

Movement patterns of African elephants (*Loxodonta africana*) in different habitat types

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In this paper we analyse the daytime movements of African elephants (*Loxodonta africana*) in different habitats in the Pongola Game Reserve, South Africa. On average adult males moved faster than females in all habitat types except when grouped together (then females moved at the faster male pace). Elephants demonstrated distinct movement patterns in different habitat types. All the movement parameters indicate that the elephants turned less the further they were from a large permanent body of water (Jozini Dam) and for males with increasing distance to the females. Male and female elephants turned more in habitat types that had favourable resources such as forage and shade, than they did in unfavourable habitats. Thus, the elephants used a direct movement strategy – turning less – when needing to get to a destination more quickly (e.g. toward water or mates), rather than significantly increasing their speed. It is hypothesized that these elephants are optimizing energy efficiency while still varying their foraging approach and search intensity. Patterns of movement through a habitat will affect ecological impacts in that habitat and so habitat-related movement pattern studies of this type could assist landscape planning (e.g. waterhole design and distribution) and large herbivore conservation.

Key words: animal speed, energy optimization, habitat selection, path analysis, sinuosity, turning angle, water availability.

INTRODUCTION

Animal movement patterns provide a unique insight for ecologists to further understand the link between landscape heterogeneity and foraging behaviour (Stephens & Krebs 1986; Turchin 1991; Bartumeus *et al.* 2005). These patterns can be resolved across a range of temporal and spatial scales to establish how animals perceive their environment (Nams 2005). The distinct ranging behaviour of an individual is a function of many different factors, including body size, behavioural state, sociality, predation risk, habitat structure and topography (Beier *et al.* 1995; Dickson *et al.* 2005). As this field of study has grown, a number of mathematical models (e.g. random walk, correlated random walk and Lévy walk models) have been developed and adapted to investigate movement in a diverse range of species from invertebrates to mammals (Turchin 1991; Dickson *et al.* 2005; Dai *et al.* 2007). Large herbivores provide a particularly interesting group

of species for ecological research, due to their extensive ranges, broad dietary breadth and the important role they play in ecosystem function (Gordon *et al.* 2004).

The African elephant (*Loxodonta africana* Blumenbach, 1797) is the largest terrestrial herbivore and pursues a generalized, mixed feeding strategy (foraging on grass and browse). Elephants are also considered major ecological drivers in the African savanna (Kerley *et al.* 2008), and when populations are at high densities they can have substantial impacts on woody vegetation (Laws 1970; Lewis 1986; Loarie *et al.* 2009a; Shannon *et al.* 2008). Such impacts may lead to irreversible changes in vegetation structure and ultimately a loss of biodiversity (Cumming *et al.* 1997; Wiseman *et al.* 2004). In South Africa, more than 800 African elephants were introduced to approximately 60 relatively small (<1000 km²) protected areas between 1979 and 2001 (Garai *et al.* 2004). In these small reserves, vegetation and habitat structure are possibly more threatened by the

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foraging behaviour of elephants due to the lack of space for seasonal dispersal and limited availability of refuges for sensitive plant species (Lombard *et al.* 2001; Duffy *et al.* 2002).

Elucidating the spatio-temporal movement pattern of elephants is important in understanding their ecology and also in making informed management decisions (Dai *et al.* 2007; van Aarde *et al.* 2008). For example, elephants use their available range in a heterogeneous manner and may move to a patch for a specific food species or for a particular phenological phase, such as leafing, flowering and/or fruiting (Swanepoel 1993; Gadd 2002). Due to their large body size and high water-turnover rate, elephants' movement patterns are crucially influenced by water availability and distribution (Stokke & du Toit 2002; Shannon *et al.* 2009). Therefore elephants are likely to actively select habitats (*e.g.* riverine), which provide a range of different resources including water, forage and shade (Shannon *et al.* 2006a). In this study, we aimed to show the relationship between elephant movement patterns and the utilization of different habitat types.

