



Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali

Jake Wall^{a,b,*}, George Wittemyer^{c,b}, Brian Klinkenberg^a, Valerie LeMay^d, Iain Douglas-Hamilton^{b,e}

^a Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia, 1984 West Mall, Vancouver B.C., Canada V6T 1Z2

^b Save the Elephants, P.O. Box 54667, Nairobi 00200, Kenya

^c Wittemyer Lab, Department of Fish, Wildlife and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523, USA

^d Department of Forest Resources Management, Faculty of Forestry, University of British Columbia, Forest Sciences Centre #2045 – 2424 Main Mall, Vancouver, B.C., Canada V6T 1Z4

^e Department of Zoology, Oxford University, Oxford OX1 3PS, UK

ARTICLE INFO

Article history:

Received 29 December 2011

Received in revised form 9 July 2012

Accepted 17 July 2012

Keywords:

GPS tracking

Home-range

Loxodonta africana

Migration

Movement ecology

Sahel

ABSTRACT

Wide-ranging, landscape-level movements by terrestrial herbivores are increasingly threatened globally. Understanding the ecology of spatio-temporal movement patterns is critical for conservation of wide-ranging terrestrial species and the ecosystems on which they rely. The range of the Gourma elephant population inhabiting the Sahelian eco-region near Tombouctou (Timbuktu), Mali encompasses the largest areal extent in this species (29% greater than range sizes reported in other populations). Over the course of a year, the Gourma elephants (*Loxodonta africana*) move in a coordinated north–south movement pattern that is relatively unique for the species. We apply two new approaches to this system to characterize space use patterns; a time-density algorithm that provides a probability surface of normalized time spent per unit grid cell of GPS tracked animals and a velocity-grid algorithm that summarizes linear movements (directions, speeds and directional similarity) in cartographic form. The derived movement vector raster was analyzed using standard clustering methods to categorize areas by movement properties. Using these techniques we inferred regions of relative ecological importance to the Gourma elephants, protection of which is essential for the preservation of this unique terrestrial movement system. Analysis suggests the observed spatio-temporal pattern is a complex function of availability of surface water, vegetation productivity (as measured using the Normalized Difference Vegetation Index, NDVI) and possibly vegetation nutrient content. The approaches and applications demonstrated here can further our understanding of the movement ecology of other wildlife landscapes and facilitate the identification of crux points for their improved management.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Free and wide-ranging movements by terrestrial herbivores at landscape scales are an important characteristic in many ecological systems, both for survival of individuals and successful functioning of ecosystems (Berger, 2004; Bolger et al., 2008). Long distance movements of animals can affect ecological characteristics such as community structure, population size or carrying capacity (Fryxell and Sinclair, 1988a), community interactions between nutrient transport and vegetation growth (McNaughton et al., 1988), and predator–prey dynamics (Fryxell and Sinclair, 1988a).

Movement strategies are generally related to system-specific spatio-temporal resource heterogeneity (Jonzén et al., 2011; Holt

and Fryxell, 2011) and itinerant movements of animals tend to coincide with seasonal resource pulses as a way to improve energy and nutrient intake in variable environments (Fryxell and Sinclair, 1988a,b; Wilmschurst et al., 1999; Holdo et al., 2009). These movements are typically categorized as seasonal nomadism, migration or dispersal and thought to be more common in landscapes with limitations on resource availability although exactable definitions are still needed (Börger et al., 2011).

Many systems involving long-distance movements by animals are under critical threat or have been lost due to human impacts and environmental change (Harris et al., 2009; Dobson et al., 2010). A species' inability to maintain long-distance ranging habits can have a domino effect on the entire ecosystem (Dobson et al., 2010). Maintaining the integrity of systems with large scale animal movements is often contingent on just a few, relatively innocuous, spatial bottlenecks that are movement crux points, easily disturbed and vulnerable to human influence (Berger et al., 2006, 2008; Sawyer et al., 2009). Further research enabling a detailed ecological understanding of these movement systems and associated cruxes

* Corresponding author at: Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia, 1984 West Mall, Vancouver B.C., Canada V6T 1Z2.

E-mail address: walljcg@gmail.com (J. Wall).

is a conservation priority (Wilcove and Wilkelski, 2008). As highlighted in recent frameworks for the study of movement ecology (Nathan et al., 2008), it is critical for conservation to define the *where*, *when*, *how* and *why* of large scale animal movement systems. Here, we provide an analysis focused on addressing these questions of one of the planet's widest-ranging terrestrial movement systems; that of desert-adapted African elephants (*Loxodonta africana*) living in the Gourma region of Mali.

Expansion of the Sahara 5500 years BP (Kröpelin et al., 2008) and over-exploitation led to the widespread eradication of elephants in North Africa (Bouché et al., 2011). As a result, the Gourma elephants are now the northernmost population in Africa (Blake et al., 2003) and a critical population with respect to the conservation status of the endangered elephants of north-west Africa (Blanc et al., 2007; Bouché et al., 2011). They inhabit an ecological extreme for the species where the environment is harsh and highly variable, spanning a wide ecological gradient. Initial investigation has found that the Gourma elephants move seasonally in what appears to be a large-scale migration (Blake et al., 2003) but the movement tactics and drivers of their unique space-use patterns have not yet been critically assessed.

In this study, we use Global Positioning System (GPS) tracking data on the elephants coupled with remotely sensed landscape covariate data to characterize the Gourma elephant movements and their drivers. We first focus on spatially quantifying the movements by using both traditional home-range metrics and a novel non-parametric 'time-density' approach for mapping animal movements and identifying high density use areas. We also develop and apply a 'velocity-grid' method for both summarizing movements at the landscape-scale and identifying spatially-clustered regions of similar movement behavior. In principle, the velocity-grid approach is similar in function to state-space techniques for analyzing and categorizing movement trajectories (Patterson et al., 2008). These methods allow us to characterize the *where*, *when* and *how* of their space use patterns.

Water availability and forage abundance and quality are factors known to affect the movements and distribution of elephants in arid and savannah ecosystems (Western, 1975; Western and Lindsay, 1984; Chamaillé-Jammes et al., 2007; Loarie et al., 2009). As a result of their long gut-length and massive energy intake requirements, elephants are thought to be heavily reliant on forage abundance (Owen-Smith, 1988) and respond spatially to vegetation availability (Harris et al., 2008; de Beer and van Aarde, 2008). Also, as obligate drinkers their movements are constrained by access to water. We address *why* the observed spatial patterns and movements might emerge as a result of these biological properties by analyzing their movements and range in relation to vegetation and rainfall.

In combination, this information provides a detailed overview of the movement ecology of the Gourma elephants that can help in the understanding and protection of this unique population of African elephants.

