

The ranging behaviour of a large sexually dimorphic herbivore in response to seasonal and annual environmental variation

GRAEME SHANNON,^{1*} BRUCE R. PAGE,¹ KEVIN J. DUFFY² AND ROB SLOTOW¹

¹*Amarula Elephant Research Programme, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville Campus, University of KwaZulu-Natal, Private Bag X54001, Durban 4000, South Africa (Email: shannongraeme@gmail.com), and* ²*Centre for Systems Research, Durban University of Technology, Durban, South Africa*

Abstract The allometric relationships of body size play a principle role in determining how large herbivores respond to the marked spatial and temporal heterogeneity of the savanna biome. Using location data collected over an 8-year period from five distinct study sites, we investigated the influence of environmental variation (using phenological and rainfall data) on the ranging behaviour of the African elephant (*Loxodonta africana*), a species that exhibits pronounced sexual dimorphism. Both sexes expanded their annual ranges during years of high rainfall and contracted their ranges during periods of resource scarcity, concurring with the hypothesis that abiotic factors dictate the distribution of large generalist herbivores at the landscape scale. However, female elephant did not exhibit the same consistent response to rainfall at the seasonal scale. Furthermore, male elephant demonstrated a reduction in their daily displacement distances during the dry winter season, and altered their movement rates on the basis of seasonal rainfall. These results suggest that male elephant are able to consistently adapt their movement behaviour according to forage quality and abundance. Smaller-bodied female elephant on the other hand, are unlikely to exhibit the same flexibility in their ranging behaviour because of their higher relative nutritional demands, lower tolerance to fibrous forage and the social and energetic constraints of group living with juveniles. Our study highlights the major role that body size and sociality plays in the decision making of sexually dimorphic herbivores. These differences can have important implications for effective conservation and management, particularly with regard to demographic (e.g. survival) and ecological (e.g. habitat use) factors.

Key words: elephant (*Loxodonta africana*), movement, plant phenology, rainfall, savanna.

INTRODUCTION

Large herbivores experience wide scale temporal fluctuations in forage availability and quality (Owen-Smith 1994; Illius & O'Connor 2000). This is particularly apparent in the savanna biome where primary productivity is determined by the two distinct seasons (wet summer and dry winter) and annual rainfall (McNaughton & Georgiadis 1986). Furthermore, there is pronounced spatial heterogeneity in resource distribution and quality from the landscape to the plant scale (Pickett & Cadenasso 1995; Skarpe *et al.* 2000).

In order to maximize nutritional return and adapt to variable forage availability and quality, herbivores make a series of hierarchical decisions that are nested across a range of spatial and temporal scales, from the selection of individual plant parts to seasonal movement patterns (Senft *et al.* 1987; Ward & Saltz 1994; Searle *et al.* 2005). Therefore, as plant biomass and

quality changes between seasons and years, an individual herbivore is predicted to adapt its ranging and foraging behaviour optimally (Stephens & Krebs 1986). Effective decision making becomes particularly important during periods of resource scarcity as poor strategies can lead to a reduction in individual fitness, resulting in lower reproductive output and even death (McNaughton & Georgiadis 1986; Mysterud *et al.* 2001a).

Body size is a key determinant in the effective decision making of large herbivores as it directly influences a range of physiological and behavioural processes, including metabolism (Demment & Van Soest 1985), movement (Jetz *et al.* 2004; Carbone *et al.* 2005), temperature regulation (Calder 1984) and reproduction (McElligott *et al.* 2001). Furthermore, as body size increases, the energy required per unit mass scales with a factor of 0.75M (M = body mass), because of greater muscle efficiency and lower heat loss (Kleiber 1975; Demment & Van Soest 1985). Larger bodied herbivores are therefore predicted to have lower relative energy demands (per kg) and are also able to tolerate lower quality diets because of their increased

*Corresponding author.

Accepted for publication September 2009

gut capacity and longer retention times (the Jarman Bell principle, Bell 1971; Jarman 1974). Ultimately, smaller-bodied species are predicted to have a relatively narrow dietary breadth, selecting rare, high quality feeding opportunities in comparison with large herbivores, which trade off quality for abundance (McNaughton & Georgiadis 1986).

As foraging and movement are inextricably linked, ranging behaviour is a key ecological correlate used to study the interactions between herbivores and their environment (Mårell *et al.* 2002; Fryxell *et al.* 2004). The geographical distribution (Hernández Fernández & Vrba 2005), home ranges (Harestad & Bunnell 1979; Mysterud *et al.* 2001b), and daily movement distances (Carbone *et al.* 2005) of terrestrial herbivores have all demonstrated a positive correlation with body size.

In this study, the ranging behaviours of male and female African elephant (*Loxodonta africana*) are compared across a range of spatial and temporal scales. Elephant exhibit distinct behavioural, social and physiological differences between the sexes (Poole 1994; Stokke & Toit 2000; Shannon *et al.* 2006a; Woolley *et al.* 2009). These characteristics, particularly the pronounced body size dimorphism (mature adult males are approximately twice the body weight of females) and distinct social organization – females and their young live in permanent family groups, while males (>15 years old) range independently or in loosely associated bachelor groups (Moss & Poole 1983) – make the elephant an ideal species to investigate the ranging responses of the sexes to environmental variation.

The hypotheses tested in this study were: (i) Large-bodied and generalist herbivores expand their ranges (seasonal and annual) during periods of resource abundance in order to maximize their nutritional intake, this is as a result of pursuing a strategy that seeks to optimize forage quantity over quality. (ii) Seasonal and annual environmental variation will affect the fine-scale movement behaviours (daily displacement and speed) of large herbivores as these reflect the feeding decisions at the plant, patch and habitat scale. (iii) Pronounced sexual dimorphism will result in larger bodied males demonstrating greater flexibility in movement and foraging behaviour compared with smaller bodied females and their young, because males exhibit social independence coupled with the allometric relationships associated with increased body size.

METHODS

Study sites

The five protected areas (PAs) that were chosen as study sites (Table 1) were located in South Africa and

Table 1. Site descriptions for the five protected areas used in this study

	Pongola Game Reserve (PGR)	Phinda Private Game Reserve (PPGR)	Tembe Elephant Park (TEEP)	Pilanesberg National Park (PNP)	Hluhluwe imfolozi Park (HiP)
Province	KwaZulu-Natal	KwaZulu-Natal	KwaZulu-Natal	North West	KwaZulu-Natal
Location	(27°54'–27°35' S; 32°01'–31°86' E)	(27°92'–27°68' S; 32°44'–32°20' E)	(27°07'–26°86' S; 32°59'–32°40' E)	(25°8'–25°22' S; 26°57'–27°13' E)	(28°42'–28°01' S; 32°15'–31°70' E)
Extent (km ²)	80	150	330	550	900
Vegetation (Acocks 1988)	Zululand Thornveld, Lowveld & Arid Lowveld	Sand forest, Natal low & Coastal bushveld	Coastal Forest, Thornveld & Sand forest	Sour bushveld	Zululand Thornveld & Lowveld
Mean rainfall (mm year ⁻¹)	650	750	700	630	765
Elephant population (2005)	52	78	165	160	400
Maximum distance to water (km)	5	6	8	8	10
Period of data collection & method used	1999–2004 (radio collar)	2003–2005 (radio collar) 2004–Jul 2005 (GPS collar)	2004–2005 (GPS collar)	1998–2000 & 2002–2003 (radio collar) 2004–2005 (GPS collar)	2000–2002 (radio collar) 2004–2005 (GPS collar)
Number of males	3	2	0	6	6
Number of family groups	2	3	3	4	3

ranged from 80 to 900 km² in extent. The average annual rainfall was 680 mm (range of 630–770 mm), with each of the PAs experiencing a dry cool winter season (from May to September) and a hot wet summer season (from October to April). The main habitats were predominantly composed of savanna vegetation (grasslands interspersed with trees), although the species composition varied between study sites. The elephant densities ranged from 0.3 to 0.6 elephant km⁻², and each of the PAs was fully fenced so that the populations were effectively closed to either emigration or immigration.