The degree of tortuosity of search paths is expected to be important for the space use, dispersal and food searching of animals (Benhamou 2004). An individual animal's path tortuosity can be measured either by a straightness index or a sinuosity index (Benhamou 2004) and should coincide with the size of turning angles. Hein *et al.* (2003) state that animals will adopt low movement speed, large turning angles and high movement sinuosity to stay in favourable habitats as long as possible but adopt high movement speed, small turning angles, straight movement and low edge permeability to avoid hostile and unprofitable habitats. Therefore, we predicted that in preferred habitats elephants would move slowly and make sinuous paths related to feeding or resting behaviours (Bartumeus *et al.* 2005; Dai *et al.* 2007), and that in comparatively risky or lower quality habitats elephants would move with greater speed and in straighter lines (Turchin 1991). As elephants are dependent on water, we also predict that distance from water will also influence these movement characteristics. The study of habitat and water-related movement patterns may provide greater understanding with regard to predicting the occurrence of habitat use/impacts and the factors dictating elephant distribution. Such knowledge can inform landscape planning, habitat conservation and elephant management in protected areas.

METHODS

Study area

Pongola Game Reserve (PGR) is located in Northern KwaZulu-Natal, South Africa and encompasses an area of 82 km² along the western shoreline of the Jozini Dam (27°25'S; 31°57'E). A railway line passes through the reserve from the southern border to the northwest fence line. The terrain is relatively flat, with several ephemeral drainage lines.

There are seven habitat types in the reserve: *Acacia* & *Marula* woodland, *Combretum* woodland, *Euclea* & *Acacia* thicket, floodplain grassland, mixed *Acacia* woodland, old farmland and riverine thicket (Fig. 1). These habitat types were defined by Shannon *et al.* (2006a) as follows. *Acacia* & *Marula* woodland are located on shallow soils of mid- to upper-slopes on higher hills and have the dominant species *Acacia nigrescens*, *Sclerocarya birrea*, *Ziziphus mucronata*, *A. tortilis*, *Grewia flava*, *Gymnosporia buxifolia*, *Grewia villosa*, *Dichrostachys cinerea*, *Ozoroa engleri*, *Canthium inerme*. *Combretum* woodlands are located on rocky, well-drained soils of upper slopes and tops of hills and have the following dominant species: *Combretum apiculatum*, *A. nigrescens*, *O. engleri*, *G. buxifolia*, *G. villosa*, *Grewia hexamita*, *Grewia caffra*, *S. birrea* and *Z. mucronata*. *Euclea* & *Acacia* thickets are located on alluvial soils in flat areas close to water at lower altitudes and are dominated by *Euclea racemosa*, *Euclea divinorum*, *Euclea natalensis*, *Pappea capensis*, *Gymnosporia nemorosa*, *A. nilotica*, *Capparis tomentosa*, *Salvadora australis*, *A. luederitzii*, *Ehretia rigida*. Floodplain grasslands are located on deep alluvial clay soils of the dam shore with mixed grasses and forbs. Mixed *Acacia* woodlands are located on higher-nutrient soils on lower slopes and have the dominant species *A. nilotica*, *A. tortilis*, *A. luederitzii*, *D. cinerea*, *E. rigida*, *Capparis tomentosa*, *Rhus gueinzii*, *Spirostachys africana*. Old farmland are areas transformed to grassland habitat by cattle farming prior to the proclamation of the reserve. Riverine thicket is located on clay-rich, deep soils of drainage lines with dominant species *E. rigida*, *C. tomentosa*, *S. australis*, *Gymnosporia senegalensis*, *A. nilotica*, *A. tortilis*, *Schotia brachypetala*, *R. gueinzii*, *A. luederitzii*, *A. senegal*, *G. buxifolia* and *D. cinerea*. *Euclea* & *Acacia* thicket and old farmland were excluded from our analysis as there were either too few long-length movement segments or only a limited