2. Materials and methods

2.1. Study area

The Gourma elephants, numbering around 350 individuals (Bouché et al., 2009), are presently found in the region south of the Niger river lying between the towns of Douentza and Gossi and extending south into northern Burkina-Faso (bounding coordinates: 3.1°W, 0.8°E, 16.6°N, 14.3°S). The region (Fig. S1) lies in the Sahelian eco-region (Grove, 1978). The physiography is a mixture of undulating dune structures of sandy substrate covered in grasses (*Cenchrus biflorus*) and Acacia scrub (Sinclair and Fryxell,

1985; Blake et al., 2003), with patches of denser vegetation and forest found in water drainage areas that together make up 54% of the region. Large flat clay pans, laterite plateaus and sandstone inselbergs cover a further 46% of the ground area. Vegetation communities include *Balanites aegyptiaca*, *Acacia raddiana*, *Acacia seyal*, *Pterocarpus lucens*, *Grewia bicolour*, *Boscia senegalensis*, *Acacia nilotica* and *Salvadora persica* among others. The only tarred road is the RN16 highway. Traditional nomadism and transhumance (Breman and de Wit, 1983) is practiced by the majority Fulani and Touareg ethnic groups, who follow their livestock to water and pasture. Recent sedenterization is leading to changes in land use and expansion of an agricultural lifestyle.

Rainfall follows a north–south gradient with cumulative annual totals ranging between 110 mm in the north and 600 mm in the south. Based on average annual rainfall totals from 1998 to 2008 measured at three rain gauge sites at *Boni*, *Gossi* and *I-n-adianatafane* (Fig. S2), the months early June to late September were defined as the wet season with rainfall peaking in July–August (Fig. S2). Temperatures follow a seasonal cycle with the months of November–January being relatively cool with night-time temperatures below 10 °C, and peaking during the hot season in May, when daytime highs can reach above 50 °C.

During the dry season, surface water is limited to a series of shallow lakes that are recharged by precipitation. These lakes often occur along drainage paths or the interface between dunes and plateaus. *Adiora*, *Agofou*, *Banzena* and *Gossi* are the only lakes within the current elephant range that usually retain water throughout the year, although even they can also dry up completely. Droughts have affected the region over the years (Agnew and Chappel, 1999) with the most recent one occurring in 2009 (Douglas-Hamilton and Wall, 2009).

2.2. Elephant position data

In March 2008, nine Global Positioning System (GPS) tracking collars were deployed on four female and five male elephants (Table S1). Individuals were randomly selected from across the study area, but each female was selected so as to represent a separate herd. Each collar (Followit, 2011) was set to acquire a GPS position every hour.

GPS data collected from collars were filtered using an upper, biologically based threshold speed of 7 km/h (elephant hourly movement distances do not exceed 6.5 km (Douglas-Hamilton pers. obs)) to weed out erroneous fixes caused by GPS error. We calculated the consistency of collars at reporting accurate GPS fixes every scheduled hour during the working lifetime of the collar (Table S1). All spatial data were projected to the Universal Transverse Mercator (UTM) WGS-84 reference system (Zone 30 N). All further calculations were made on this filtered and projected dataset.

2.3. Home range metrics: MCP, Kernel, α -LoCoH and time-density

One hundred percent Minimum Convex Polygon (MCP) home ranges (Mohr, 1947) and Localized Convex Hull (LoCoH) home ranges parameterized using maximum displacement (α -LoCoH) (Getz et al., 2007) were calculated for both total available data ($n = 8$; data from the bull 'El Mozaar' was dropped from all analyses because of its poor quality – see Tables 2 and S1) and, for those individuals with at least 1 year of data; 1st year data only ($n = 6$). 50% and 90% Gaussian kernel home ranges using least-squares cross validation (LSCV) were also calculated using Hawth's Tools (Beyer, 2004).

Grid areas were calculated using total and 1st year data as follows: a 500 m resolution grid (selected to be approximately double the median hourly movement distance and aligned with

the closest whole number 500 m UTM division in both easting and northing) was draped over the terrain and any grid that contained a fractional track segment was counted towards the grid area. Ratios of MCP ranges to grid ranges were calculated using 1st year movement data. The ratio provides a metric of how concentrated the movement of each animal is within the space delineated by the MCP area.

A 'time-density' grid was generated for each elephant to look at the distribution of time spent per unit of landscape across the study region, in effect, an estimation of an elephant's utilization distribution (UD) (Marzluff et al., 2001). The number of hours an elephant spent within each 500 m grid cell was determined by summing the fractional linear path lengths between successive GPS points that fell within a particular 500 m grid cell. Consider a pixel G at row i and column j . The time spent within G is then calculated as:

$$T_G = \sum_{k=1}^N \frac{d_k}{s_k} \quad (1)$$

where d_k is the fractional length of track segment k that intersects pixel G , N is the total number of track segments in the animal's trajectory and s_k is the animal's linear speed over track segment k .

Time-density grids for each elephant were normalized by dividing each grid cell value by the total tracked time for the particular elephant. A merged grid was generated for both males and females where each pixel represents a percentage of the total tracked hours spent within the grid cell. The male and female percentage grids were then multiplied to generate a percentage overlap grid.

A search was made for time-density hot-spots by identifying particular groups of pixels where elephants were spending the majority of their time. We used the upper 5% percentile value, calculated from the respective male and female time-density grid values, to define a cut-off point for each grid. Only those pixels in the upper 5% were considered further. We then ranked clusters of adjacent pixels (hot-spots) in descending order based on the total number of pixels in the grouping (adjacency of a pixel to another was defined as requiring two pixels to touch on any of the four possible sides or four corners).

2.4. Linear movements

First-year total movement distance was calculated for those elephants with at least 95% temporal coverage for the first full year of data collection. The maximum linear path distance moved by each elephant within a 24 h period was calculated using a running window in which any 24 h section that contained less than 95% temporal coverage was excluded. Maximum hourly displacements were calculated as the maximum straight-line distances between any two successive data-positions collected within 1.1 h of each other.

We developed a 'velocity-grid' designed to illustrate the relative movement patterns and speeds of elephants throughout the range by first rasterizing the landscape and calculating statistics related to velocity within each raster grid cell. Raster grids were aligned to the time-density grids calculated previously but with a larger 5 km pixel size chosen to better generalize the movement tracks. Statistics were calculated using all track segments that originated from within the given grid and included mean speed, mean heading and the mean positive dot-product of unit track segments calculated as follows:

$$\frac{\sum_{i \neq j}^N |\cos \theta_{ij}|}{\sum_0^{N-1} n} \quad (2)$$

where θ_{ij} is the angle between track segment j and segment i and the summation of the absolute cosine value is made over N seg-

ments but only for unique combinations of i and j since $i \cdot j = j \cdot i$. The average dot-product value results in a range between 0 (undirected movement) and 1 (directed movement). For each pixel, a single output vector with its origin at the center of the given pixel was created pointing in the mean track direction and colored according to the mean dot-product value (0 – green, 0.5 – yellow, 1 – red). The length of the vector was scaled to represent the mean of the speeds within each grid. Separate male and female velocity-grids were created from merged data from each sex.

