The ranging patterns of elephants in Marsabit protected area, Kenya: the use of satellite-linked GPS collars

Shadrack M. Ngene1,2*, Hein Van Gils1, Pipke E. Van Wieren3, Henrik Rasmussen4, Andrew K. Skidmore1, Herbert H. T. Prins3, Albertus G. Toxopeus1, Patrick Omondi4 and Iain Douglas-Hamilton5

1International Institute of Geo-information Science and Earth Observation, Hengelosestraat 99, PO Box 6, 7500 AA Enschede, The Netherlands, 2Kenya Wildlife Service, Meru National Park, PO Box 11, Mara, Kenya, 3Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3A, 6708 PB, Wageningen, The Netherlands, 4Kenya Wildlife Service, PO Box 40241, Nairobi 00100, Kenya and 5Save the Elephant, PO Box 54667, Nairobi

Abstract

We investigated the ranging patterns of elephants in the Marsabit protected area, north eastern Kenya, to ascertain the range of bachelor and female family herds in different seasons, and to identify corridor and noncorridor areas. Data were acquired for five bachelor and four female family herds equipped with satellite-linked geographical positioning system collars, and monitored from December 2005 to December 2007. Distinct dry (about 260 km²) and wet seasons (about 910 km²) ranges were observed, with connecting corridors (north-eastern corridor: about 90 km long, about 2-7 km wide; southern corridors: about 10-20 km long, about 2-3 km wide). The dry season range corresponded with Marsabit evergreen forest, while the wet season range matched with dry deciduous lowland shrubs. The ranging elephants moved at speed of about 0.2-20 km/h. Bachelor herds moved faster than female family herds. Elephants moved fast during the intermediate and wet seasons than during the dry season. The speed of ranging elephants was over 1 km/h in the corridor areas and about 0.2 to less than 1 km/h in the non-corridor areas. Expansion of settlements towards corridor areas needs to be controlled to avoid future blocking of connectivity between wet and dry season elephant ranges.

Key words: conservation of connectivity, corridor, elephant migration, GPS collars, ranging patterns, satellite, speed

Résumé

Nous avons étudié les schémas spatiaux des éléphants dans l’aire protégée de Marsabit, au nord-est du Kenya, pour évaluer le domaine vital des hardes de mâles et des hardes matriarcales à différentes saisons, et pour identifier les zones qui sont, ou pas, des corridors. Nous avons récolté des données pour cinq hardes de mâles et quatre hardes matriarcales équipées de colliers émetteurs reliés par satellite à un système de positionnement mondial, et nous les avons suivies de novembre 2005 à décembre 2007. Nous avons observé des domaines distincts de saison sèche (environ 260 km²) et de saison des pluies (environ 910 km²) ainsi que les corridors qui les relient (corridor du nord-est : pres de 90 km de long, entre 2 et 7 km de large environ ; corridors du sud : entre 10 et 20 km de long, de 2 à 3 km de large). Le domaine vital de saison sèche correspondait à la forêt sempervirente de Marsabit, tandis que celui de saison des pluies correspondait à des arbustes décidus secs de plaine. Les éléphants se déplaçaient à une vitesse comprise entre 0,2 et 20 km/h. Les hardes de mâles allaient plus vite que les familles de femelles. Les éléphants se déplaçaient plus vite à l’entre-saison et en saison des pluies qu’en saison sèche. La vitesse des éléphants en mouvement était de plus d’un km/h dans l’étendue des corridors et elle variait de 0,2 à moins d’un km/h dans les zones qui ne faisaient pas partie des corridors. Il faut contrôler les extensions vers les aires qui servent de corridors pour éviter tout futur blocage de la connectivité entre les espaces vitaux de saison sèche et de saison des pluies.