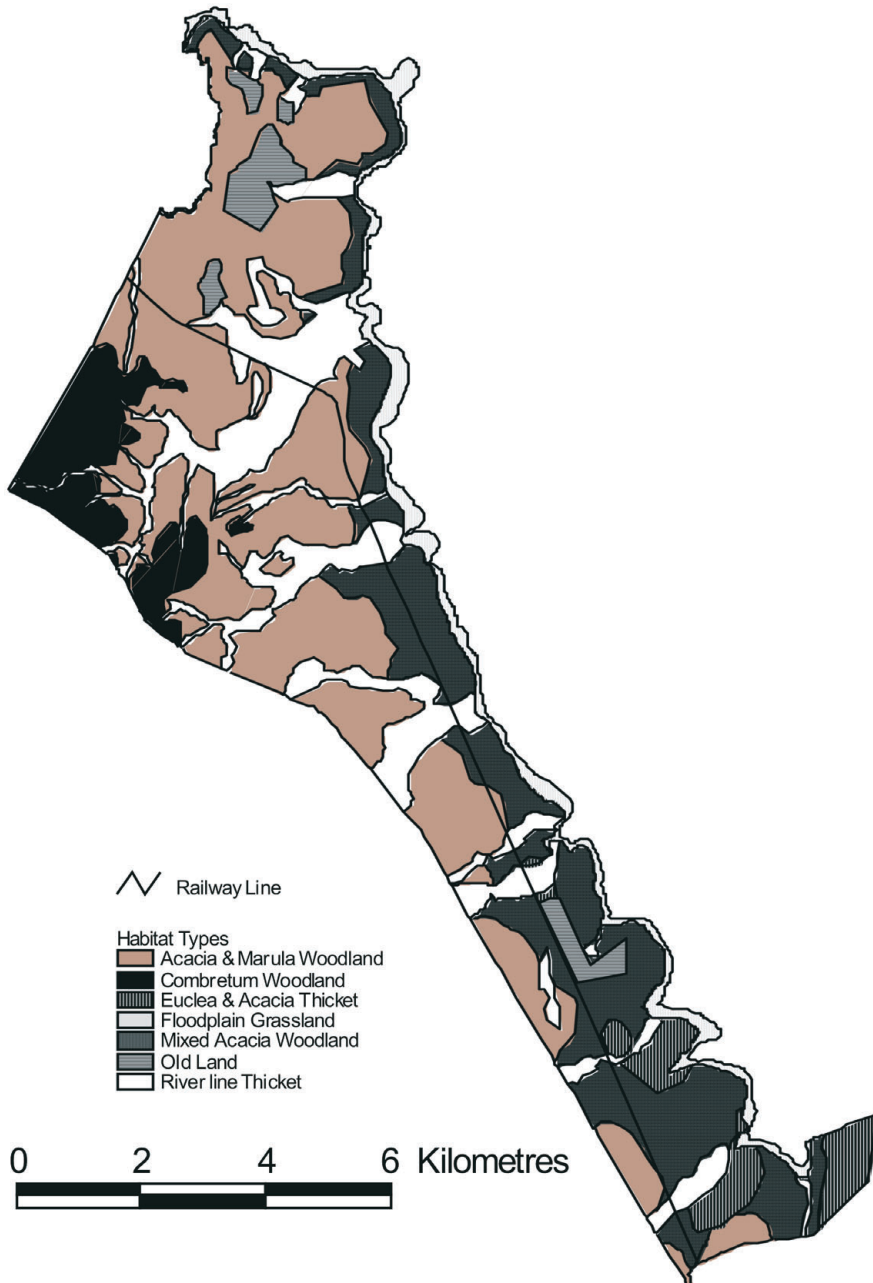


Fig. 1. Habitat types in Pongola Game Reserve (Shannon *et al.* 2006a).

number of locations recorded in these habitat types.

The climate is hot and semi-arid with 400–600 mm of rainfall per annum, more than 60% of the rain falls in the summer season (mid-October to mid-March). During the study period, PGR had three distinct elephant groups, a large family group

of 38 elephants, a second smaller family group consisting of four 15–20-year-old females and their three calves, and four free-ranging adult males. The adult males and the small family group crossed the railway, while the large family group remained on the eastern section of the reserve adjacent to the dam.

Movement data

Between December 2002 and October 2004, four radio-collared elephants (two adult males and an adult female within each family group) were followed during the day (06:00–18:00). The radio collars were fitted by a qualified veterinarian in accordance with South African law and American Society of Mammalogists guidelines. The initial position of an individual male or family group was determined using radio telemetry, while subsequent locations were then calculated using the GPS position of the observer and a sighting distance and angle. Behavioural data, date and time, were also recorded. The aim was to record data at 10 to 20-min intervals for observation periods of between one and seven hours. All elephant latitude–longitude locations were projected into UTM 1983 (Zone 36, WGS84 datum) with the ESRI ArcView® 3.3 Projector Extension. As the adult males could completely separate themselves from the large female group by crossing the railway line, data were separated into three sets; adult females without adult males, adult males without females and females and males combined. Adult females have young males with them as part of their social grouping but these young males are not referred to further in this paper.