A k means cluster analysis (Tou and Gonzalez, 1974) was used to classify the male and female mean speed and mean dot-product grids into two classes. The classification was made to segment the velocity-grid into areas of slower, non-directional movement and those of fast, directed movement. To quantify the degree of spatial-connectedness of directed and undirected grid cells, we calculated a mean 'contiguity' index (LaGro, 1991) for clustered patches of both directed and undirected grid cells using the 'CONTIG' algorithm in Fragstats 3.3 (McGarigal et al., 2002).

2.5. Movement pattern

We assessed localized changes in range use over the study period by calculating and plotting the centroid coordinate of positions that fell within successive week-long periods (weekly arithmetic mean of X and Y hourly UTM coordinates) for every male and female elephant. North–South movements and east–west movements were considered independently.

2.6. NDVI

Vegetation biomass and verdancy are both measurable using spectral indices (Peñuelas and Filella, 1998). NDVI is an indicator of vegetation productivity phenology (Rouse et al., 1973). To understand drivers of the elephant migration, we examined NDVI selection patterns throughout the range. NDVI was measured using the SPOT-Image 10-day aggregate S10 data product (available at <http://free.vgt.vito.be>), which has a 1000 m pixel resolution. A global MCP (GMCP) range calculated from all available data from both male and female elephants was used to delineate an overall region (Fig. S1) from which the mean NDVI values ($NDVI_{GMCP}$) were calculated over each 10-day period between April 1, 2008 and September 30, 2010. A localized mean NDVI value ($NDVI_{LoCoH}$) was calculated from concomitant 10-day α -LoCoH home ranges and compared to the ecosystem-wide value. The difference between the localized α -LoCoH mean NDVI value and the global mean MCP value ($NDVI_{GMCP}$) was termed 'DiffNDVI'.

$$DiffNDVI = NDVI_{LoCoH} - NDVI_{GMCP} \quad (3)$$

2.7. Statistical analyses

We used paired and unpaired t -tests to look at inter-sex, season and photo-period differences of mean hourly path distances as well as for comparison of mean first-year cumulative distances between sexes. We also used t -tests to compare 1st year home range metrics between male and female elephants. Wilcoxon Rank Sum tests were used when assumptions of normality were violated as dictated by Shapiro–Wilk normality tests (Crawley, 2007).

Differences in selection for NDVI between males and females and during wet and dry seasons were assessed using a linear mixed-effects model (Pinheiro and Bates, 2000) with a continuous time autoregressive lag-1 correlation (corCAR1) structure to account for temporal and spatially correlated observations of NDVI between successive 10-day periods. Statistical modeling was performed using the 'nlme' package in R (Pinheiro et al., 2011). Our model specification was:

$$DiffNDVI_{it} = \beta_0 + \beta_1 SEX_i + \beta_2 SEASON_{it} + \beta_3 SEX_i SEASON_{it} + \varepsilon_i + \delta_{it} \quad (4)$$

where *DiffNDVI* is the difference between *NDVI_{LoCoH}* and *NDVI_{GMCP}* for elephant *i* at time measurement *t*, ε_i are the random effects associated with elephant *i* and having variance $Var(\varepsilon_i) \sim N(0, \sigma_s^2 I)$ where *I* is the identity matrix, *N* is the normal distribution and σ_s^2 a constant. δ_{it} are the model residuals with variance $Var(\delta_{it}) \sim N(0, R)$ and covariance matrix:

$$R = \begin{cases} C(k) & i = i' \\ 0 & i \neq i' \end{cases} \quad (5)$$

where *C(k)* is defined as:

$$C(k) = \sigma^2 e^{-\frac{|t_{ij}-t_{i'j'}|}{\phi}} \quad (6)$$

where $k = t_{ij} - t_{i'j'}$, *j* indexes successive measurement times, σ^2 is a constant and ϕ is a constant related to the practical range of the correlated time-series (Schabenberger and Pierce, 2002).

3. Results

3.1. Movement pattern

A strong north–south annual movement component was observed among all individuals (Fig. 1). A strong east–west movement was also observed in all female elephants and one male, that when combined with the north–south movements, took the form of a circular pattern traversed in a counter-clockwise direction (Fig. S1). The remaining four males adopted different patterns including ‘figure 8’ and ‘L’ shape landscape movements and thus the east–west movements were not as clearly defined. Movements south coincided with the onset of rains while movements north were less coordinated and varied by sex with males taking longer to return to the northern range.

3.2. NDVI selection

Elephants tended to use areas of greater NDVI in the study ecosystem throughout the study duration, with the strongest differentiation between areas used (α -LoCoH) versus ecosystem total (GMCP) during the start of the wet seasons (Fig. 2). Model selection, based on log-likelihood ratio deletion tests, indicated covariates of sex, and the interaction of sex by season, did not provide additional explanatory power of NDVI selection. The reduced model explained a significant amount of the variation in the data ($p < 0.001$). Both wet ($\bar{y} = 5.86$; $p < 0.001$) and dry ($\bar{y} = 2.57$; $p < 0.001$) season mean NDVI selection values were significantly greater than zero while wet season selection was significantly greater than dry season selection ($p < 0.001$). The estimated within-individual practical range parameter (Eq. (6)) between repeat time measures was $\phi = 0.52$. The estimated standard deviation of the random inter-elephant variation was $\sigma_{\varepsilon} = 0.0005$ and the standard deviation parameter (Eq. (6)) of intra-elephant variation was $\sigma = 6.925372$.

3.3. Home-range

No significant difference was found between female 1st Year MCP home ranges (mean = 24,196 km²) and those of males (mean = 15,860 km²) ($t = 1.986$, $p = 0.1303$, Table 1). The largest recorded total MCP range was 32,062 km² by female ‘Ramata’. Grid ranges were smaller than MCP ranges and no significant difference between 1st year female (mean = 1415 km²) and male (mean = 1200 km²) grid ranges was found ($t = 0.987$, $p = 0.380$, Table 1). Ratios of 1st year MCP to 1st year grid range areas ranged between 22.0 and 11.7 (Table 2) with a mean ratio for females of 17.1 and 13.2 for males, indicating male range was more concentrated in space than that of females. Total and 1st year α -LoCoH home range, and total 50% and 90% kernel home-ranges are provided in Table 2.

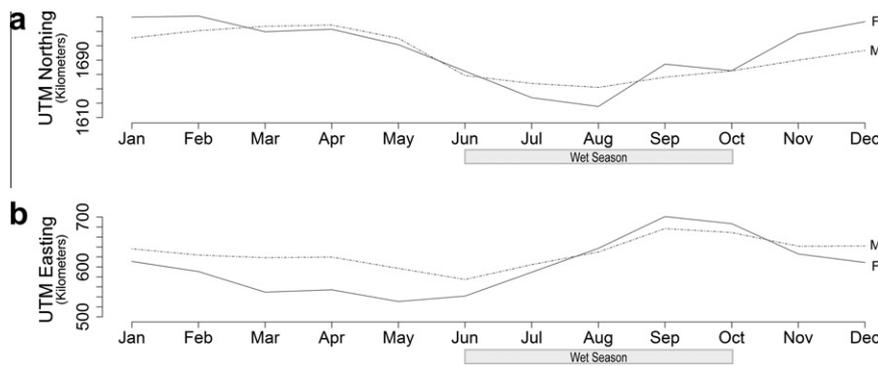


Fig. 1. Weekly mean position centroid Northing (a) and Easting (b) coordinates for female (solid line) and male (dashed line) elephants plotted against the month in which they occurred. Wet season months are shaded gray.