The unique biology of the elephant and the fenced nature of the study sites also minimized the influence of four other key factors that have been shown to influence decision making in large herbivores – predation, competition, reproductive state (Stephens & Krebs 1986; Poole 1994) and water availability (Redfern *et al.* 2003). First, because of their large body size, elephant experience very low levels of predation (Ruggiero 1991). Second, elephant do not exhibit territorial behaviour, and intra-specific competition has only been shown to occur between family groups in situations where resources become very limited, population densities are high (>1 elephant km⁻¹) and there is a clear and defined dominance hierarchy (Wittmyer *et al.* 2007). The elephant densities in this study were comparatively low (between 0.3 and 0.5 elephant km⁻²) and the social hierarchy had not fully developed due the relatively young age of the adult females (15–40 years of age). Thirdly, elephant do not exhibit a distinct breeding season (Poole 1989), and as such no distinct temporal patterns in movement of the sexes are anticipated solely on the basis of reproductive state. Furthermore, the spatially restricted nature of the study sites limited the necessity for male elephant to adopt a strategy of extensive mate searching when they are reproductively active (Whitehouse & Schoeman 2003), a behaviour that is commonly observed in open populations (Poole 1989, 1994; Owen-Smith 1992).

Finally, elephant are a water-dependent species that have been shown to select habitats close to water, particularly during the dry season when supplies become scarce (Viljoen 1989; Stokke & Toit 2002). The fenced nature of the PAs used in this study has resulted in water points being augmented year round to ensure that the large water volumes required by elephant were readily available throughout the year across the five sites. Although summer rainfall can create ephemeral water points, these are often too small and shallow for elephant, and they prefer to use established water points for both drinking and bathing (Owen-Smith 1992; Nowak 1999). Furthermore, the maximum distance to permanent water in this study was approximately 10 km (see Table 1), which is within the daily ranging distance of an elephant (Owen-Smith 1992). As a result, surface water availability was excluded as a major driving factor in range variation over time and space.

Accepting these broad assumptions allows the unique opportunity to investigate the role of body size and sociality in the decision making of a sexually dimorphic large herbivore across independent PAs.

Location data

The elephant (independent males or family groups) were located on the ground using either radio telemetry – individual

elephant were fitted with radio collars – or traditional tracking methods (dung and spoor). Once an elephant was sighted, a GPS position was recorded along with date, time and habitat type. The elephant were then followed at a discrete distance (≥ 50 m), until they moved out of sight or the observation period ended (2–8 h). During this time, location points were recorded at approximately 20-min intervals. Satellite GPS collars and GPS/GSM (Global System for Mobile Communication) collars were also used, and these automatically recorded positional data throughout the day at pre-determined times (minimum of 4 times per day). These fine-scale location data were collected for 15 family groups and 17 males during an 8-year period from 1998 to 2005, with each PA being sampled for varying time periods (see Table 1). However, for an individual male elephant or family group to be included in the dataset, each location had to be accurately recorded with a GPS, and the time and date logged. Furthermore, in accordance with the literature, a minimum of 35 days of data (1 point per day) were required to calculate a reliable estimate of seasonal home range (Seaman *et al.* 1999; Druce *et al.* 2006), and at least one full biological year of data was necessary for an individual elephant or family group (a consecutive summer and winter season) to be included in the analyses. Because male elephant continue to grow after reaching sexual maturity in their late teens (see Poole 1994), only individuals ≥ 28 years of age were included in the study, to fully explore the effects of body size on ranging behaviour. Meanwhile, family groups of related adult females and their offspring (Moss & Poole 1983) were used for the female data points. Elephant were considered to range independently following approaches used in previous research (see Druce *et al.* 2008), and the fact that associations of two individuals or two groups accounted for only 5–30% of locations, across both sexes and the five study populations.

Climate data

Daily rainfall data were collected in each of the PAs for the duration of the study. The regional ecologist supplied rainfall data for Tembe Elephant Park (TEP), while reserve management provided data for Pilanesberg National Park (PNP), Pongola Game Reserve (PGR) and Phinda Private Game Reserve (PPGR). The Hluhluwe-imfolozi Park (HiP) data were collected by the Zululand Grass Project (Botany Department, University of Cape Town). Rainfall was highly variable during the study period, with 2000 being the wettest year in all of the PAs, while 2002–2004 was significantly drier (Fig. 1). The average rainfall (all sites) over the 6 years varied from 673 to 770 mm, TEP demonstrated the greatest within site variation with 1391 mm in 2000 and 257 mm in 2002.

Phenological data collection

As rainfall was used as a key indicator of environmental variation, it was necessary to test the assumption that rainfall is positively correlated with forage quality and abundance in the savanna biome. Phenological data were therefore collected in PGR and PNP from 2002 to 2004, with 3500 trees sampled at random in all height classes

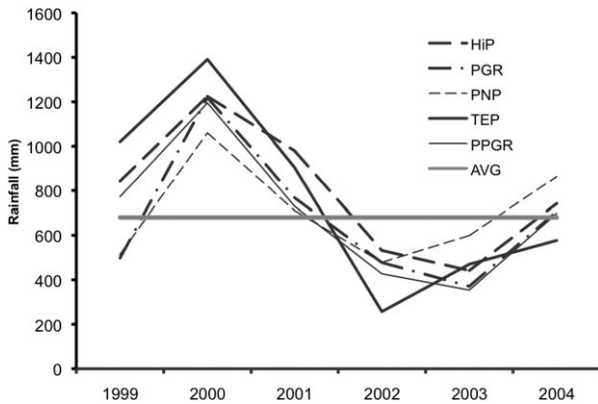


Fig. 1. The variation in annual rainfall from 1999 to 2004 for the five protected areas used in the study and the long-term mean (AVG). AVG, average; HiP, Hluhluwe imfolozi Park; PGR, Pongola Game Reserve; PNP, Pilanesberg National Park; TEP, Tembe Elephant Park; PPGR, Phinda Private Game Reserve.

above 1 m. The location of each tree (GPS) was recorded along with the aspect and topographic position. The basal diameter, total height, height below canopy and diameter of the longest and shortest canopy axis were measured. The available biomass was estimated as a percentage by visually calculating the density of the canopy, with 100% corresponding to a theoretically solid canopy. The proportions of old wood (primary and secondary branches), new wood (shoots) and non-woody biomass (leaves, fruit and flowers) were then estimated. Each of these categories was given as a percentage of the total available biomass. A further breakdown of the non-woody biomass was used to calculate the relative proportions of new leaves, mature leaves, senescent leaves, fruits and flowers. A minimum of 40 trees were sampled each month, in order to ensure a wide range of tree species and canopy sizes for the calculation of mean biomass availability.