Movement statistics

We used Dickson *et al.*'s (2005) CGRMVMNT extension for ESRI ArcView® to estimate the speed of elephants in each habitat type v during movement path j ,

$$s_{v,j} = \frac{\sum_{i=1}^n (s_i \times \alpha_{v,i})}{\sum_{i=1}^n \alpha_{v,i}} \quad (1)$$

where n is the number of movement segments of path j , s_i is the average speed (km/h) of segment i , and $\alpha_{v,i}$ is the area of habitat type v within a 100 m buffered area of segment i . The average speed in a particular habitat type is

$$s_v = \frac{1}{p} \sum_{j=1}^p s_{v,j} \quad (2)$$

where p is the number of movement paths. Since this extension excludes the segments with length = 0, the speed calculated here would generally be greater than the speed directly calculated using sum length divided by duration time. Differences in speed were analysed using a one-way ANOVA with Tukey HSD (honestly significant differences test).

Hawth's Analysis Tools for ESRI ArcGIS® v3.x

was used to calculate elephant movement parameters including movement length l (*i.e.* distance moved in metres), moving angle β (*i.e.* movement direction with 0° indicating north) and turning angle α (*i.e.* the absolute angle between move i and move $i + 1$, with 0° indicating no change in direction). Since moving angle and turning angle are circular quantities, all angular measurements are treated as points on one unit circle. We used the circular package and CircStats package of R (R Development Core Team 2005) to compute mean direction of the calculated points (on the unit circle) and the mean resultant length p . p provided a measure of concentration of turning angles and falls in the interval $[0, 1]$, p is close to 1 for data highly concentrated in one direction and close to 0 for widely dispersed data. Essentially, p is a measure of dispersion and it is reasonable to reject angle uniformity when p is large (Mardia & Jupp 1999).

Benhamou (2004) proposed a sinuosity index:

$$SN = 2[E(D^2) / L]^{-0.5} = 2 \left[p \left(\frac{1-c^2-s^2}{(1-c)^2+s^2} \right) \right]^{-0.5} \quad (3)$$

where $E(D^2)$ is the expected value of the squared diffusion distance D , L is the accumulated travel distance along the path ($L = \sum l_i$), p and b are the expectation and the coefficient of variation of the movement length l , and c and s are the mean cosine and sine of the turning angle α . If the turning angle is a symmetric distribution, then $s = 0$, and equation (3) can be simplified as:

$$SN = 2 \left[p \left(\frac{1+c}{1-c} + b^2 \right) \right]^{-0.5} \quad (4)$$

As the path becomes more tortuous SN increases in value. SN was calculated for each habitat type.

For these movement statistics it was necessary to consider paths with at least three consecutive points. The numbers of sets of data with three points was 43 for adult females when separate from adult males, 83 for adult males when separate from females and 362 for females and males together.

This research was conducted in compliance with South African laws.

RESULTS

There were no distinct differences between adult male movement rates or between female movement rates across the various habitat types

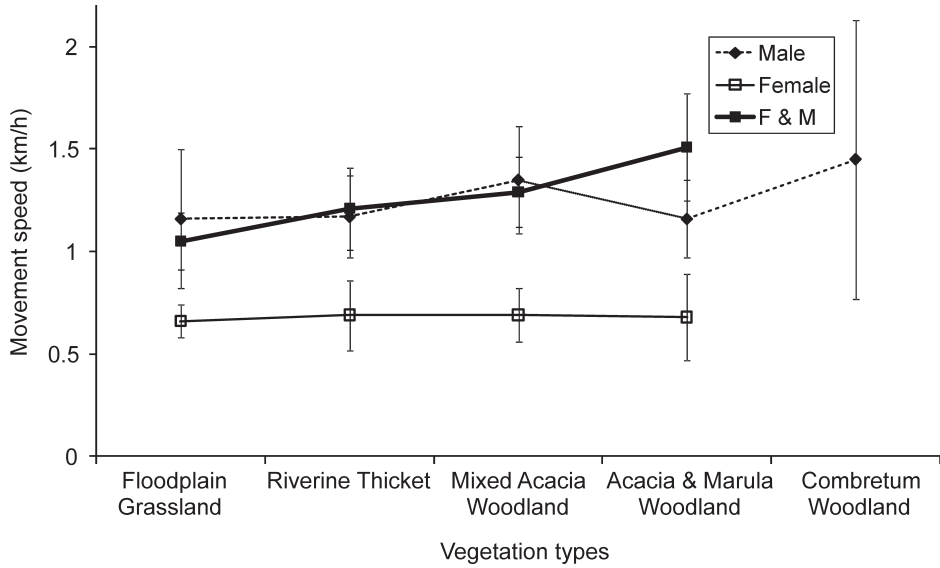


Fig. 2. Mean travel speeds (km/h) by habitat types for male and female elephants on their own, and together (error bars are 1 S.D.). Habitats are organized, as far as is possible, so the distance from water increases from left to right along the x axis.