Introduction

The distribution of food resources for mega-herbivores in natural environments is not homogeneous (Senft et al.,
1987). The distribution is influenced by an interaction of factors, which include topography, elevation, soil type, amount of rainfall and human interference (Pomeroy & Service, 1992; Bailey and Provenza, 2008). In addition, seasonal change in the distribution of food resources has an impact on the spatial structure, demography and movement patterns in mega-herbivores (Turchin, 1998) including elephants (Wittemyer et al., 2007). As a result, for mega-herbivores to maximise food resource intake, they have to move from one area to another within the landscape (Prins & Van Langevelde, 2008). The movements have to match the distribution of the food resources. At a given time of the day, they will occur at feeding and resting areas, and then move to drinking water points or salt lick sites (Prins & Van Langevelde, 2008; Douglas-Hamilton, Krink & Vollrath, 2005; Prins & Van Langevelde, 2008). Such movements arise within two frameworks: natural selection acting over generations (Pyke, 1984) and new experiences that animals learn within their life time (Pyke, 1984; Senft et al., 1987; Laca, 2008). The goal of such movements is to enhance the food resource intake as it is necessary for their daily body energetic requirements. Elephants, being important mega-herbivores in an ecosystem, employ the same strategies as other mega-herbivores while foraging in ecosystems with heterogeneously distributed food resources (Pomeroy & Service, 1992; Laca, 2008). The importance of elephants in an ecosystem is further exemplified by their role in modifying landscapes and revenues emanating from tourism.

Elephants are ecological landscape ‘gardeners’, local and national revenue earners and destroyers of crops (Douglas-Hamilton et al., 2005). In addition, elephants cause serious conservation–farming conflict in areas adjacent to protected areas (Hoare & Dutoit, 1999). In such cases, a common solution is to fence them, but this hastens habitat destruction (Douglas-Hamilton et al., 2005). Regrettably, the elephant’s range is declining due to habitat fragmentation resulting from an increase of human population and associated land use and land tenure changes (Ipavec et al., 2007). The mosaic of forest and savannah in Marsabit protected area in northern Kenya is no exception. However, the Marsabit elephants have not been studied in the past due to technological limitations. As a result, collection of quality data in insecure and remote areas like Marsabit was not guaranteed. Therefore, there is need to monitor and analyse the ranging patterns of elephants in the Marsabit protected area. Monitoring is at present easier and more reliable because of recent advances in radio tracking using GPS technology (Blake, Douglas-Hamilton & Karesh, 2001). The use of satellite linked GPS collars allows for acquisition of high resolution spatio-temporal data, which is important for studying the elephants ranging patterns (Douglas-Hamilton et al., 2005). Harris et al. (1990) provide an excellent and concise review of the concept of tracking and data analysis.

Past studies on African elephants have concentrated on their movement patterns and estimation of home range extent. A home range is an area that an animal uses to satisfy its requirements for mating, food, water, escape routes from enemies, resting sites, and look up positions (Jewell, 1966; Delany, 1982). Estimates of elephant home range have been achieved using three methods: minimum convex polygon (Leuthold & Sale 1973; Lindeque & Lindeque 1991, Thouless, 1996; Whyte, 1996; Foguekem et al., 2007; and Ipavec et al., 2007), squared grids (Douglas-Hamilton et al., 2005), and fixed kernel density estimation (Leggett, 2006). Douglas-Hamilton et al. (2005) reported that elephant ranges, studied over a two-year period and for separate regions, have a highly complex structure. Individual elephants ranged over areas from 10^4 to 10^5 km^2 (Leuthold & Sale 1973; Lindeque & Lindeque 1991; Thouless, 1995, 1996; Whyte, 1996; Douglas-Hamilton et al., 2005; Leggett, 2006; Foguekem et al., 2007; and Ipavec et al., 2007). For example, the Samburu-Laikipia elephants ranged from about 100 km^2 to more than 700km^2, whereas in Amboseli, Shimba Hills and Meru National Park, their home range was from about 100 km^2 to about 200km^2, more than 10km^2 to about 80km^2, and 200km^2 about 300km^2 respectively (Douglas-Hamilton et al., 2005). The home ranges in fenced and open areas were small (over 10km^2 to about 80km^2) and large (over 90km^2 to about 800km^2; Douglas-Hamilton et al., 2005; Leggett, 2006; Dolmia et al., 2007). Migrations of over 400km have been reported from Mali (Blake et al., 2003) and Namibia (Leggett, 2006; Lindeque & Lindeque, 1991). As the elephants move within their dry and wet seasons range or migrate from their dry to wet seasons range and vice versa, they do so in varying speeds (Leggett, 2006).