An index of woody vegetation quality was established using a ratio of the percentage of mature leaf/percentage of senescent leaf, as green leaves have a higher nutritional value than browning senescent leaves (Chidumayo 1994). These individual data points were plotted against the rainfall values from the previous month, accounting for the lag in growth response (Archibald & Scholes 2007). A linear regression was then used to establish whether there was a relationship between monthly rainfall and available non-woody biomass. The mean monthly value of available non-woody biomass (biomass rank) was used as the dependent variable, while the preceding month's rainfall was used as the independent. The analyses were carried out separately for the two PAs.

Spatial analysis

The four distinct temporal scales used in the study for ranging behaviour analyses were based on approaches that have been used in previous studies: (i) yearly range (a biological year, comprising a single continuous wet and dry season); (ii) summer and winter seasonal range (Owen-Smith 1992; De Villiers & Kok 1997; Mysterud *et al.* 2001b); (iii) daily displacement (the straight line distance between two

location points spanning a 24-h period); and (iv) movement rate (km per hour) (Whitehouse & Schoeman 2003). The spatial scales included the 95% kernel (total range) and the 50% kernel (core range), which are considered robust and ecologically valid methods by which to calculate the home ranges of large mammal species (Worton 1989).

To avoid autocorrelation while also establishing a standardized protocol (taking into account the different methods of data collection and daily sampling intensity), one location point was selected per day (at random) for each set of home range analyses (Swihart & Slade 1985; 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 clipped according to the boundaries of the PA and their size calculated using the X-tools extension.

Home ranges were calculated for each biological year (summer and winter season) and for individual seasons. The length of a season was defined by the rainfall of that year, with the summer beginning 10 days after >15 mm of rain in September/October while winter began when there had been no significant rainfall (<15 mm) for 2 weeks, from 15 March of each year.

The location data were also used to generate the displacement distance from 1 day to the next using the Animal Movement extension. The straight-line distance between two location points that were 24 ± 1 h apart were calculated in the GIS for a minimum of 35 days within each season. The values were summed and divided by the total number of days to get an average straight-line displacement for each elephant during different years and seasons. Movement rates were calculated using the same method. Days with regular location points (minimum of six for 12-h 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 because of 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 can be made.

Statistical analysis

The analyses were carried out in SPSS 13 and the Kolmogorov Smirnov test was used to establish whether data were normally distributed before proceeding. Initially, a linear regression was used to investigate the relationship between rainfall and range size for each sex. However, to remove the effect of PA size, the standardized residual was calculated for each data point using a one-way ANOVA. The limited size of the PGR and PPGR prevented range expansion and the residuals remained relatively similar for all of the data points. The PAs were therefore split into two distinct categories, small (<150 km²), which included PPGR and PGR, and large (>300 km²), 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 PAs. Annual rainfall was classified as high or low, depending whether it was above or below the long-term mean for all five PAs (680 mm). The long-term PGR data set was analysed independently using a Wilcoxon paired-sample test to establish

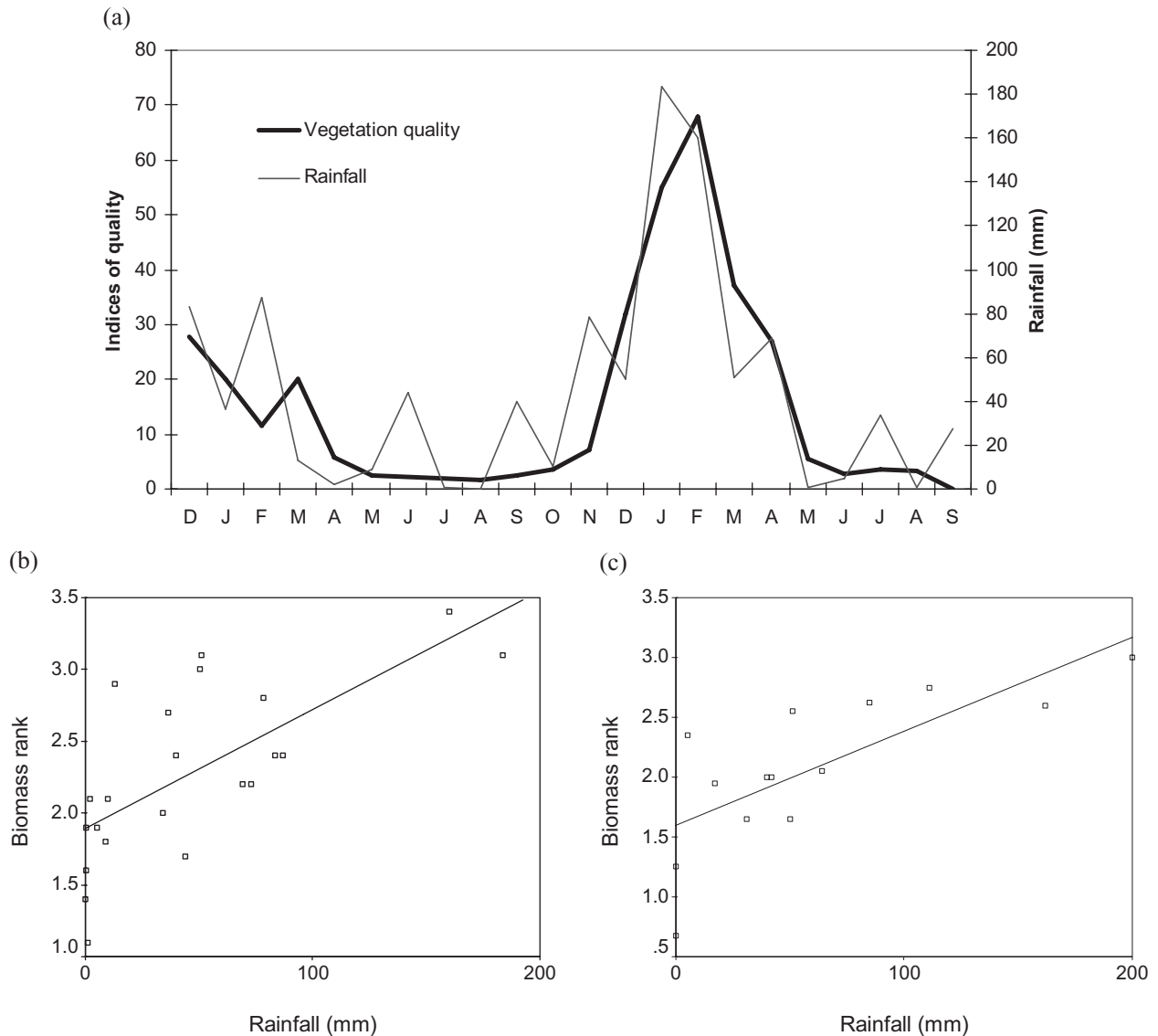


Fig. 2. The relationship between rainfall and plant phenology in the savanna biome. (a) The temporal variation in vegetation quality from 2002 to 2004 using a ratio of mature leaf/senescent leaf and monthly rainfall. The temporal variation in non-woody biomass and monthly rainfall in (b) Pongola Game Reserve and (c) Pilanesberg National Park from 2002 to 2004.

whether winter and summer ranges were significantly different for males and females. The displacement and movement rate analyses involved comparing all the male and female results using a one-way ANOVA. The data were then separated by sex and a two-way ANOVA was used to analyse the influence of season and rainfall. The influence of PA size was also investigated using a one-way ANOVA.

