68**, 221-234.

De Villiers, P.A. & Kok, O.B. (1997) Home range, association and related aspects of elephants in the eastern Transvaal Lowveld. African *Journal of Ecology*, **35**, 224-236.

Demment, M.W. (1983) Feeding ecology and evolution of body size of baboons. *African Journal of Ecology*, **21**, 219-233.

Demment, M. W. (1985) Feeding ecology and the evolution of body size of baboons. *African Journal of Ecology*, **21**, 219-233.

Demment, M.W. & Van Soest, P.J. (1985) A nutritional explanation for body size patterns of ruminant and non-ruminant herbivores. *The American Naturalist*, **125,** 641-672.

Diamond, J. (1978) Niche shift and the rediscovery of interspecific competition. *American Scientist*, **66**, 322-331.

du Toit, J.T. (1990) Feeding height stratification among African browsing ruminants. *African Journal of Ecology*, **28**, 55-61.

du Toit, J.T. & Cumming, D.H.M. (1999) Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation*, **8,** 1643-1661.

du Toit, J.T. & Yetman, C.A. (2005) Effects of body size on the diurnal activity budgets of African browsing ruminants. *Oecologia,* **143**, 317-325.

Dublin, H.T., Sinclair, A.R.E., Boutin, S., Anderson, E., Jago, M. & Arcese, P. (1990a) Does competition regulate ungulate populations? Further evidence from Serengeti, Tanzania. *Oecologia*, **82**, 283-288.

Dublin, H.T., Sinclair, A.R.E. & McGlade, J. (1990b) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology*, **59**, 1147-1164.

Dudley, J.P., Criag, G. C., Gibson, D. St. C., Haynes, G. & Klimowicz, J. (2001) Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology*, **39**, 187-194.

Dunbar, R.I.M., Hannah-Stewart, L. & Dunbar, P. (2002) Forage quality and the cost of lactation for female gelda baboons. *Animal Behaviour*, **64**, 801-805.

East, R. (1984) Rainfall, Soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*, **22,** 245-270.

Etzenhouser, M.J., Owens, M.K., Spalinger, D.E. & Murden, S.B. (1998) Foraging behaviour of browsing ruminants in a heterogeneous landscape. *Landscape ecology*, **13**, 55-64.

Farnsworth, K.D., Focardi, S. & Beecham, J.A. (2002) Grassland-herbivore interactions: How do grazers coexist? *The American Naturalist*, **159**, 24-39.

Forsyth, D.M. (2000) Habitat selection and coexistence of the Alpine chamois (*Rupicapra rupicapra*) and Himalayan tahr (*Hemitragus jemlahicus*) in the eastern Souther Alps, New Zealand. *Journal of Zoology, London*, **252**, 215-225.

Frid, A. (1994) Observations on habitat use and social organization of huemul *Hippocamelus bisulcus* coastal population in Chile. *Biological Conservation*, **67**, 13-19.

Fritz, H. & Duncan, P. (1994) On the carrying capacity for large ungulates of African savanna ecosystems. Proceedings of the Royal Society of London Series B-Biological Sciences, **256**, 77-82.

Fritz, H. & De Garine-Whichatitsky, M. (1996) Foraging in a social antelope: Effects of group size on foraging choices and resource perception in impala. *Journal of Animal Ecology*, **65**, 736-742.

Fritz, H., Duncan, P., Gordon, I.J. & Illius A. W. (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. *Oceologica,* **131,** 620-625.

Fryxell, J.M. & Sinclair, A.R.E. (1988) Causes and consequences of migration by large herbivores. *Trends in Ecology and Evolution.* **3,** 237-241.

Fryxell, J.M., Wilmshurst, J.F. & Sinclair, R.E. (2004) Predictive models of movement by Serengeti grazers. *Ecology*, **85,** 2429-2435.

Galanti, V., Tosi, G, Rossi, R. & Foley C. (2000) The use of GPS radio collars to track elephants (*Loxodonta Africana*) in the Tarangire National Park (Tanzania) *Hystrix,* **11,** 27-37.

Garaï, M.E., Slotow, R., Carr, R.D. & Reilly, B. (2004) Elephant reintroductions to small fenced reserves in South Africa. *Pachyderm*, **37**, 28-36.