Famini & Hutchinson (2003) provide a detailed review of the literature pertaining to the speed of moving elephants dating back to 1899. Since then, different authors have reported varying speeds for moving elephants, the lowest and highest being almost 0kmh^{-1} to about 0.03kmh^{-1} and about 2kmh^{-1} to about 50kmh^{-1}, respectively (Hutchinson et al., 2003; Hutchinson et al.,
While using the latest GPS telemetry to study the speed of elephant movements in Samburu/Laikipia, Meru, Shimba Hills and Amboseli (Douglas-Hamilton et al., 2005), Kunene region (Leggett, 2006), Tarangire (Galanti et al., 2000), northern Cameroon (Foguekem et al., 2007), and Zokouma (Dolmia et al., 2007), the researchers showed that distinct elephant range sectors were connected by narrow corridors. A range sector is an area larger than 2km², in which neighbouring grid squares were visited at least three times each by an elephant whereas a corridor refers to a segment of continuous movements over at least 10km distance that connects two range sectors (Douglas-Hamilton et al., 2005). Based on the definitions, in Samburu/Laikipia, Meru, Shimba Hills and Amboseli ecosystems, bachelor herds and female family herds have been recorded to move faster in corridor areas (95% confidence interval (CI) = about 1-2kmh⁻¹) than in non-corridor areas (range sectors; 95% CI = about 0.3-0.4kmh⁻¹; Douglas-Hamilton et al., 2005). Generally, the discrepancies in the reported speeds of moving elephants by different authors were because they used different methods to obtain data on elephant speeds. The methods include the use of moving vehicles, photographs, videos (Hutchinson et al., 2003; Hutchinson et al., 2006; Ren & Hutchinson, 2008), global system for mobile communication (GSM)-geographic positioning (GPS) collars (Douglas-Hamilton et al., 2005). In addition, most of these studies have used elephant day-time location data because the contemporary tracking technology did not allow for data recording at night. However, with the GPS collars functioning for 24 h, ranging patterns of elephants can be studied in more details to ascertain threats to their range.

The ranging space for elephants in Marsabit is reportedly decreasing due to demographic and economic development (Oroda et al., 2005). Settlements and farms are found around the Marsabit forest mountain. The human population around the forest mountain increased by 153% from about 17,000 people in 1979 to about 43,000 people in 2006 (Oroda et al., 2005) Accordingly, the land under crop farming increased from about 35km² ha in 1973 to about 300km² in 2005 (Oroda et al., 2005). In addition, land under settlements increased from about 1km² in 1973 to about 4km² in 2005 (Oroda et al., 2005). Based on these changes, understanding the ranging pattern is therefore important to identify the threatened elephant range as well as other areas used by elephants to effectively provide them with security throughout the year. As such, it will be possible to plan for security patrols with more precise knowledge of actual elephant range. In this paper, we establish the ranging patterns of elephants in and around the Marsabit Protected Area. Potential effects of human developments on the future of elephant conservation in Marsabit are discussed.

To understand the elephants’ ranging patterns and speed of movements, we (i) compare the speed of moving bachelor and female family herds (ii) compare speed of movements in different seasons (iii) compare long distance movement and speed, and (iv) compare speed of movement in corridor and non-corridor areas. We aim to test the following hypotheses.

Firstly, group composition determines its speed of movement. Because bachelor herds are composed of individuals of almost the same age, while female family herds consist of young individuals who slow female family herds, we hypothesise that bachelor herds moved significantly faster than female family herds.

Secondly, since the speed of moving elephants is likely to vary in relation to the spatial arrangements of food resources, inter-patch speed of movements, common during the dry season, will differ from those during the intermediate or wet seasons. We thus hypothesise that the speed of moving elephants should be significantly faster during the intermediate season, when the elephants migrate from their dry season range to wet season range and vice versa.

Thirdly, because human infrastructures (e.g., farms, settlements, and roads) disturb and repel elephants (Ngene et al., 2009), elephants move significantly faster in corridors where human infrastructures are present than in non-corridors.