RESULTS

Vegetation quality, biomass availability and rainfall

Regression analyses confirmed the positive relationship between vegetation quality and rainfall ($F_{1,20} =$

43.66, $P < 0.001$, $r^2 = 0.69$) (Fig. 2a), and between biomass availability and rainfall in both the 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. 2b,c).

Home range

Home range size increased significantly with PA size for both males ($F_{1,44} = 134.79$, $P < 0.01$, $r^2 = 0.75$) and females ($F_{1,36} = 58.377$, $P < 0.01$, $r^2 = 0.62$). After factoring out the PA size effect using residuals, the annual range size for males 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 five study sites (Fig. 3). There was no

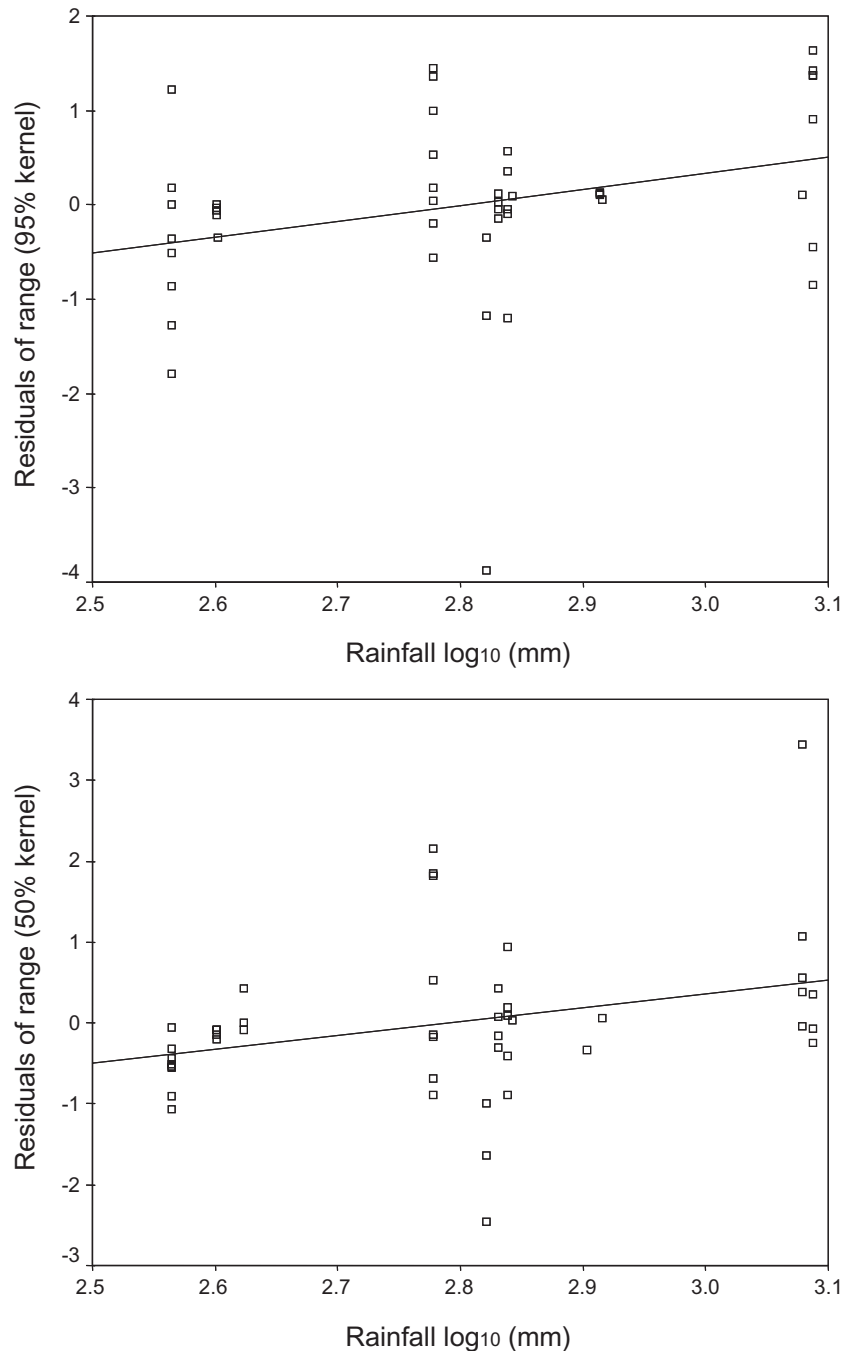


Fig. 3. The effect of rainfall on the range size (95% and 50% of kernels) of male elephant, using data from the five study sites.

such effect of rainfall on range sizes of females and their associated family groups (total: $F_{1,36} = 0.65$, $P > 0.5$, $r^2 = 0.006$; core: $F_{1,36} = 0.009$, $P > 0.9$, $r^2 = 0$).

However, both male and female elephant demonstrated a positive relationship between range size and rainfall for the total annual home range ($F_{1,54} = 1522.91$, $P < 0.025$) and the core annual range ($F_{1,54} = 403.76$, $P < 0.05$) in the three large PAs. The

seasonal data were not as conclusive, because of the level of variation in the female response (winter total range: $F_{1,53} = 75.18$, $P = 0.07$, summer total range: $F_{1,33} = 8.51$, $P = 0.21$). Males responded consistently, however, expanding their winter (total range: $F_{1,33} = 20.32$, $P < 0.001$, core range: $F_{1,33} = 18.58$, $P < 0.001$) and summer (total range: $F_{1,20} = 7.80$, $P = 0.012$, core range: $F_{1,33} = 6.16$, $P < 0.025$) ranges in years with above average rainfall (Fig. 4).