Ginnett, T.F. & Demment, M.W. (1997) Sex differences in giraffe foraging behaviour at two spatial scales. *Ocelogica* **110,** 291-300.

Ginnet, T.F & Demment, M.W. (1999) Sexual segregation by Masai giraffes at two spatial scales. *African Journal of Ecology*, **37**, 93-106.

Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. (2004) The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, **41,** 1021-1031.

Gross, J.E., Zank, C., Hobbs, N.T., Spalinger, D.E. (1995) Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern. *Landscape Ecology*, **10**, 209-217.

Guy, P.R. (1976) The feeding behaviour of elephants (Loxodonta Africana) in the Sengwa area Rhodesia. *South African Journal of Wildlife Research*, **6**, 55-63.

Hall-Martin, A.J. (1987) Role of musth in the reproductive strategy of the African elephant (*Loxodonta Africana*) *South African Journal of Science* **83**, 615-620.

Henriksen, S., Aanes, R., Saether, B., Ringsby, T. Tufto, J. (2003) Does availability of resources influence grazing strategies in female Svalbard reindeer? *Rangifer,* **23**, 25-37.

Hoare, R.E. (1999) Determinants of human-elephant conflict in a land-use mosaic. *Journal of Applied Ecology*, 36, 689-700.

Hoare, R.E. & du Toit, J.T. (1999) Coexistence between people and elephants in African savannas. *Conservation Biology*, **13**, 633-639.

Hobbs, N.T. (1996) Modification of ecosystems by ungulates. *Journal of Wildlife Management*, **60**, 695-713.

Hooge, P.N., & Eichenlaub, B. (1997) Animal movement extension to Arcview. Ver 1.1 Alaska Biological Science Center, U.S Geological Survey, Anchorage, USA.

Houston, D. & Shine, R. (1993) Sexual dimorphism and niche divergence: feeding habits of the *Arafura filesnake*. *Journal of Animal Ecology*, **62**, 737-748.

Hubbs, A.H. & Boonstra, R. (1998) Effects of food and predators on the home-range sizes of Arctic ground squirrels (*Spermophilus parryii*). *Canadian Journal of Zoology*, **76**, 592-596.

Huisman, J. & Olff, H. (1998) Competition and facilitation in multispecies plant-herbivore systems of productive environments. *Ecology Letters*, **1**, 25-29.

Hunter, L.T.B. (1998) *The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, KwaZulu-Natal, South Africa.* PhD Thesis, University of Pretoria, 205pp.

Illius, A. W. & O'Connor, T.G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos*, **89**, 283–294.

Jachmann, H. (1983) Spatial organisation of the Kusungu elephant. *Bijdragen tot de Dierkunde*, **53**, 179-186.

Jarman, P.J. (1972) Seasonal distribution of large mammal populations in the unflooded Middle Zambezi Valley. *Journal of Applied Ecology*, 9, 283-299.

Jarman, P.J. (1974) The social organization of antelope in relation to their ecology. *Behaviour*, **48**, 215-267.

Jarman, P. (1983) Mating systems and sexual dimorphism in large, terrestrial, mammalian herbivored. *Biological Reviews,* **58**, 485-520.

Jenkins, K.J. & Wright, R.G. (1988) Resource partitioning and competition among cervids in the northern Rocky Mountains. *Journal of Applied Ecology*, **25**, 11-24.

Jeschke, J.M. & Tollrain, R. (2005) Predicting herbivore feeding times. *Ethology,* **111**, 187-206.

Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004) The scaling of animal space use. *Science* **306**, 266-268.

Johnson, C.F., Cowling, R.M. & Philipson, P.B. (1999) The flora of the Addo Elephant National Park, South Africa: Are threatened species vulnerable to elephant damage? *Biodiversity and Conservation*, **8**, 1447-1456.

Kie, J.G. & Bower, R.T. (1999) Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection and dietary niche. *Journal of Mammalogy*, **80**, 1004-1020.

Krebs, J.R. & Davies, N.B. (1993) *An introduction to behavioural ecology, third edition.* Blackwell Science Ltd, Oxford.