(Fig. 2). However, when separate, females moved significantly slower than males (Tukey HSD, $P < 0.05$). When the females were with the adult males they moved at the average rates of the males (Fig. 2).

Both male and female elephants tended to move forward (mean turning angle $\bar{\alpha}$ closer to 0) in most habitat types. However, the degree to which there is a concentration of movement in one direction p

tends to increase across habitat types when the sexes were separate (Fig. 3) and corresponds to a decrease in the values of sinuosity SN (Fig. 4). When the males were with the females these trends are less evident (Figs 3 & 4). Floodplain grasslands were only frequented by females on their own and when with males. In other words, males did not frequent this habitat on their own. However, in this habitat when the females were on

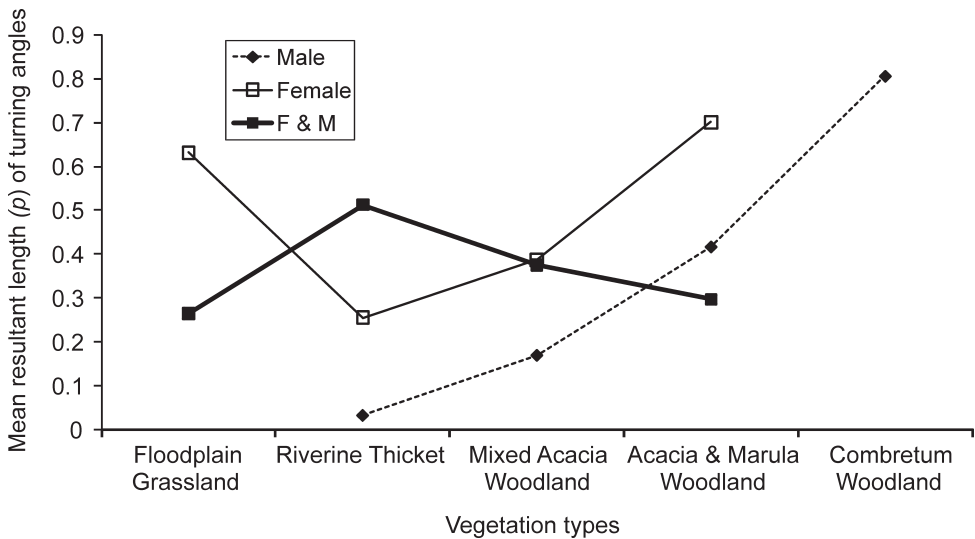


Fig. 3. Mean resultant length of turning angles p (representing the degree to which there is a concentration in one direction) for male and female elephant on their own and together.

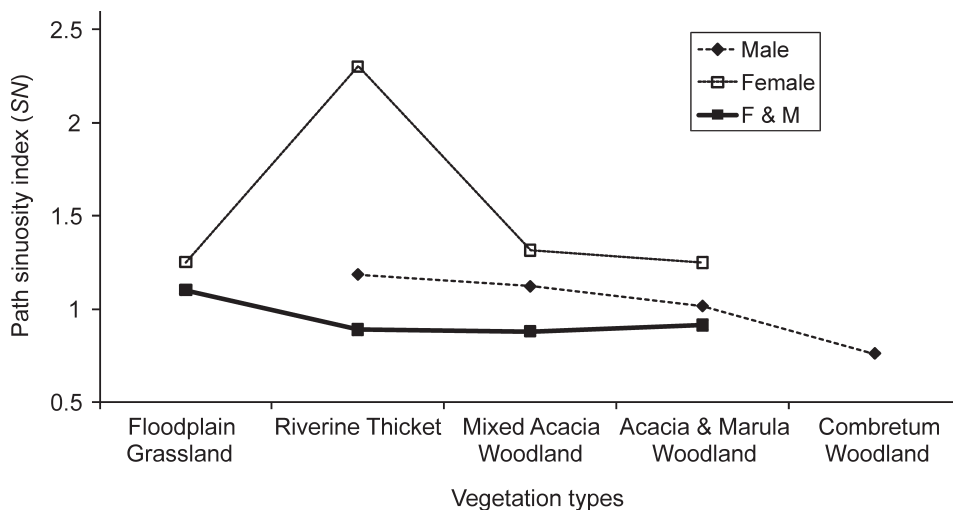


Fig. 4. The path sinuosity (SN) index by habitat types for male and female elephant on their own, and together.

their own p was much higher than when they were together with males but the values for SN were largely the same (Figs 3 & 4). The females did not access the Combretum woodland because they remained on the eastern side of the railway line (see Fig. 1).