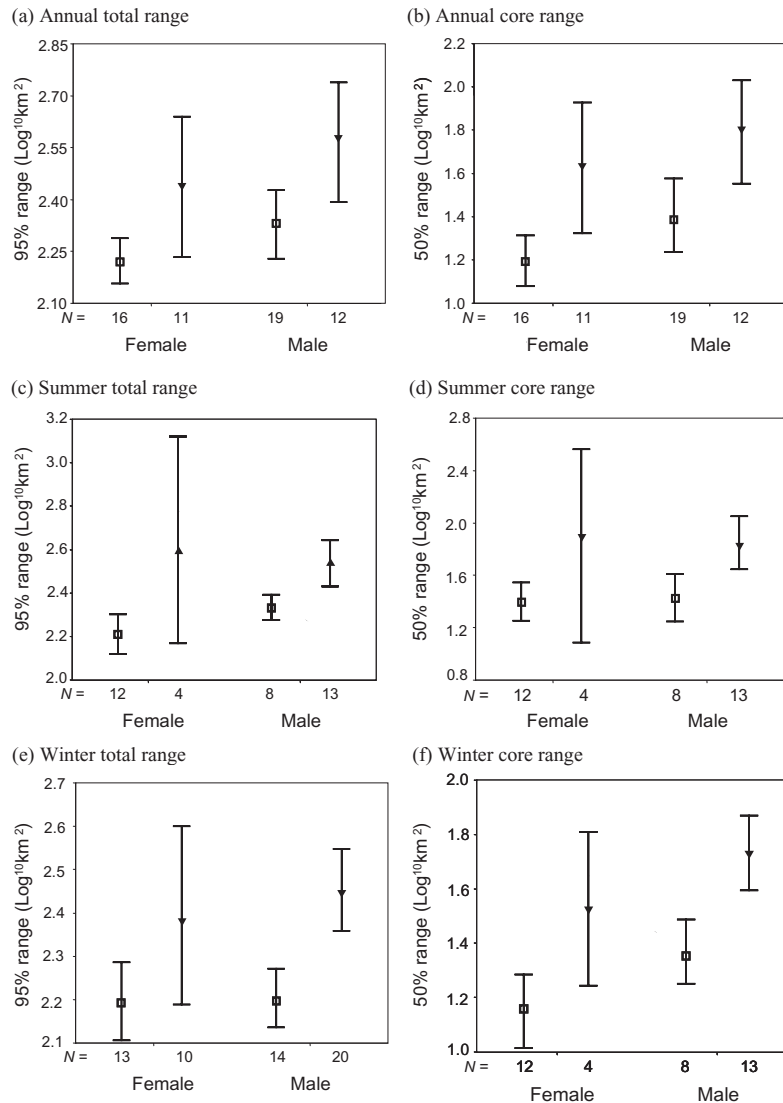


Fig. 4. The effect of rainfall on range size for male and female elephant in large protected areas, low rainfall \square <math><680</math> mm per year and high rainfall \blacktriangledown >680 mm per year.

In small PAs, there was no overall relationship between home range size and rainfall (total range $F_{1,22} = 2.41$, $P > 0.25$ and core range $F_{1,22} = 0.43$, $P > 0.75$). Despite this, the continuous data set from PGR showed that male range size tracked the drop in rainfall from 1999 to 2003 (Fig. 5a,b) for both the total and core annual range. The total range increased in 2004, which coincided with the end of a severe drought. The females did not exhibit the same relationship (Fig. 5c,d). However, the females in PGR exhibited larger core winter ranges compared with the preceding summers. While not significant, the trend was evident ($Z = -1.826$, d.f. = 3, $P < 0.1$). The males did not demonstrate the same relationship ($Z = 0.008$, d.f. = 3, $P > 0.95$). However, during the dry period of 2002–2004 they reduced their core ranges.

Displacement

The mean displacement distances were similar for male and female elephant ($F_{1,50} = 0.26$, $P > 0.5$). However, males demonstrated a seasonal relationship with larger displacement distances in the summer compared with the winter ($F_{1,52} = 4.03$, $P = 0.05$) (Fig. 6a). Season alone did not influence the displacement distances of female elephant ($F_{1,52} = 0.01$, $P > 0.9$), but they did have smaller summer displacement distances during years of above average rainfall ($F_{1,20} = 5.08$, $P < 0.05$) (Fig. 6b). Males decreased their winter displacement distances during years with below average rainfall ($F_{1,29} = 4.52$, $P < 0.05$). There was no influence of PA size on the annual displacement distances of females, but males demonstrated greater average displacement

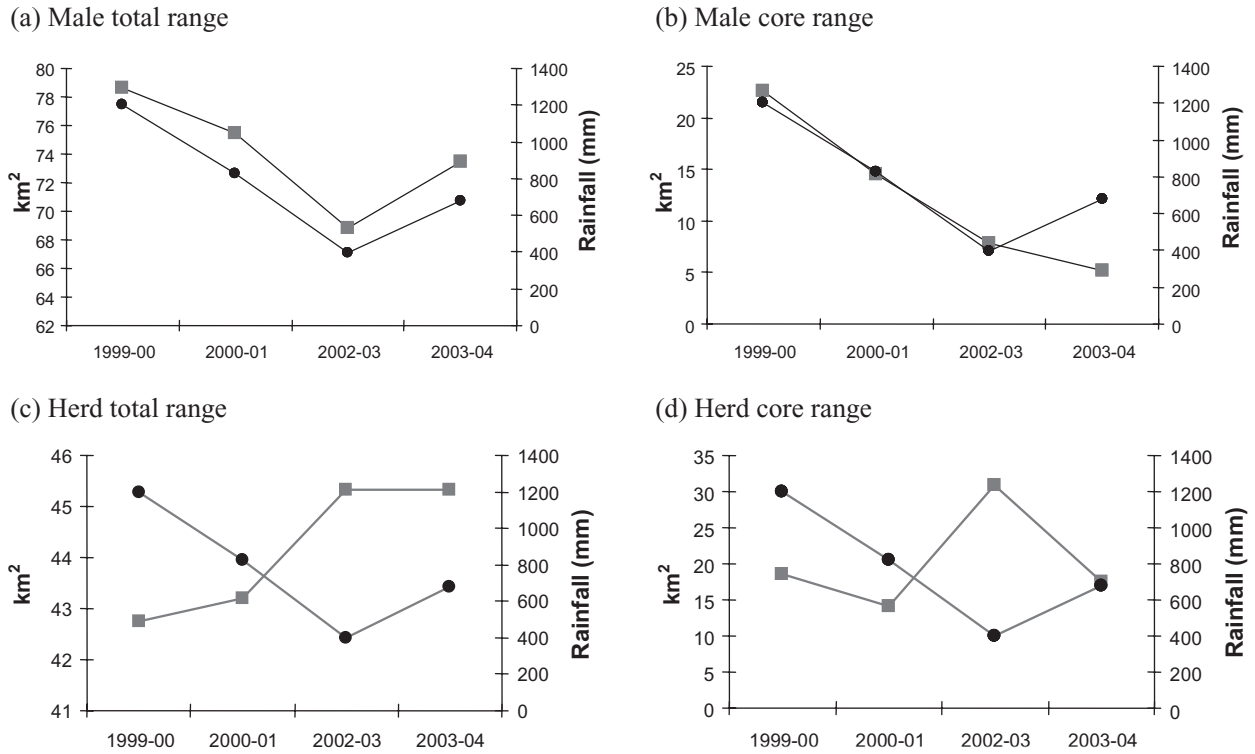


Fig. 5. The effect of annual rainfall ● on the total and core ranges ■ of male and female elephant in PGR.