Kruuk, L.E.B., Slate, J., Pemberton, J.M., Brotherstone, S., Guiness, F. & Clutton-Brock, T. (2002) Antler size in red deer: Heritability and selection but no evolution. *Evolution,* **56**, 1683-1695.

Laws, R.M. (1970) Elephants as agents of habitats and landscape change in East Africa. *Oikos*, **21,** 1-15.

Laws, R.M., Parker, I.S.C. & Johnstone, R.C.B. (1975) *Elephants and their habitats. The ecology of elephants in Northern Bunyoro, Uganda.* Oxford, Clarendon Press.

Le Blanc, M., Festa-Bianchet, M. & Jorgenson, J.T. (2001) Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. *Canadian Journal of Zoology*, **79,** 1661-1670.

Le Pendu, Y., Guilhem, C., Briedermann, L., Maublanc, M. & Gerard, J. (2000) Interactions and associations between age and sex classes in mouflon sheep (*Ovis gmelini*). *Behavioural Processes,* **52**, 97-107.

Leader-Williams, N., Smith, R.J. & Walpole, M.J. (2001) Elephant hunting and conservation. *Science*, **293**, 2203-2204.

Lee, P.C. & Moss, C.J. (1995) Satural growth in known-age African elephants (*Loxodonta Africana*). *Journal of Zoology, London*, **236**, 29-41.

Leuthold, W. (1977)Spatial organisation and strategy of habitat utilization of elephants in Tsavo National Park, Kenya *Z. säugetierkunde* **42,** 358-379.

Lindeque, M. & Lindeque, P.M. (1991) Satellite tracking of elephants in northwestern Namibia. *African Journal of Ecology*, 29, 196-206.

Loison, A., Gaillard, J., Pelabon, C. & Yoccoz, N.G. (1999) What factors shape sexual size dimorphism in ungulates? *Evolutionary Ecology Research*, **1**, 611-633.

Lombard, A.T., Johnson, C.F., Cowling, R.M. & Pressey, R.L. (2001) Protecting plants from elephants: Botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biological Conservation*, **102**, 191-203.

Low, A.B. & A.G. Rebelo (eds) (1996) *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs and Tourism, Pretoria.

Main, M.B., Weckerly, F.W. & Bleich, V.C. (1996) Sexual segregation in ungulates: new directions for research. Journal of Mammalogy, **77,** 449-461.

Mapaure, I.N. & Campbell, B.M. (2002) Changes in miombo woodland cover in and around Sengwa Wildlife Research Area, Zimbabwe, in relation to elephants and fire. *African Journal of Ecology*, **40,** 212-219.

Marell, A., Ball, J.P. & Hofgaard, A. (2002) Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks and Levy flights. *Canadian Journal of Zoology*, **80,** 854-865.

Marshal, J.P., Krausman, P.R. & Bleich, V.C. (2005) Dynamics of mule deer forage in the Sonoran Desert. *Journal of Arid Environments*, **60**, 593-609.

Matthews, W. (2005) Large herbivore population estimates for Tembe Elephant Park. KwaZulu-Natal Nature Conservation Services unpublished report.

McComb, K., Moss, C., Durant, S.M., Baker, L. & Sayialel, S. 2001. Social knowledge in African elephants. *Science,* **292,** 491-494.

McElligott, A.G., Gammell, M.P., Harty, H.C., Paini, D.R., Murphy, D.T., Walsh, J.T. & Hayden, T. J. (2001) Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behavioural Ecology and Sociobiology*, **49,** 266-272.

McNaughton, S.J. & Georgiadis, N.J. (1986) Ecology of African grazing and browsing mammals. *Annual Review of Ecology,Evolution and Systematics*, **17**, 39-65.

Mduma, S.A.R., Sinclair, A.R.E. & Hilborn, R. (1999) Food regulates the Serengeti wildebeest: A 40 year record. *Journal of Animal Ecology*, **68**, 1101-1122.

Meissner, H.H., Spreeth, E.B., De Villiers, P.A., Pieterson, E., Hugo, T.A & Terblanche, B.F. (1990) Quality of food and voluntary intake by elephant as measured by lignin index. *South African Journal of Wildlife Research*, **20**, 104-110.

Merz, G. (1986) Counting elephants (*Loxodonta africana cyclotis*) in tropical rain forest with particular reference to the Tai National Park, Ivory Coast. *African Journal of Ecology*, 24, 61-68.