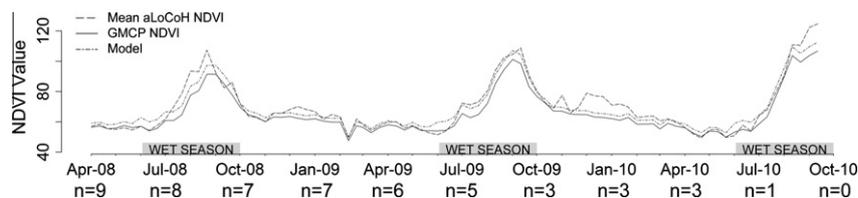


Fig. 2. Time series NDVI values showing the 10-day global MCP mean value – *NDVI_{GMCP}* (solid line), the 10-day α -LoCoH values – *NDVI_{LoCoH}* averaged over all nine elephants (dashed line) and the predicted values from our NDVI selection model (dash-dot line). *n* is the number of samples used in calculating the means.

Table 1
Summary of statistical analyses of linear metrics and home-ranges.

Calculation	Statistic	Female	Male	Significance (female > male)
Hourly displacement (km/h)	Mean	0.47	0.45	No Diff ($p = 0.397$)
1st Year path distance (km)	Mean	3968	3984	No Diff ($p = 0.977$)
Total MCP range (km ²)	Max	32,062	20,906	–
1st Year MCP range (km ²)	Mean	24,196	15,860	No Diff ($p = 0.130$)
1st Year grid range (km ²)	Mean	1415	1200	No Diff ($p = 0.380$)
MCP/grid ratio	Mean	17.1	13.2	–
Time spent north of N16	Sum	65.2%	47.7%	–

Table 2
Summary of home-range metrics. Where insufficient data was available to calculate a given metric, the table entry was left blank.

Elephant	1st Year MCP area (km ²)	Total MCP area (km ²)	1st Year LoCoH area (km ²)	Total LoCoH area (km ²)	1st Year 500 m grid area (km ²)	Total 500 m grid area (km ²)	1st Year MCP/grid ratio	Total 50% kernel area (km ²)	Total 90% kernel area (km ²)
Bahati (F)	–	15515	–	2051	–	584	–	64	503
Mariam (F)	19573	20347	4081	4235	1182	1291	16.6	120	898
Ramata (F)	31139	32062	5061	5379	1380	1727	22.6	199	1337
Tombouctou (F)	21877	23658	4835	5399	1682	2221	13.0	276	1816
Achar (M)	11745	12023	2504	3660	1005	1516	11.7	126	689
Ali Farka Touré (M)	16275	17612	4210	5407	1072	2057	15.2	93	902
Amadou (M)	–	18262	–	4001	–	1175	–	84	794
El Mozaar (M)	–	–	–	–	–	–	–	–	–
Salif Keita (M)	19561	20906	5484	7479	1522	2979	12.8	220	1755
Mean:	20028	20048	4362	4701	1307	1694	15	148	1087
SD:	6481	6003	1051	1603	266	733	4	75	492

Of the total time-density home-range grid cells occupied within the landscape, male and female overlap was 23.9% (Fig. S1, green pixels). Max grid cell values were 1.32% of total tracked hours for females and 1.07% for males (Fig. 3). The top six male and female time-density hot-spots were found to correspond with the top six 50% kernel home-range areas as ranked in order of size (Fig. 3) and encompassed 28.2% (female) and 31.6% (male) of the total tracked hours.

3.4. Linear movements

Hourly speeds and displacements had a maximum value of 6.10 km/h for females and 6.43 km/h for males (Table 3). There was no significant difference in mean hourly speed between males ($\bar{s}_{male} = 0.45$ km/h) and females ($\bar{s}_{female} = 0.47$ km/h) ($t = 0.904$, $p = 0.397$, Table 1) but night-time speeds ($\bar{s}_{night} = 0.52$ km/h) were significantly greater than daytime speeds ($\bar{s}_{day} = 0.36$ km/h) for all elephants (Paired t -test; $t = 7.783$, $p < 0.001$). A significant difference in seasonal hourly speeds was found (Paired t -test; $t = 2.933$, $p = 0.019$) with a higher wet season value ($\bar{s}_{wet} = 0.48$ km/h) compared to a lower dry season value ($\bar{s}_{dry} = 0.41$ km/h).

Six collars yielded datasets longer than a year in duration. From these six, the mean male 1st year distance of 3984 km was not significantly different from the mean female distance of 3968 km. ($t = 0.031$, $p = 0.977$; Table 1). The greatest distance covered by any of the elephants in a single 24 h period was performed by the female 'Bahati' who moved 64.7 km. This occurred immediately after her collar was fitted suggesting this high value does not represent normal behavior. The longest 24-h male movement was 49.0 km.

Velocity-grids (Fig. 4a and b) segmented into directed versus undirected grid cells using k means clustering show that females (Fig. 4c) had proportionally fewer directed grids than males (Fig. 4d) (19.3% of total grid cells compared to 26% for males). Females had an area-weighted mean contiguity index value of 0.20 (directed movement) and 0.61 (undirected movement) while males had an area-weighted mean contiguity index value of 0.28 (directed movement) and 0.63 (undirected movement).

4. Discussion

4.1. Circular movement patterns

The north–south annual movements performed by all individuals, and east–west movements performed by some, suggest that resource gradients are important to the Gourma elephants' ecology and survival. Numerous factors exist that contribute to the timing of the latitudinal movement pattern. Principal among these is thought to be the annual rainfall cycle and elephant movements are generally known to be strongly controlled by water availability during the dry season (Western, 1975; Smit et al., 2007; Chamaillé-Jammes et al., 2007; de Beer and van Aarde, 2008). At the peak of the dry season, water within the elephant home-range is limited to a series of shallow, surface fed lakes that exist only in the northern range and are prone to drying completely during drought years (Douglas-Hamilton and Wall, 2009). Furthermore, available water is used heavily by livestock and people, leading to competition with elephants (Ganamé et al., 2009). The movement south (Fig. 1) coincides with the onset of sufficient rain for surface water pooling and alleviates the reliance on larger lakes. Closely associated with rainfall quantity is plant productivity, and a north–south NDVI gradient emerges that peaks in September (Fig. S3). Both male and female elephants reached the southern bounds of their range prior to peak rainfall in July/August, with the movement south being faster than the more gradual return north between August and January (females) and from August to April (males). The elephants tended to leave the southern point of the range before peak NDVI had occurred in September but at a time when NDVI was also relatively high in the north. NDVI declines to a minimum by the months of February–April, when cow/calf groups are again located in proximity to permanent water (Fig. S3). Selection for higher than average NDVI occurred during both the wet and dry season, but particularly during the wet season when elephants were not dependent on surface water points (Fig. 2). The timing and rate of desiccation of water sources in the south have not yet been measured, but may also influence movement behavior.