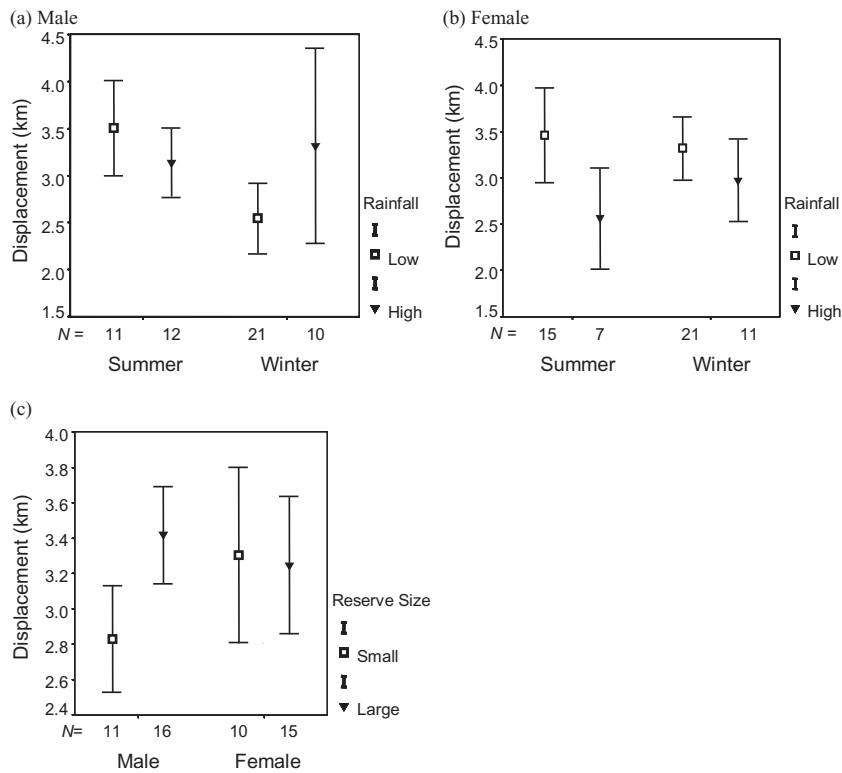


Fig. 6. The influence of season and PA (protected area) size on the 24-h displacement distance of male and female elephant in all five PAs.

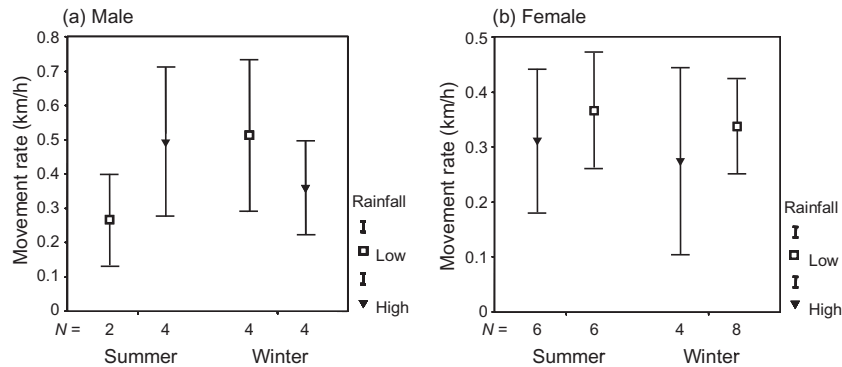


Fig. 7. The effect of rainfall on movement rates of male and female elephant during the two distinct climactic seasons (winter and summer) in all five protected areas.

distances in the larger PAs ($F_{1,25} = 9.42$, $P < 0.01$) (Fig. 6c).

Movement rates

Males moved at a significantly faster rate than females ($F_{1,37} = 5.25$, $P < 0.05$) and also increased their movement rates during wet summers and dry winters ($F_{1,10} = 8.37$, $P < 0.05$) (Fig. 7a), a relationship which was not evident for female elephant (Fig. 7b) ($F_{1,21} = 0.25$, $P > 0.75$). Females in small PAs had higher average movement rates ($>0.5 \text{ km h}^{-1}$) compared with large PAs where movement rates did not exceed 0.3 km h^{-1} ($F_{1,23} = 73.71$, $P < 0.001$). The limited size of the male data set prevented a comparison of movement rates and PA size.

DISCUSSION

Ranging behaviour has commonly been used to investigate the broad-scale decision making of large herbivores in heterogeneous environments, including the wildebeest – *Connochaetes taurinus* (Wilmshurst *et al.* 1999), Thomson's gazelle – *Gazella thomsoni thomsoni* (Fryxell *et al.* 2004), red deer – *Cervus elaphus* (Myrsterud *et al.* 2001a), reindeer – *Rangifer tarandus* (Mårell *et al.* 2002) and elk – *Cervus canadensis* (Boyce *et al.* 2003), all of which exhibit seasonal habitat selection and a change in movement behaviour in response to plant phenological development. However, there has been only limited research focussing on the temporal variation in ranging behaviour of the sexes (Harestad & Bunnell 1979; Myrsterud *et al.* 2001b), while differences in habitat selection have generally been used to explain sexual segregation (Conradt 1999; Bon *et al.* 2001). Interestingly, Shannon *et al.* (2006b) presented results demonstrating that male and female elephant do not exhibit distinct habitat preferences and were therefore

unlikely to be segregated as a result of habitat selection. Notwithstanding, clear differences in the extent of male and female annual and seasonal ranges have been reported (Viljoen 1989; Owen-Smith 1992; Stokke & Toit 2002).

At a continental scale, the home range sizes of African elephant were inversely correlated with long-term mean annual rainfall (Osborn 2004), but at the finer spatial resolution used in this study both male and female elephant responded to local variation by expanding their annual ranges during years with above average rainfall. This result concurs with the prediction that abiotic factors dictate the distribution of large herbivores at the landscape scale (Boyce *et al.* 2003; Redfern *et al.* 2003). Rainfall directly influences primary productivity in the savanna ecosystem (Prins & Loth 1988) and has been used to predict carrying capacities (Coe *et al.* 1976; East 1984) and to explain ungulate population dynamics (Owen-Smith 1990; Illius & O'Connor 2000). Similarly in this study, biomass availability and vegetation quality were positively related to monthly rainfall in the PGR and PNP, with the drought of 2002–2003 leading to a dramatic reduction in the available biomass when compared with 2004.

Previously, the range use of elephant (as with other water-dependent species) was largely described as a function of distance to surface water, with elephant contracting their movements around permanent water sources during the dry season (Western & Lindsay 1984; Owen-Smith 1992; Stokke & Toit 2002). The results presented in this study suggest that there is also likely to be a positive relationship between rainfall, forage abundance and home range size (Myrsterud *et al.* 2001a,b; Henriksen *et al.* 2003), providing further evidence that despite their generalist foraging behaviour, elephant are responding to heterogeneity in savanna ecosystems (Grainger *et al.* 2005; Dai *et al.* 2007). In fact, unlike small-bodied and selective herbivores, elephant appear to be

adopting a strategy that maximizes the rate of nutritional intake by targeting the abundant, but often-lower quality foraging opportunities, through the expansion of their home ranges during years when rainfall is above average.

Annual rainfall had a greater influence on ranging behaviour than season, because productivity and rainfall are directly correlated, while temporally distinguished seasons are associated with variable forage quality (Prins & Loth 1988). During low rainfall years and winter seasons, elephant (of both sexes) reduced their ranges and foraged in habitats that maintained a relatively high abundance of biomass, such as riverine vegetation and thickets in low lying areas (Ottichilo 1986; Viljoen 1989). The compression of winter ranges in large herbivores has been linked to their tolerance of low quality forage in habitats where it remains relatively abundant (Myserud *et al.* 2001b). These differences may be more pronounced in large-bodied browsers and mixed feeders, which focus their foraging on the remaining discrete patches of woody vegetation during the winter season (Myserud *et al.* 2001b; Dussault *et al.* 2005). In comparison, large bodied grazers have a relatively uniform and two dimensional food source, which enables them to utilize comparatively smaller annual ranges (Owen-Smith 1992). As a result, their seasonal ranges are unlikely to contract to the same extent as browsing species during the dry season, and in species such as the African buffalo (*Syncerus caffer*) ranges have actually been shown to increase (Ryan *et al.* 2006).