Michelena, P., Bouquet, P.M., Dissac, A., Fourcassie, V., Lauga, J., Gerard, J. & Bon, R. (2004) An experimental test of hypotheses explaining social segregation in dimorphic ungulates. *Animal Behaviour*, **68,** 1371-1380.

Møller, A.P. (1991) Concordance of mammalian ejaculate features. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **246,** 237-241.

Moolman, H.J. & Cowling, R.M. (1994) The impact of elephant and goat grazing on the endemic flora of South African succulent thicket. *Biological Conservation*, **68**, 53-61.

Mooring, M.S., Fitzpatrick, T.A., Benjamin, J.E., Fraser, I.C., Nishihira, T.A., Reisig, D.D. & Rominger, E.M. 2003. Sexual segregation in desert bighorn sheep (*Ovis Canadensis mexicana*). *Behaviour*, **140**, 183-207.

Morales, J.M. & Ellner, S.P. (2002) Scaling up animal movements in heterogenous landscapes: the importance of behaviour. *Ecology*, **83**, 2240-2247.

Moss, C.J. (2001) The population demography of an African elephant (Loxodonta Africana) population in Amboseli, Kenya. *Journal of Zoology, London*, **255,** 145-156.

Moss, C.J. & Poole, J.H. (1983) *Relationships and social structure of African elephants*. In: R.A Hinde (ed) Primate social relations.315-325 Blackwell scientific publications. Oxford.

Murray, M. & Brown, D. (1993) Niche separation of grazing ungulates in the Serengeti: an experimental test. *Journal of Animal Ecology*, **62,** 380-389.

Mysterud, A. (1998) The relative roles of body size and feeding type on activity time of temperate ruminants. *Oceologica,* **113,** 442-446.

Mysterud, A. (2000) The relationship between ecological segregation and sexual body size dimorphism in large herbivores. *Oecologia*, **124,** 40-54.

Mysterud, A., Langvatn, R., Yoccoz, N.G. & Stenseth, N.C. (2001a) Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology*, **70**, 915-923.

Mysterud, A., Javier Pérez-Barbería, F. & I.J. Gordon (2001b) The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oceologica*, **127,** 30-39.

Mysterud, A., Langvatn, R. & Stenseth, N.C. (2004) Patterns of reproductive effort in male ungulates. *Journal of Zoology, London*, 264, 209-215.

Nellemann, C., Moe, S.R. & Rutina, L.P. (2002) Links between terrain characteristics and forage patterns of elephants (*Loxodonta africana*) in northern Botswana. Journal of Tropical Ecology, **18**, 835-844.

Neuhaus, P. & Ruckstuhl, K.E. (2004) Can the activity budget hypothesis explain sexual segregation in desert big horn sheep? *Behaviour,* **141,** 513-520.

Norton-Griffiths, M. (1975) The numbers and distribution of large mammals in Ruaha National Park, Tanzania. *East African Wildlife Journal*, 13, 121-140.

Ntumi, C.P. (2003) Space and habitat use by elephants (*Loxodonta Africana*) in the Maputo Elephant Reserve, Mozambique. M.Sc. Thesis, University of Pretoria, Pretoria, South Africa.

Olff, H., Ritchie & Prins, H.H.T. (2002) Global environmental controls of diversity in large herbivores. *Nature,* **415**, 901-904.

Osborn, F.V. (2003) Seasonal influence of rainfall and crops on home-range expansion by bull elephants. *Pachyderm*, **35**, 53-59.

Osborn, F.V. (2004) The concept of home range in relation to elephants in Africa. *Pachyderm*, **37**, 37-44.

Osborn, F.V & Parker, G.E. (2003) Linking two elephant refuges with a corridor in the communal lands of Zimbabwe. *African Journal of Ecology*, **41**, 68-74.

Ottichilo, W.K. (1986) Population estimates and distribution patterns of elephants in the Tsavo ecosystem, Kenya in 1980. *African Journal of Ecology*, **24**, 53-57.

Owen-Smith, N., (1990) Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *Journal of Animal Ecology*, **59**, 893–913.

Owen-Smith, R. N. (1992) *Megaherbivores: The influence of very large body size on ecology.* Cambridge University Press, Cambridge, UK.