**Materials and methods**

**Study site**

The Marsabit National Park and Reserve (northern Kenya), together labelled a Protected Area, cover approximately 360km² and 1,130km² respectively (Fig. 1) and is centred on longitude 37°0’E and latitude 2°0’20’N. A characteristic feature of the protected area is Mount Marsabit (1680 m), and its conspicuous evergreen forest covering about 125km² (Oroda et al., 2005). Mount Marsabit is a dormant shield volcano dating from the tertiary (Mclaughlin, Dougherty & Mclaughlin, 1973). The surrounding areas are characterized by a gently sloping shrub-land plateau. The humid upper peak of Mount...
Marsabit supplies ground water to the surrounding areas. Permanent rivers are absent on Mount Marsabit (Loltome, 2005). However, water points (wells, boreholes, crater lakes and springs) occur inside the forest and along the forest edges (Loltome, 2005).

The precipitation regime in Marsabit is characterized by two rainy seasons, with peaks in April and November. The annual rainfall varies between 50 and 250 mm (on the lowlands) and 800–1000 mm (in the mountain forest; Loltome, 2005). The evaporation rate is high, at about 2400–2600 mm per year (Synott, 1979). The eco-climatic zone of the forest is categorized as sub-humid and the surrounding shrub-lands fall within the very arid category (Eiden, Keith & Lonnes, 1991).

The vegetation within the protected areas ranges from perennial grassland, evergreen—semi-deciduous open and thick shrub-lands to evergreen forest (Harlocker, 1979). Their flora and fauna are described in detail by Githae et al. (2007), Harlocker (1979) and Mclaughlin et al. (1973). The grasses occur amongst the shrubs and in some cases amongst trees in the forest. The tree cover is over 75% and has less developed undergrowth (<10%; Ngene & Omondi, 2005). The percentage cover of shrubland is from 10%, within open shrub-lands, to over 75% in thick shrub-lands (Ngene & Omondi, 2005). The area under forest and woodland decreased from about 180km² to about 125km² and 100 km² to about 1km² from 1973 to 2005, respectively due to increase of settlements (about 1 km² to about

Elephant location data

Four female and five male elephant in different parts of the protected area were equipped with Iridium satellite-link GPS collars supplied by Televilt Positioning AB of Sweden. The animals were immobilized following procedures described by Whyte (1996). The elephant locations’ data were recorded at a spatial and temporal accuracy of 5-15 meters and 5-10 minutes, respectively (Televilt, 2005). The first group of seven elephant were collared from 4 to 16 December 2005. The elephant were collared on the north west, western, south western, and southern slopes of the Marsabit mountain forest. The second group of two female elephants was collared from 7 to 11 July 2006 on the north eastern and south eastern part of the mountain forest.

All collars were set to collect and record a position once every hour. The collected positions were transmitted to the satellite every 48 h. The original time recorded was in GMT; 3 h were added to obtain the local time. The position data were sent from the satellite to an e-mail account and downloaded automatically using the Save the Elephant (STE) downloader software (save the Elephant, Nairobi, Kenya). The STE tracking database interface software downloaded the elephant tracks onto Arc Map 9.2. The tracks’ attribute data had information on distance between two points and track speed, which were calculated as described by Turchin (1998). The data was exported to an excel file using Arc Map 9.2 (ESRI, 2006) for further analysis as outlined by Harris et al. (1990).

Data analysis

We analysed data for the period December 2005 to December 2006 and tested the following hypotheses: H1: Bachelor herds moved significantly faster than female family herds; H2: The speed of moving elephants was significantly faster during the intermediate season than the dry and wet seasons, and, H3: Elephants moved significantly faster in corridors area where human infrastructure is present than noncorridor areas.

The elephant herds were categorized into female family herds and bachelor herds. Seasons were divided into three categories: dry (January, February, July, August and September), intermediate (March, June and October) and wet (April, May, November and December). Elephant location data were categorized into corridor and noncorridor data sets. Corridor areas were described as areas where elephants moved continuously for more than 10 km, whereas noncorridor areas were depicted as areas where elephants moved continuously for less than 10 km (Douglas-Hamilton et al., 2005). All the datasets were visually inspected and tested for normality and homogeneity of variances using the Kolmogorov-Smirnov and and Brown-Forsythe tests, respectively (Fowler et al., 1998). Normality and homogeneity of variances were assumed when p > 0.05. The datasets were not normally distributed and the variances were heterogeneous. Therefore, we log transformed the datasets to normalize them and ensure homogeneity of variances. We then used one-way ANOVA F-tests to analyse the data (Fowler et al., 1998) following procedures described by Statsoft (2002). Post hoc analysis (Scheffe test) was used to isolate the seasons when the speed of moving bachelor and female family herds was significantly different (Statsoft, 2002). Significant differences were at P ≤0.05 (Fowler et al., 1998).