DISCUSSION

In PGR male elephants moved faster than females (when separate) across all habitat types, concurring with a recent study on the differences in ranging behaviour between the sexes (Shannon *et al.* 2010). However, there was no significant difference in movement speeds between habitat types for either the male or female groups when in single sex groups. This result would seem to indicate that the sex differences in behaviour are unrelated to habitat selection (Shannon *et al.* 2006b).

Male elephants demonstrate loose social bonds and would be expected to have greater freedom in their movement behaviour, compared with females who are more constrained by the social and nutritional demands of group living. Interestingly the average speeds of females increase when accompanied by males, despite that male elephants choose when to associate with the females and not the other way around. Thus, female movement behaviour changed in the presence of males. Mature males are generally only found in association with females when in musth – a sexually active state that generates interest amongst family groups (Poole 1987). One can speculate that females and males are moving faster in each other's presence because the males are pursuing

the adult females and their family groups. This explanation might be over simplified with the reality a more generalized increase in movement of the groups caused by disturbance related to individuals mating.

Elephants in PGR have no predators so their primary risks, and related behavioural drivers, should relate to the need for water, food and shade. As different habitats offer varying amounts of water, shade and nutrition, resource availability and distribution should be a major factor controlling their movement rates (Shannon *et al.* 2010). Riverine thicket has the highest densities of palatable trees (Duffy *et al.* 2002; Shannon *et al.* 2006a) and shade trees. Thus, it is not surprising that this habitat had the highest values for sinuosity index (SN) and lowest values of p for both females and males when moving independently of each other. In riverine thicket these results correspond to more tortuous movement that could be related to foraging. Habitat preference ratios averaged annually gave similar results (Shannon *et al.* 2006a,b), which shows that these movement parameters could in certain circumstances be used as indicators of habitat use.

Floodplain grassland is the habitat located in closest proximity to the Jozini Dam, followed by mixed *Acacia* woodland, *Acacia* & *Marula* Woodland and *Combretum* woodland the farthest; riverine thicket runs perpendicular to the dam (Fig. 1). For adult male elephants without females and the female group without adult males, the turning angle concentrations increased and sinuosity decreased with distance to the dam (excluding

floodplain grassland). In other words, paths further from water are less sinuous. Thus, it appears that these elephants when not sexually active are driven by their demand for water. For males, distance from the females is on a similar gradient and could be a further explanation. Water has been shown to strongly influence the ranging patterns of elephants (Redfern *et al.* 2003; de Beer *et al.* 2006; Loarie *et al.* 2009b; Shannon *et al.* 2009). Moreover, elephants are attracted to habitats near rivers and dams, which not only provide drinking water but also an abundance of forage (Shannon *et al.* 2006a). That the trend changes when the males are with the females might indicate that sexual activity overwhelms, or at least influences, water as a driver of movement.

The fact that tortuosity varies more across habitat type than movement speed would seem to indicate that elephants use a strategy of turning more in favourable habitats when foraging and turning less when on the move (toward water or mates), and not by significantly increasing their speed. This result could be the result of elephants optimizing energy efficiency (speed of walking) while still varying foraging and searching intensity (by altering the degree of path tortuosity).

Movement patterns of elephants at the habitat scale can provide valuable information with regard to habitat preference and could be useful for the management of both elephants and the savanna ecosystem. Elephant management is usually based on data measured at the population and reserve scale. Our study highlights that this scale may in fact be too coarse (see also Morgan *et al.* 2009) because habitats that are associated with differing movement rates and path structures are likely to be impacted differently. The strong effect of water proximity on movement rates indicates that managers when provisioning artificial water, particularly in smaller reserves, should consider the influence on movement rates on the vegetation (see also de Beer *et al.* 2006; Loarie *et al.* 2009b; Shannon *et al.* 2009). The distinct ranging patterns exhibited in this study further demonstrate how animal movement relates to habitat preferences and water availability, even for a large generalist herbivore such as the elephant (Dai *et al.* 2007; Shannon *et al.* 2010). Understanding movement behaviour has significant consequences for both large herbivore ecology and conservation as it can provide a direct measure of spatial distribution, habitat utilization and resource selection over time.

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