Owen-Smith, R.N. (1993) Comparative mortality rates of male and female kudus: the costs of sexual size dimorphisms. *Journal of Animal Ecology*, **62**, 428-440.

Owen-Smith, R.N. (1994) Foraging responses of kudus to seasonal changes in food resources: Elasticity in constraints. *Ecology*, **75**, 1050-1062.

Owen-Smith, R.N. (1996) Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, **26**, 107-112.

Owen-Smith, N. (1998) How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). *Journal of Zoology, London*, **246**, 183-192.

Pelletier, F. & Festa-Bianchet, M. (2004) Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis Canadensis. Behavioral Ecology and Sociobiology,* **56**, 546-551.

Pérez-Barbería, F.J. & Gordon I.J. (1998) The influence of sexual dimorphism in body size and mouth morphology on diet selection and sexual segregation in cervids. *Acta Veterinaria Hungarica,* **46,** 357-367.

Pérez-Barbería, F.J., Robertson, E. & Gordon, I.J. (2005) Are social factors sufficient to explain sexual segregation in ungulates? *Animal Behaviour,* **69**, 827-834.

Peters, R.H. (1983). The Ecological Implications of Body Size. Cambridge: Cambridge University Press.

Pickett, S.T.A. & Cadenasso, M.L. (1995) Landscape ecology: Spatial heterogeneity in ecological systems. *Science* **269,** 331-334.

Poole, J.H. (1987) Rutting behaviour in African elephants: The phenomenon of musth. *Behaviour,* **102,** 283-316.

Poole, J.H. (1989) Announcing intent: the aggressive state of musth in African elephants. *Animal Behaviour*, **37**, 140-152.

Poole, J.H. (1994) Chapter 14. Sex *differences in the behaviour of African elephants.* In: Short, R.V. & Balaban, E. (Eds). The difference between the sexes 331-346. Cambridge University Press, UK.

Poole, J.H. & Moss, C.J. (1981) Musth in the African elephant, *Loxodonta africana. Nature*, **292**, 830-831.

Post, E. & Stenseth, N.C. (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology*, **80,** 1322-1399.

Prins, H.H.T. & Loth, P.E. (1988) Rainfall patterns as a background to plant phenology in northern Tanzania. *Journal of Biogeography*, **15,** 451-46.

Prins, H.T. & Van der Jeugd, H.P. (1993) Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology*, **81,** 305-314.

Putman, R.J., Culpin, S. & Thirgood, S.J. (1993) Dietary differences between male and female fallow deer in sympatry and in allopatry. *Journal of Zoology, London*, **229**, 267-275.

Ramsey, F.L. & Usner, D. (2003) Persistence and heterogeneity in habitat selection studies using radio telemetry. *Biometrics*, **59**, 332-340.

Rands, S.A., Colishaw, G., Pettifor, R.A., Rowcliffe, J.M. & Johnson, R.A. (2003) Spontaneous emergence of leaders and followers in foraging pairs. *Nature*, **423**, 432-434.

Redfern, J.V., Grant, R., Biggs, H. & Getz, W.M. (2003) Surface water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, **84**, 2092-2107.

Rosenzweig, L. M. (1981) A theory of habitat selection. *Ecology*, **62**, 327-335.

Rouault, M. & Richard, Y. (2003) Intensity and spatial extension of drought in South Africa at different time scales. *Water South Africa*, **29,** 489-500.

Ruckstuhl, K.E. (1998) Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour,* **55,** 99-106.

Ruckstuhl, K.E. (1999) To synchronise or not to synchronise: A dilemma for young big horn males? *Behaviour*, **136,** 805-818.

Ruckstuhl, K.E. & Neuhaus, P. (2000) Sexual segregation in ungulates: a new approach. *Behaviour*, **137,** 361-377.

Ruckstuhl, K.E. & Neuhaus, P. (2001) Behavioural synchrony in Ibex groups: Effects of age, sex and habitat. *Behaviour,* **138**, 1033-1046.

Ruckstuhl, K.E. & Kokko, H. (2002) Modelling sexual segregation in ungulates: effects of group size, activity budgets and synchrony. *Animal Behaviour*, **64,** 909-914.