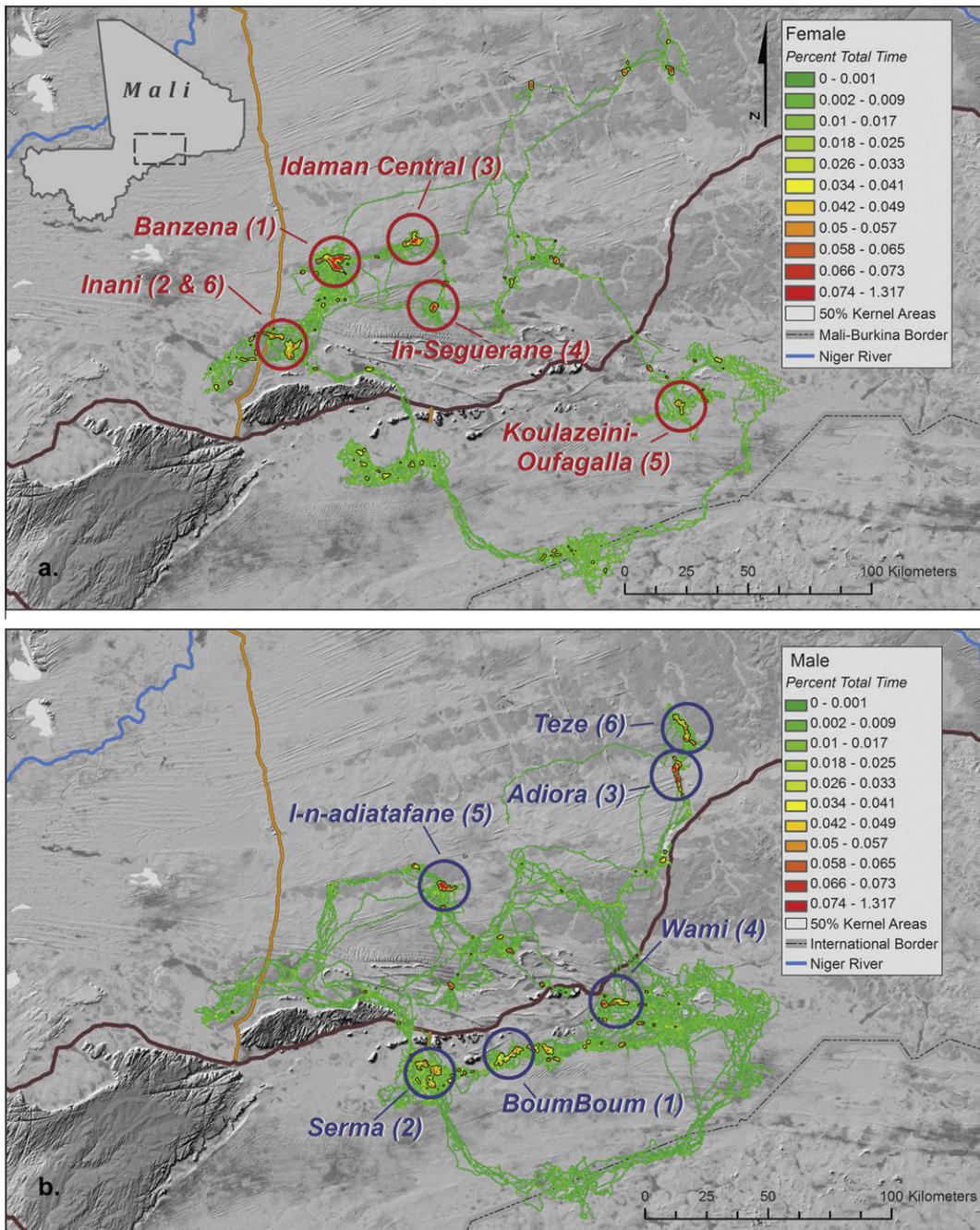


Fig. 3. (a) Female Time-Density home-range as percent of total hours tracked. Values range from 0% (green) to 1.32% (red). (b) Male Time-Density home-range as percent of total hours tracked. Values range from 0% (green) to 1.07% (red) and use the color scheme as females. The top six hot-spot areas are named while the 50% kernel density areas have been encircled in black.

Previous work in the Malian Sahel by Breman and de Wit (1983) demonstrates that plant nutritional quality increases along a south to north gradient. Their study showed that north of the 300 mm/yr isohyet is where water availability, as compared to nitrogen and phosphorous, begins to limit plant growth, and protein levels were found to increase, peaking in July and August. As such, this southern movement may indicate temporary selection for higher biomass and plant verdancy rather than a search for limiting nutrients as described in other migration systems (Holdo et al., 2009). Prior to peak NDVI, the elephants began moving north into lower biomass areas. It is possible the movements are driven by the faster greening of the southern portion of their range once the rains begin, followed by a slower diffusion north-

ward to access higher quality resources prior to their desiccation as the rains cease.

The east–west movement patterns are not well understood but possibly emerge from elephants trying to reach specific, localized resources, such as mineral deposits (Weir, 1972) or east–west gradients in vegetation species, while still maintaining an overall optimal latitudinal movement strategy, and results in the observed circular pattern. Further study of elephant diet and vegetation nutritional quality in the different parts of the range is needed in order to gain a more comprehensive understanding of the relationship between the temporal movements of elephants and the dynamics of vegetation protein, nutrient levels, and biomass and their resulting selection for vegetation type at varying times of the year.

Table 3

Summary of linear path metrics from each elephant. In some cases, insufficient tracking data was acquired to calculate a given metric and values have been left correspondingly blank.

Elephant	1st Year Path Distance (km)	Max Hourly Displacement (km)	Max 24 Hour Path Distance (km)
Bahati (F)	–	5.39	64.68
Mariam (F)	3541	6.10	34.08
Ramata (F)	3629	6.08	32.63
Tombouctou (F)	4734	6.06	49.33
Achar (M)	3725	5.74	35.05
Ali Farka Touré (M)	3602	5.22	46.62
Amadou (M)	–	5.24	49.00
El Mozaar (M)	–	–	–
Salif Keita (M)	4624	6.43	31.61
Mean	3976	5.78	42.87
SD	549	0.45	11.58

4.2. Spatio-temporal partitioning of movement behavior

The velocity-grid method is a conceptually straightforward, spatially-explicit method of empirically characterizing modes of movement behavior and complements other sophisticated model-based, state-space approaches (Morales et al., 2004; Preisler et al., 2004). Our velocity-grid methodology was able to differentiate explicit movement patterns by classification of combined directional similarity and speed of movement metrics using the k means classification algorithm (Fig. 4) which resulted in mapped ranges of quick, directed movement compared to ranges of slow, undirected movement and is highly useful for geolocating and identifying characteristics of a migration path. Beyond the two base classes, it is theoretically possible to extend the method to include other biologically interesting modes of movement behavior.