Results

Speed of movement, herds’ composition, and seasons

The speed of moving elephants ranged between about 0.2kmh$^{-1}$ and about 19kmh$^{-1}$ (bachelor herds range: about 0.4kmh$^{-1}$ to about 19kmh$^{-1}$; female family herds range: about 0.2kmh$^{-1}$ to about 18kmh$^{-1}$). The bachelor herds moved slightly faster than female family herds during all the seasons. The 95% confidence interval (CI) of mean speed of moving bachelor and female family herds during the dry, intermediate and wet seasons were: about 0.30-0.31kmh$^{-1}$ and about 0.25-0.27kmh$^{-1}$; about 0.30-0.35kmh$^{-1}$ and about 0.31-0.33kmh$^{-1}$; about 0.33-0.35kmh$^{-1}$ and about 0.32-0.34kmh$^{-1}$, respectively. Fig. 2 below presents a summary of the speed of moving bachelor and female family herds during the dry, intermediate and wet seasons. Bachelor and female family herds in each season moved at the same speeds (Fig. 2). However, they moved significantly faster during the intermediate and wet seasons than in the dry season (one-way ANOVA F = 52; df = 5; P < 0.05; Fig. 2).

Long distance movements and seasonal elephant range

Four elephant herds were followed for 17 h. Each herd was represented by a single collared elephant (ID). Table 1
presents a summary of the total and average distance moved by the four herds from 22 October 2006 at around 6:00 p.m. to 25 October 2006 at around 12:00 p.m. The total distance moved by the four herds differed significantly with Mrs Kamau’s herd moving at a longer distance in 17 h than the other three herds ($\chi^2 = 107$, df = 3, $P < 0.05$; Table 1).

One female elephant (Mrs Kamau), collared on the eastern part of Marsabit forest, in a herd of 12 family members, moved over 90 km north-east of Marsabit forest (Fig. 2a; Table 1). This long distance movement started about 6:00 p.m. on 22 October 2006 and ended about 8:00 a.m. on 25 October 2006, though some rest stops were made. For example, on 23 October 2006, the family herd rested for four hours, from approximately 11:00 a.m. to approximately 3:00 p.m. after continuously walking for about 42 km. Also, on 24 October 2006, the family herd rested again for four hours, from about 1:00 p.m. to about 5:00 p.m., after continuously walking for approximately 41 km. On 23 October 2006, from around 8:00 p.m. to around 9:00 p.m., the family herd entered a lava field, thereby reducing their average speed from approximately 2 km h$^{-1}$ to approximately 1 km h$^{-1}$ (Fig. 3-3A). Between 24 October 2006 (around 6:00 p.m.) and 25 October 2006 (around 5:00 a.m.), the family herd only moved for short distances, with an average speed of approximately 0.4 km h$^{-1}$. During this period, the family herd speed ranged from approximately 0.01 km h$^{-1}$ to approximately 2 km h$^{-1}$. Before the long distance migration, the family herd walked at an average speed of approximately 0.3 km h$^{-1}$. During ninety percent of the time, family herd speed was less than or equal to approximately 0.5 km h$^{-1}$. In the remaining ten percent of the time, the family herd’s speed was greater than or equal to approximately 0.6 km h$^{-1}$, while for only 3.4% of the time was their speed greater than or equal to approximately 1 km h$^{-1}$.

A second female elephant (Rita), collared in a herd of 10 family members, moved for about 16 km without stopping between 7:00 p.m. of 24 October 2006 and 12:00 p.m. of 25 October 2006 before settling to utilize an area about 28 km south of Marsabit forest (Table 1; Figs 3b and 4). All the other elephant herds utilized the area south of Marsabit forest during the wet season (Fig. 4).