Large-bodied herbivores also acquire considerable fat reserves during the wet summer season, which they can exploit during periods of resource scarcity (Millar & Hickling 1990; Myserud *et al.* 2001b). In fact, the mobilization of fat reserves has been proposed as the strategy by which white rhinoceros (*Ceratotherium simum*), the second largest African herbivore, meet their nutritional demands during the dry season, while maintaining approximately the same foraging approach year round (Shrader *et al.* 2006).

Although there are clear advantages of body size, the demands of group living, can negatively impact the foraging efficiency of individuals (Fritz & De Garine Whichatitsky 1996) and it was notable that the female elephant in PGR consistently exhibited larger winter ranges, a result which may be a function of restricted range size (40 km²), seasonal habitat selection and the very large number of elephant ($n = 42$) in the herd (Shannon *et al.* 2006c).

Across the five study sites male elephant adapted their ranging behaviour (home range, displacement and movement rate) at a range of different time scales (annual, seasonal, daily, hour), while females only exhibited significant variation at the seasonal and yearly scale in the large PAs. We suggest that the differences in

ranging behaviour are a result of male elephant exhibiting social independence and significantly larger body sizes, which are associated with greater digestive tolerance and lower relative energy requirements (Stokke & Toit 2000; Shannon *et al.* 2006a). When forage availability becomes limited, it appears that they are able to consistently reduce these expansive ranges to target remaining food resources in comparatively small, focussed ranges, while also utilizing their substantial fat reserves. Moreover, male elephant have been shown to tolerate diets with significantly lower levels of nutrients such as phosphorous and nitrogen when compared with females and calves (Woolley *et al.* 2009). Home range contraction is also likely to be assisted by a dietary switch from grass to browse as phenological changes take place (Myserud *et al.* 2001b). Meanwhile, the female response to variation in productivity is less flexible because of group dynamics (Woolley *et al.* 2009), and the elevated mass-specific energy requirements, which in addition to higher water turnover rates (Stokke & Toit 2002) may explain their greater susceptibility to starvation during droughts compared with males (Corfield 1973; Dudley *et al.* 2001). The strengths of our approach have been the ability to collect and analyse detailed data from five distinct populations of elephant across an 8-year period. However, the interpretation of the results has taken into account broad assumptions on the behaviour of elephant coupled with the unique conditions of the five study sites. A number of questions that are beyond the scope of this study are now raised with regard to the precise role of social factors (e.g. reproduction and competition) in the ranging behaviour of male and female elephant.

Despite these considerations, the pronounced differences in ranging behaviour highlighted above, indicate that body size is likely to play a significant role in the decision making of a sexually dimorphic species. Large herbivores are a major component of terrestrial ecosystems and understanding their behavioural responses to temporal and spatial heterogeneity is important for effective management (Boyce *et al.* 2003; Fryxell *et al.* 2004; Gordon *et al.* 2004). Elephant are a prime example as they have the potential to alter habitat structure when densities are elevated (Lombard *et al.* 2001). Males in particular, because of their larger body size and independent ranging behaviour, may have greater localized impacts than the more selective females and their family groups (Shannon *et al.* 2006a). Despite this, these impacts are unlikely to be homogenous across their range but will depend upon the distribution of resources and the scale of resolution (Shannon G., Druce D. J., Mackey R. L., Page B. R., Grant R. & Slotow R. unpub. data). Commonly, large herbivore management has focussed at the population and PA scale; however, this may well be too coarse to detect

the relevant ecological scales at which individual species and the sexes are responding.

ACKNOWLEDGEMENTS

We would like to thank the reserve management and owners of the Pongola Game Reserve, Phinda Private Game Reserve, Hluhluwe iMfolozi Park, Tembe Elephant Park and Pilansberg National Park, without whom this research would not have been possible. We thank and acknowledge all of the research assistants who worked in the various reserves over the years, and that provided data. Thanks also to the Zululand Grass Project, Botany Department, University of Cape Town for providing us with rainfall data for HiP. This study was funded by Distell (Amarula), PPC Cement, Wildlands Conservation Trust, the National Research Foundation (GUN #: 2053623), the University of KwaZulu-Natal and the Durban Institute of Technology. Logistical support was provided by Ezemvelo KZN Wildlife, Northwest Parks and Tourism Board, Pongola Game Reserve and CC Africa (Phinda). We thank Norman Owen-Smith for useful comments during manuscript review.

REFERENCES

- Acoccks J. P. H. (1988) *Veld Types of South Africa*, 3rd edn. Botanical Research Institute, Pretoria.
- Archibald S. & Scholes R. J. (2007) Leaf green-up in a semi-arid African savanna – separating tree and grass responses to environmental cues. *J. Veg. Sci.* **18**, 583–94.
- Bell R. H. V. (1971) A grazing ecosystem in the Serengeti. *Sci. Am.* **225**, 86–93.
- Bon R., Rideau C., Villaret J. & Joachim J. (2001) Segregation is not only a matter of sex in Alpine ibex *Capra ibex*. *Anim. Behav.* **62**, 495–504.
- 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**, 421–31.
- Calder W. A. (1984) *Size Function and Life History*. Harvard University Press, Cambridge.
- Carbone C., Collishaw G., Isaac N. J. B. & Rowcliffe J. M. (2005) How far do animals go? Determinants of day range in mammals. *Am. Nat.* **165**, 290–7.
- Chidumayo E. N. (1994) Phenology and nutrition of miombo woodland trees in Zambia. *Trees* **9**, 67–72.
- 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**, 341–54.
- Conradt L. (1999) Social segregation is not a consequence of habitat segregation in red deer and feral soay sheep. *Anim. Behav.* **57**, 1151–7.
- Corfield T. F. (1973) Elephant mortality in Tsavo National Park, Kenya. *East Afr. Wildl. J.* **11**, 339–68.
- Dai X., Shannon G., Slotow R., Page B. & Duffy K. (2007) Short-duration daytime movements of a cow herd of African elephants. *J. Mamm.* **88**, 151–7.
- De Villiers P. A. & Kok O. B. (1997) Home range and related aspects of elephant in the eastern Transvaal Lowveld. *Afr. J. Ecol.* **33**, 224–36.
- Demment M. W. & Van Soest P. J. (1985) A nutritional explanation for body size patterns of ruminant and non-ruminant herbivores. *Am. Nat.* **125**, 641–72.
- Druce H., Pretorius K., Druce D. & Slotow R. (2006) The effect of mature elephant bull introductions on ranging patterns of resident bulls: Phinda Private Game Reserve, South Africa. *Koedoe* **49**, 77–84.
- Druce H. C., Pretorius K. & Slotow R. (2008) The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biol. Conserv.* **141**, 3127–8.
- Dudley J. P., Criag G. C., Gibson D. S. T. C., Haynes G. & Klimowicz J. (2001) Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *Afr. J. Ecol.* **39**, 187–94.
- Dussault C., Courtois R., Ouellet J. & Girard I. (2005) Space use of moose in relation to food availability. *Can. J. Zool.* **83**, 1431–7.
- East R. (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals. *Afr. J. Ecol.* **22**, 245–70.
- Fritz H., De Garine Whichatitsky M. (1996) Foraging in a social antelope: effects of group size on foraging choices and resource perception in impala. *J. Anim. Ecol.* **65**, 736–42.
- Fryxell J. M., Wilmshurst J. F. & Sinclair R. E. (2004) Predictive models of movement by Serengeti grazers. *Ecology* **85**, 2429–35.
- Gordon I. J., Hester A. J. & Festa-Bianchet M. (2004) The management of wild large herbivores to meet economic, conservation and environmental objectives. *J. Appl. Ecol.* **41**, 1021–31.
- Grainger M., van Aarde R. & Whyte I. (2005) Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *Afr. J. Ecol.* **43**, 369–75.
- Harestad A. S. & Bunnell F. L. (1979) Home range and body weight – a re-evaluation. *Ecology* **60**, 389–402.
- 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.
- Hernández Fernández M. & Vrba E. S. (2005) Body size, biomic specialization and range size of African large mammals. *J. Biogeogr.* **33**, 1243–56.
- Hooge P. N. & Eichenlaub B. (1997) *Animal Movement Extension to Arcview*. Ver 11. Alaska Biological Science Center, US Geological Survey, Anchorage, AK.
- Illius A. W. & O'Connor T. G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos* **89**, 283–94.
- Jarman P. J. (1974) The social organization of antelope in relation to their ecology. *Behaviour* **48**, 215–67.
- Jetz W., Carbone C., Fulford J. & Brown J. H. (2004) The scaling of animal space use. *Science* **306**, 266–8.
- Kleiber M. (1975) *The Fire of Life: An Introduction to Animal Energetics*. Krieger, Huntington, New York.
- 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. *Biol. Conserv.* **102**, 191–203.
- McElligott A. G., Gammell M. P., Harty H. C. *et al.* (2001) Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behav. Ecol. Sociobiol.* **49**, 266–72.