As seen in Fig. 4c and d, and as indicated with the contiguity index, grids of directed and undirected movement tended to form

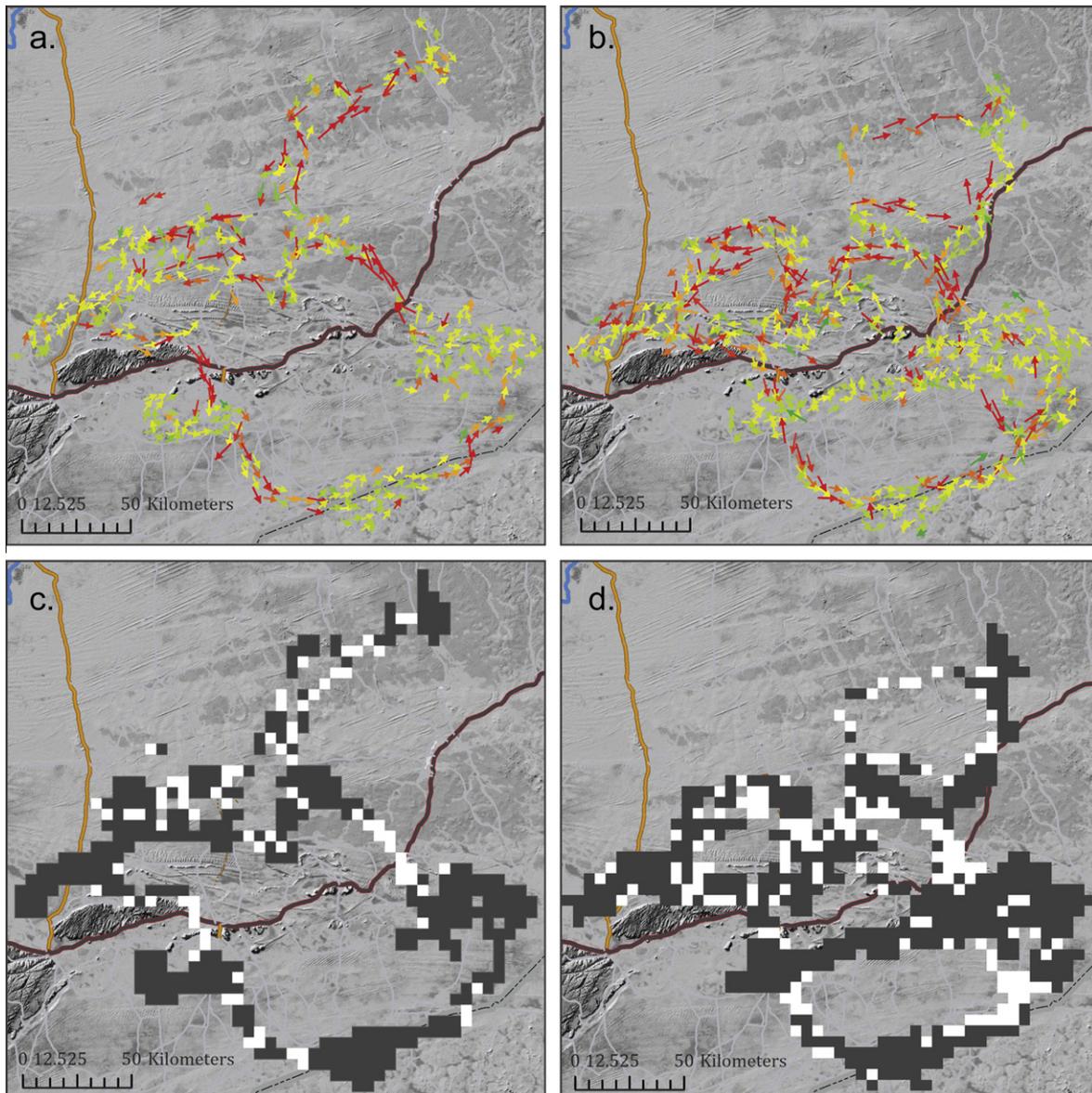


Fig. 4. (a) Female and (b) male velocity-grids. Arrows originate from the center of 5 km grid cells from which calculations were made. Arrow direction indicates mean track direction, arrow length indicates the mean speed and the coloring indicates similarity in track direction as calculated using the mean of the absolute value of track dot-products (red = high; green = low). Results of the k means classification for (c) females and (d) males. The 'Directed' class (high mean dot-product and high mean speed) is shown in white and the 'Undirected' class (low mean dot-product and low mean speed) is shown in gray.

Table 4
Results of statistical comparison between Mali elephants and Kenya elephants.

Calculation	Statistic	Mali	Kenya	Significance (Mali > Kenya)
1st Year path distance (km)	Mean	3976	3523	No Diff ($p < 0.056$)
1st Year MCP range (km ²)	Mean	20,028	1388	Greater ($p < 0.001$)
1st Year Grid range (km ²)	Mean	1307	468	Greater ($p < 0.001$)

connected spatial blocks indicating aggregated regions of similar movement behavior. Notably, the two largest contiguous female directed-clusters occurred where their movement track crossed the RN16 highway. Similar road response behavior has been recorded in *Loxodonta cyclotis* (Blake et al., 2008). Although there was no significant difference between overall male/female movement speeds, males had 6.7% more directed grid cells than females and this could be the result of male 'musth' behavior driving periods of increased speed and directed movement (Rasmussen, 2005).

Like seasonal differences recorded elsewhere in Africa (Western and Lindsay, 1984; Wittemyer et al., 2007; Young et al., 2009), the greater distances moved in the wet compared to dry season are likely a function of water availability and elephants not being tied to specific dry season water points. The significantly greater night-time movement speeds likely arise from the cooler temperatures and the potential for fewer interactions with people (Graham et al., 2009).

4.3. Spatial utilization heterogeneity

Our time-density methodology quantifies the amount of time spent by an elephant per unit area, providing a time-weighted UD which gives fine-grained detail of relative and absolute elephant spatial-temporal use across the study site. It is more straightforward to interpret than other methods which require smoothing (though time-density requires choosing a bin size) or assume certain distributional forms, and similar to the idealized nonparametric estimator proposed by White and Garrott (1990). Time-density grids showed heterogeneous utilization of the landscape by both males and females (Fig. 3), indicating a spatial partitioning between different spatial resources. Interestingly, none of the aggregated high-use areas (hot-spots) overlapped amongst the sexes and suggests different resource priorities and life strategies between males and females.

Higher female MCP/Grid area ratio values indicate more concentrated local movements and 'negative' space (areas not visited) compared to males. Clustering of water and vegetative resources, which correlate with underlying physiography, most likely explains the emergent spatial distribution. Only 23.9% of occupied landscape units were shared.