Ruckstuhl, K.E. & Neuhaus, P. (2002) Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Review*, **77**, 77-96.

Ruckstuhl, K.E., Festa-Bianchet, M. & Jorgenson, J.T. (2003) Bite rates in rocky mountain bighorn sheep (*Ovis Canadensis*): effects of season, age sex and reproductive status. *Behavioural Ecological Sociobiology,* **54,** 167-173.

Ruggiero, R.G. (1991) Opportunistic predation on elephant calves. *African Journal of Ecology*, **29**, 86-89.

Schimel, D., Stillwell, M.A & Woodmansee R.G. (1985) Biogeochemistry of C, N and P in a soil Catena of the shortgrass steppe. *Ecology*, **66**, 276-282.

Schultze, R.E. (1982) Agrohydrology and agroclimatology of Natal. Agricultural catchments research unit. *Report No.14.* University of Natal, Pietermaritzburg.

Schoener, T.W. (1974) The compression hypothesis and temporal resource partitioning. *Proceedings of the National Academy of Sciences of the United States of America,* **71,** 4169-4172.

Schoener, T.W. (1982) The controversy over interspecific competition. *American Scientist*, **70**, 586-595.

Schoener, T.W. (1983) Field experiments on interspecific competition. *American Naturalist*, **122**, 240-285

Seagle, S.W. & McNaughton, S.J. (1992) Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. *Landscape Ecology*, 7, 229-241.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987) Large herbivore foraging and ecological hierarchies. *Bioscience,* **37,** 789-799.

Shannon, G., Page, B., Duffy, K. & Slotow, R. (In Press) African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology.*

Shine, R. (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology*, **64**, 419-461.

Shipley, L. (1999) Grazers and browsers: How digestive morphology affects diet selection. In: Launchbaugh, K.L., Sanders, K.D. & Mosley, J.C. Grazing behaviour of livestock and wildlife 20-27.

Siegel, S. & Castellan, N.J. (1988) *Nonparametric statistics for the behavioural sciences, second edition.* McGraw-Hill International Editions, New York.

Sinclair, A.R.E. (1985) Does interspecific competition shape the African ungulate community. *Journal of Animal Ecology*, **54**, 899-918.

Sitati, N.W., Walpole, M.J., Smith, R.J. & Leader-William, N. (2003) Predicting spatial aspects of human elephant conflict. *Journal of Applied Ecology*, **40**, 667-677.

Skarpe, C., Bergström, R., Bråten, A-L. & Danell, K. (2000) Browsing in a heterogenuos savanna *Ecography* **23**: 632-640.

Slotow, R. & van Dyk, G. (2001) Role of delinquent young 'orphan' male elephants in high mortality of white rhinoceros in Pilansberg National Park, South Africa. *Koedoe*, **44**, 85-94.

Slotow, R. & van Dyk, G. (2002) Ranging of older male elephants introduced to an existing small population without older males: Pilanesberg National Park. In: *Proceedings of a workshop on elephant research held at the Knysna Elephant Park, 9-11th May, 2002 (EMOA Workshop Proceedings*), Compiler Marion E. Garai, pp 16-20. Elephant Management and Owners Association, Vaalwater.

Slotow, R. & van Dyk,, G. (2004) Ranging of older male elephants introduced to an existing small population without older males: Pilansberg National Park. *Koedoe*, **47**, 91-104.

Slotow, R., van Dyk, G., Poole, J., Page, B. & Klocke, A. (2000) Older bull elephants control young males. *Nature*, **408**, 425-426.

Sommerlatte, M.W.C. (1976) *A survey of elephant populations in north-eastern Botswana.* Report to the Botswana Department, National Parks, and Tourism, Gabarone, Botswana.

Spinage, C.A. (1994) *Elephants*. T and AD Poyser ltd, UK.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging theory*. Princeton University Press, Princeton, New Jersey. USA.

Stokke, Stokke, S. (1999) Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. *Canadian Journal of Zoology* **77**, 1723-1732.

Stokke, S. & du Toit, J. (2000) Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography*, **23,** 70-80.

Stokke, S. & du Toit, J. (2002) Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology*, **40,** 360-371.

Sukumar, R. & Gadgil, M. (1988) Male-female differences in foraging on crops by Asian elephants. *Animal Behaviour,* **36**, 1233-1235.