- McNaughton S. J. & Georgiadis N. J. (1986) Ecology of African grazing and browsing mammals. *Annu. Rev. Ecol. Evol. Syst.* **17**, 39–65.
- Mårell A., Ball J. P. & Hofgaard A. (2002) Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks and Levy flights. *Can. J. Zool.* **80**, 854–65.
- Millar J. S. & Hickling G. J. (1990) Fasting endurance and the evolution of mammalian body size. *Funct. Ecol.* **4**, 5–12.
- Moss C. J. & Poole J. H. (1983) Relationships and social structure of African elephants. In: *Primate Social Relations* (ed. R. A. Hinde) pp. 315–25. Blackwell scientific publications, Oxford.
- 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. *J. Anim. Ecol.* **70**, 915–23.
- Mysterud A., Javier Pérez-Barbería F. & Gordon I. J. (2001b) The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia* **127**, 30–9.
- Nowak R. M. (1999) *In: Walker's Mammals of the World*, 6th edn. The John Hopkins University Press, Baltimore, MD.
- Osborn F. V. (2004) The concept of home range in relation to elephants in Africa. *Pachyderm* **37**, 37–44.
- Ottichilo W. K. (1986) Population estimates and distribution patterns of elephants in the Tsavo ecosystem, Kenya in 1980. *Afr. J. Ecol.* **24**, 53–7.
- Owen-Smith N. (1990) Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *J. Anim. Ecol.* **59**, 893–913.
- Owen-Smith R. N. (1992) *Megaherbivores: The Influence of Very Large Body Size on Ecology*. Cambridge University Press, Cambridge.
- Owen-Smith R. N. (1994) Foraging responses of kudus to seasonal changes in food resources: Elasticity in constraints. *Ecology* **75**, 1050–62.
- Pickett S. T. A. & Cadenasso M. L. (1995) Landscape ecology: spatial heterogeneity in ecological systems. *Science* **269**, 331–4.
- Poole J. H. (1989) Announcing intent: the aggressive state of musth in African elephants. *Anim. Behav.* **37**, 140–52.
- Poole J. H. (1994) Sex differences in the behaviour of African elephants. In: *The Difference between the Sexes*, Chap 14 (eds R. V. Short & E. Balaban), pp. 331–46. Cambridge University Press, Cambridge.
- Prins H. H. T. & Loth P. E. (1988) Rainfall patterns as a background to plant phenology in northern Tanzania. *J. Biogeogr.* **15**, 451–46.
- Ramsey F. L. & Usner D. (2003) Persistence and heterogeneity in habitat selection studies using radio telemetry. *Biometrics* **59**, 332–40.
- 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**, 2092–107.
- Ruggiero R. G. (1991) Opportunistic predation on elephant calves. *Afr. J. Ecol.* **29**, 86–9.
- Ryan S. J., Knechtel C. U. & Getz W. M. (2006) Range and habitat selection of African Buffalo in South Africa. *J. Wildl. Manage.* **70**, 764–76.
- Seaman D. R., Millsaugh J. J., Kernohan B. J., Brundige G. C., Raedeke K. J. & Gitzen R. A. (1999) Effects of sample size on kernel home range estimates. *J. Wildl. Manage.* **63**, 739–47.
- Searle K. R., Thompson Hobbs N. & Shipley A. (2005) Should I stay or go? Patch departure decisions by herbivores at multiple scales. *Oikos* **111**, 417–24.
- 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**, 789–99.
- Shannon G., Page B. R., Duffy K. J. & Slotow R. (2006a) The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia* **150**, 344–54.
- Shannon G., Page B. R., Duffy K. J. & Slotow R. (2006b) The consequences of body size dimorphism: are African elephants sexually segregated at the habitat scale? *Behaviour* **143**, 1145–68.
- Shannon G., Page B., Duffy K. & Slotow R. (2006c) African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *Afr. Zool.* **41**, 37–44.
- Shrader A. M., Owen-Smith N. & Ogutu J. O. (2006) How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. *Funct. Ecol.* **20**, 376–84.
- Skarpe C., Bergström R., Bråten A. L. & Danell K. (2000) Browsing in a heterogenous savanna. *Ecography* **23**, 632–40.
- Stephens D. W. & Krebs J. R. (1986) *Foraging Theory*. Princeton University Press, Princeton, NJ.
- Stokke S. & 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. & Toit J. (2002) Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *Afr. J. Ecol.* **40**, 360–71.
- Swihart R. K. & Slade N. A. (1985) Testing for independence of observations in animal movements. *Ecology* **66**, 1176–84.
- 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. *Afr. J. Ecol.* **27**, 227–40.
- 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. & Lindsay W. K. (1984) Seasonal herd dynamics of a savanna elephant population. *Afr. J. Ecol.* **22**, 229–44.
- Whitehouse A. M. & Schoeman D. S. (2003) Ranging behaviour of elephants within a small, fenced area in Addo Elephant National Park, South Africa. *Afr. Zool.* **38**, 95–108.
- 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. *Can. J. Zool.* **77**, 1223–32.
- Wittemyer G., Getz W. M., Vollrath F. & Douglas-Hamilton I. (2007) Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behaviour. *Behav. Ecol. Sociobiol.* **61**, 1919–31.
- Woolley L. A., Millsaugh J. J., Woods R. J., Janse van Rensburg S., Page B. R. & Slotow R. (2009) Intraspecific strategic responses of African elephants to temporal variation in forage quality. *J. Wildl. Manage.* **73**, 827–35.
- Worton B. J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–8.