The maximum range size reported here was the largest in areal extent (MCP) ever recorded for elephants (150.4% larger than in Namibia (Leggett, 2006) and 29.1% larger than in Botswana (Chase, 2007)). The daily and annual travel distances of the Gourma elephants were notably similar to those of other arid lands elephant populations ($W = 41, p < 0.56$; Table 4), whereas home-ranges were significantly larger ($W = 54, p < 0.001$, Table 4), indicating the Mali elephants spend less time per unit landscape than other semi-arid elephants but expend similar energy budgets on movement. This is likely a reflection of the widely distributed nature of resources in the Sahel relative to other elephant habitats in Africa. Of interest are the seemingly viable resources outside the currently recorded range, such as the water abundant Niger River to the north, that are seldom used. Further study is needed to look at vegetation gradients in relation to elephant nutritional requirements and at human presence and settlements outside of the recorded range, to understand this lack of use. For example, vegetation abundance

along the Niger river may simply be too low and human density too high, to sustain elephant populations north of their current range.

4.4. Conservation priorities

Establishment of anthropogenic barriers and habitat-loss have historically been prime factors in the collapse of migratory systems (Bolger et al., 2008). Identification of vulnerable crux-points, both spatial bottle-necks and core spatial resources, along frequently used movement paths is a critical step towards conservation of wide-ranging systems. Here, we identified high use regions by assessing the relative proportion of time spent per grid square across the landscape. High-use regions identified using the time-density methodology corresponded well with those from the traditional kernel estimator. These hot-spots (e.g. Lake Banzena – Fig. 3) are critical to the spatial integrity of this recorded movement system and may be crux points on which the survival of the population is dependent.

The velocity-grid cartographic output and directed grid cell classification highlighted possible bottle-necks to the movements of the Mali elephants. The most prominent example based on the directed class patch size and constraining local topography was identified at position 7 (Fig. S1). Known locally in French as 'La Porte des Éléphants' (Translation: 'Elephant Doorway') it corresponds to a one mile (1.6 km) wide valley through sandstone inselbergs (Fig. S4). Our initial analyses identify these spatial cruxes, such as *La Porte des Éléphants*, which appear to be critical to the continued functioning of this exceptional system.

Acknowledgments

We thank the Government of Mali (Ministry of Eaux et Forêt) for supporting and facilitating this research, the US Embassy, Bamako for their logistical support, and Mr. El Mehdi Doumbia (Chef d'Antenne, Eaux et Forêts, I-n-adiatafane) for local elephant knowledge and community liaison. Funding for the tracking collars and collar deployment was supplied by the African Parks Foundation (APF) through the generosity of the late Paul van Vlissingen. All data collection and project management was provided by Save the Elephants. We thank the Prince Bernhard Fund for Nature, the WILD Foundation and Caroline Tisdall for their donations, and Dr Susan Canney for field collaboration. The ESRI Conservation Program (ECP) donated the latest ArcGIS software used in many of the analyses. We would also like to acknowledge the Save the Elephants elephant collaring team for their work in 2008, and the Canadian National Science and Research Council (NSERC), whose support made this doctoral work possible. We also thank two anonymous reviewers and Grant Hopcraft for their helpful comments that greatly improved the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.07.019>.