Swihart, R.K & Slade, N.A. (1985) Testing for independence of observations in animal movements. *Ecology*, **66**, 1176-1184.

Swihart, R.K., Slade, N.A. & Bergstrom, B.J. (1988) Relating body size to the rate of home range use in mammals. *Ecology*, **69**, 393-399.

Tedonkeng Pamo, E. & Tchamba, M.N. (2001) Elephants and vegetation change in the Sahelo-Soudanian region of Cameroon. *Journal of Arid Environments*, **48**, 243-253.

Thouless, C.R. (1994) Conflict between humans and elephants on private land in Northern Kenya. *Oryx*, 28, 119-127.

Thouless, C.R. (1995). Long distance movements of elephants in Northern Kenya. *African Journal of Ecology*. 33: 321-334.

Thouless, C.R. (1996) Home range and social organisation of female elephants in northern Kenya. *African Journal of Ecology*, 34, 284-287.

Tufto, J., Andersen, R. & Linnell, J. (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *Journal of Animal Ecology,* 65, 715-724.

Twine, W. (2002) Feeding time budgets of selected African ruminant and non-ruminant grazers. *African Journal of Ecology,* **40**, 410-412.

Van de Koppel, J. & Prins, H.H.T. (1998) The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. *Journal of Tropical Ecology*, **14,** 565-576.

Van der Wal, R., Madan, N., van Lieshout, S., Dormann, C., Langvatn, R. & Albon, S.D. (2000) Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia*, **123,** 108-115.

Van Soest, P.J. (1996) Allometry and ecology of feeding behaviour and digestive capacity in herbivores: A review. *Zoo Biology*, **15**, 455-479.

Van Wyk, A.E. (1996) Biodiversity of the Maputuland centre. In: *The biodiversity of African plants*. 198-207. (eds.) L.J.G. Van der Maesen, X.M. Van der Burgt, J.M. Van Medenbach de Rooy. Kluwer Academic Publishers, Dordrecht.

Van Wyk, P. & Fairall, N. (1969) The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe*, **12**, 66-89.

Viljoen, P.J. (1988) The ecology of the desert-dwelling elephants *Loxodonta Africana* (Blumenbach, 1779) of western Damaraland and Kaokoland. D.Sc. (Wildlife Management), University of Pretoria, Pretoria, South Africa.

Viljoen, P.J. (1989) Habitat selection and preferred food plants of a desert dwelling elephant population in the northern Namib Desert. South West Africa/ Namibia. *African Journal of Ecology*, **27**, 227-240.

Vivas, H.J. & Saether, B. (1987) Interactions between an generalist herbivore, the moose *Alces alces* and its food resources: An experimental study of winter foraging behaviour in relation to browse availability. *Journal of Animal Ecology*, **56**, 509-520.

Ward, D. & Saltz, D. (1994) Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev desert. *Ecology*, **75**, 48-58.

Western, D. (1975) Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal*, **13**, 265-288.

Western, D. and Lindsay, W.K. (1984) Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology*, 22, 229-244.

White, M.A., Thornton, P.E. & Running, S.W. (1997) A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biochemical Cycles*, **11**, 217-234.

Whitehouse, A. M. & Schoeman, D.S. (2003) Ranging behaviour of elephants within a small fenced area in Addo Elephant National Park, South Africa. *African Zoology*, 38, 95-108.

Whyte, I.J. (2001) Conservation management of the Kruger national Park elephant population. DSc. University of Pretoria, Pretoria.

Williamson, B.R. (1975) Seasonal distribution of elephant in Wankie National Park. *Arnoldia*, **7**, 1-16.

Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. & Henschel, C.P. (1999) Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology*, **77**, 1223-1232.

Wiseman, R., Page, B.R. & O'Connor, T.G. (2004) Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South African Journal of Wildlife Research*, **34**, 25-37.

Wittermeyer, G., Douglas-Hamilton, I. & Getz, W.M. (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, **69**, 1357-1371.

Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164-168.

Yearsley, J.M. & Perez-Barberia, F.J. (2005) Does the activity budget hypothesis explain sexual segregation in ungulates? *Animal Behaviour*, **69**, 257-267.