References

- Agnew, C.T., Chappel, T., 1999. Drought in the Sahel. *GeoJournal* 48, 299–311.
- Berger, J., 2004. The last mile: how to sustain long-distance migration in mammals. *Conserv. Biol.* 18, 320–331.
- Berger, J., Cain, S.L., Berger, K.M., 2006. Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biol. Lett.* 2, 528–531.
- Berger, J., Young, J.K., Berger, K.M., 2008. Protecting Migration Corridors: Challenges and Optimism for Mongolian Saiga. *PLoS Biol.* 6, e165. <http://dx.doi.org/10.1371/journal.pbio.0060165>.
- Beyer, H.L., 2004. Hawth's Analysis Tools for ArcGIS. <<http://www.spatial ecology.com/htools>> (accessed July 2011).
- Blake, S., Bouché, P., Rasmussen, H.B., Orlando, A., Douglas-Hamilton, I., 2003. Report: The last Sahelian elephants. Ranging Behavior, Population Status and Recent History of the Desert Elephants of Mali. Save the Elephants, Kenya. <<http://www.savetheelephants.org/publications.html>>.
- Blake, S., Deem, S.L., Strindberg, S., Maisels, F., Momont, L., Isia, I.-B., Douglas-Hamilton, I., Karesh, W.B., Kock, M.D., 2008. Roadless Wilderness Area Determines Forest Elephant Movements in the Congo Basin. *PLoS ONE* 3, e3546. <http://dx.doi.org/10.1371/journal.pone.0003546>.
- Blanc, J.J., Barnes, R.F.W., Craig, G.C., Dublin, H.T., Thouless, C.T., Douglas-Hamilton, I., Hart, J.A., 2007. African Elephant Status Report 2007: An update from the African Elephant Database. <<http://www.african-elephant.org/aed/aesr2007.html>> (accessed July, 2011).
- Bolger, D.T., Newmark, W.D., Morrison, T.A., Doak, D.F., 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecol. Lett.* 11, 63–77.
- Börger, L., Matthiopoulos, J., Holdo, R.M., Morales, M., Couzin, I., McCauley, E., 2011. Migration quantified: constructing models and linking them with data. In: Milner-Gulland, E.J., Fryxell, J.M., Sinclair, A.R.E. (Eds.), *Animal Migration: a synthesis*. Oxford University Press Inc., New York, pp. 111–128.
- Bouché, P., Doamba, B., Sissoko, B., Bouju, S., 2009. Les éléphants du Gourma, Mali: Statut et menaces pour leur conservation. *Pachyderm* 45, 47–56.
- Bouché, P., Douglas-Hamilton, I., Wittemyer, G., Nianogo, A.J., Doucet, J.-L., Lejeune, P., Vermeulen, C., 2011. Will elephants soon disappear from West African Savannas? *PLoS ONE* 6, e20619. <http://dx.doi.org/10.1371/journal.pone.0020619>.
- Breman, H., de Wit, C.T., 1983. Rangeland productivity and exploitation in the Sahel. *Science* 221, 1341–1347.
- Chamaillé-Jammes, S., Valeix, M., Fritz, H., 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *J. Appl. Ecol.* 44, 625–633.
- Chase, M.J., 2007. Home ranges, transboundary movements and harvest of elephants in northern Botswana and factors affecting elephant distribution and abundance in the Lower Kwando River Basin. Electronic Doctoral Dissertations for UMass Amherst. Paper AAI3290051. <<http://scholarworks.umass.edu/dissertations/AAI3290051>> (accessed September 2011).
- Crawley, M.J., 2007. *The R Book*. John Wiley & Sons.
- de Beer, Y., van Aarde, R.J., 2008. Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *J. Arid Environ.* 72, 2017–2025.
- Dobson, A.P. et al., 2010. Road will ruin Serengeti. *Nature* 467, 272–273.
- Douglas-Hamilton, I., Wall, J., 2009. Drought threatens Mali elephants. *Pachyderm* 45, 129–130.
- Followit, 2011. <www.followit.se> (accessed June 2011).
- Fryxell, J.M., Sinclair, A.R.E., 1988a. Causes and consequences of migration by large herbivores. *TREE* 3, 237–241.
- Fryxell, J.M., Sinclair, A.R.E., 1988b. Seasonal migration of white-eared Kob in relation to resources. *Afr. J. Ecol.* 26, 17–31.
- Ganamé, N., Bah, B., Maiga, A., 2009. Report: Study on the Liberation from Human and Livestock Pressure of Lake Banzana in the Gourma of Mali. Ministère de l'Environnement et de l'Assainissement, Mali.
- Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., Wilmers, C.C., 2007. LoCoH: Nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE* 2, e207. <http://dx.doi.org/10.1371/journal.pone.0000207>.
- Graham, M.D., Douglas-Hamilton, I., Adams, W.M., Lee, P.C., 2009. The movement of African elephants in a human-dominated land-use mosaic. *Anim. Conserv.* 12, 445–455.
- Grove, A.T., 1978. Geographical introduction to the Sahel. *The Geographical Journal* 144, 407–415.
- Harris, G.M., Russell, G.J., van Aarde, R.J., Pimm, S.L., 2008. Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx* 42, 66–75.
- Harris, G., Thirgood, S., Hopcraft, J.G.C., Cromsigt, J.P.G.M., Berger, J., 2009. Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Res.* 7, 55–76.
- Holdo, R.M., Holt, R.D., Fryxell, J.M., 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *Am. Nat.* 173, 431–445.
- Holt, R.D., Fryxell, J.M., 2011. Theoretical reflections on the evolution of migration. In: Milner-Gulland, E.J., Fryxell, J.M., Sinclair, A.R.E. (Eds.), *Animal Migration: A Synthesis*. Oxford University Press Inc., New York, pp. 17–31.
- Jonzén, N., Knudsen, E., Holt, R.D., Sæther, B.-K., 2011. Uncertainty and predictability: the niches of migrants and nomads. In: Milner-Gulland, E.J., Fryxell, J.M., Sinclair, A.R.E. (Eds.), *Animal Migration: A Synthesis*. Oxford University Press Inc., New York, pp. 91–109.
- Kröplin, S. et al., 2008. Climate-driven ecosystem succession in the Sahara: the past 6000 years. *Science* 320, 765–768.
- LaGro, J., 1991. Assessing patch shape in landscape mosaics. *Photogram. Eng. Remote Sens.* 57, 285–293.
- Leggett, K.E.A., 2006. Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. *Afr. Zool.* 41, 17–36.
- Loarie, S.R., van Aarde, R.J., Pimm, S.L., 2009. Fences and artificial water affect African savannah elephant movement patterns. *Biol. Conserv.* 142, 3086–3098.
- Marzluff, J.M., Knick, S.T., Millspaugh, J.J., 2001. High-Tech Behavioural Ecology: Modeling the Distribution of Animal Activities to Better Understand Wildlife Space Use and Resource Selection. In: Millspaugh, J.J., Marzluff, J.M. (Eds.), *Radio-Tracking and Animal Populations*. Academic Press, Oxford, pp. 309–326.
- McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer Software Program Produced by the Authors at the University of Massachusetts, Amherst. <<http://www.umass.edu/landeco/research/fragstats/fragstats.html>> (accessed October 2011).
- McNaughton, S.J., Ruess, R.W., Seagle, S.W., 1988. Large mammals and process dynamics in African ecosystems. *Bioscience* 38, 794–800.
- Mohr, C.O., 1947. Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* 37, 223–249.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E., Fryxell, J.M., 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85, 2436–2445.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci.* 105, 19052–19059.
- Owen-Smith, N., 1988. Megaherbivores: The Influence of Very Large Body Size on Ecology. Cambridge University Press, Cambridge.
- Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J., 2008. State-space models of individual animal movement. *Trends Ecol. Evol.* 23, 87–94.
- Peñuelas, J., Filella, L., 1998. Visible and near infrared reflectance techniques for diagnosing plant physiological status. *Trends Plant Sci.* 3, 151–156.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-effects Models in S and S-Plus*. Springer, New York.
- Pinheiro, J.C., Bates, D.M., debRoy, S., Sarkar, D., R Core Team., 2011. nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-98. <<http://cran.r-project.org/web/packages/nlme/index.html>> (accessed August 2011).
- Preisler, H.K., Ager, A.A., Johnson, B.K., Kie, J.G., 2004. Modelling animal movements using stochastic differential equations. *Environmetrics* 15, 643–657.
- Rasmussen, H.B., 2005. Reproductive Tactics in Male African Savannah Elephants (*Loxodonta africana*). Ph.D. Thesis, Oxford University, Oxford.
- Rouse, J.W., Haas, R.H., Schell, J.A., Deering, D.W., 1973. Monitoring vegetation systems in the Great Plains with ERTS. Proceedings of the Third Earth Resources Satellite-1 Symposium (Maryland: NASA SP-351), pp. 309–317.
- Sawyer, H., Kauffman, M.J., Nielson, R.M., Horne, J.S., 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecol. Appl.* 19, 2016–2025.
- Schabenberger, O., Pierce, F.J., 2002. *Contemporary Statistical Models for the Plant and Soil Sciences*. CRC Press, Boca Raton, FL, pp. 738.
- Sinclair, A.R.E., Fryxell, J.M., 1985. The Sahel of Africa: ecology of a disaster. *Can. J. Zool.* 63, 987–994.
- Smit, I.P.J., Grant, C.C., Devereux, B.J., 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biol. Conserv.* 136, 85–99.
- Tou, J.T., Gonzalez, R.C., 1974. *Pattern Recognition Principles*. Addison-Wesley, Massachusetts, pp. 377.
- Weir, J.S., 1972. Spatial distribution of elephants in an African National Park in relation to environmental sodium. *Oikos* 23, 1–13.
- Western, D., 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *Afr. J. Ecol.* 13, 265–286.
- Western, D., Lindsay, W.K., 1984. Seasonal herd dynamics of a savannah elephant population. *Afr. J. Ecol.* 22, 229–244.
- White, G.C., Garrott, R.A., 1990. *Analysis of Wildlife Radio-Tracking Data*. Academic Press, San Diego, pp. 383.
- Wilcove, D.S., Wilkelski, M., 2008. Going, going, gone: is animal migration disappearing? *PLoS Biol.* 6, e188. <http://dx.doi.org/10.1371/journal.pbio.0060188>.
- 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, 1223–1232.
- 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 behavior. *Behav. Ecol. Sociobiol.* 61, 1919–1931.
- Young, K.D., Ferreira, S.M., van Aarde, R.J., 2009. Elephant spatial use in wet and dry savannas of southern Africa. *J. Zool.* 278, 189–205.