During the dry season, on the western part of the Marsabit forest, elephants moved from the forest to the lowlands late in the afternoon (between 5:30 p.m. and 7:30 p.m.) and were back to the forest in the morning (between 6:30 a.m. and 8:00 a.m.). On the southern and south-eastern part of the forest, some herds of elephants moved from the forest to the lowlands and vice versa in two distinct periods, first from 6:30 a.m. to 8:00 a.m. and

Table 1  Distance travelled by four elephant herds during the beginning of the rainy season between 7:00 p.m on 22 October 2006 and 12:00 p.m. on 25 October 2006

<table>
<thead>
<tr>
<th>Elephant ID</th>
<th>Herd composition</th>
<th>Minimum distance (km)</th>
<th>Maximum distance (km)</th>
<th>Total distance (km) h</th>
<th>Average (km/h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rita</td>
<td>Female family</td>
<td>0.01</td>
<td>2</td>
<td>18</td>
<td>17 1</td>
</tr>
<tr>
<td>Hula Hula</td>
<td>Bachelor</td>
<td>0.01</td>
<td>1</td>
<td>19</td>
<td>17 1</td>
</tr>
<tr>
<td>Shadrack</td>
<td>Bachelor</td>
<td>0.01</td>
<td>2</td>
<td>23</td>
<td>17 1</td>
</tr>
<tr>
<td>Mrs Kamau</td>
<td>Female family</td>
<td>0.02</td>
<td>4</td>
<td>95</td>
<td>17 6</td>
</tr>
</tbody>
</table>

One female herd (Mrs Kamau) exhibited long distance movement (migration) whereas the three other elephant herds displayed short distance movement (local dispersal). The minimum and maximum distances indicate the lowest and highest distance travelled within an hour during the 17 hour period. The total distance is the overall distance travelled during the 17 hours. The distance values (minimum, maximum, and total) are approximate values.
5:30 p.m. and 7:30 p.m., and second from 5:30 p.m. and 7:30 p.m. and 6:30 a.m. to 8:00 a.m., respectively.

Two distinct wet season elephant ranges were identified, one of about 470 km² being over 90 km north east of Marsabit forest and the other of approximately 440 km², which was about 15–30 km south of Marsabit forest (Fig. 4). The dry season range of approximately 260 km² corresponded with Marsabit evergreen forest, while the wet season range matched with dry deciduous lowland shrubs. The elephant moved from the forest to the lowlands during the wet season. Conversely, during the dry season, they moved from the lowlands to Marsabit forest and its surroundings (Fig. 4). The dry and wet season ranges were connected by corridors. The north-eastern corridor was approximately 90-km long and its width was about 2 km near the forest and increased to a maximum of about 7 km near Bule Marmar, where the elephants established their wet season range. The southern corridors were about 10–20 km long and its width ranged from about 2 km near the forest and increased to a maximum of about 3 km, where the elephants established their wet season range.

Spatial distribution of varying speed of movements and corridors

Figure 5a–c shows the distribution of varying speed of elephants in Marsabit protected area. Fig. 5c also shows the
The ranging patterns of elephants in Kenya

The majority of individuals have used most of the western side of the mountain, the area to the south between Kituruni, Gof Bongole, Karare, Kijiji and Lake Paradise. Areas within the forest where elephants were recorded to move at low speed (less than 0.2 km h\(^{-1}\)) were those near drinking water points [e.g. Crater Lake, Lake Paradise, Lehutaa and the central springs (Fig. 5a)]. Nearly all slow movements occurred in the plains around the mountain and outside the forest (Fig. 5a). Areas within the forest where elephants were recorded to move at higher speed (approximately 0.2–1 km h\(^{-1}\) or more) were associated with their movements between foraging areas along the

Fig. 4 Dry and wet seasons’ range of elephants in Marsabit protected area and its surroundings. One of the elephants’ wet season ranges was over 90 km northeast of Marsabit forest whereas the other was within approximately 15–30 km from Marsabit forest. The elephants use migratory/dispersal corridors to migrate/disperse from dry to wet season ranges and vice versa. The wet season range is dominated by Acacia spp., Bauhinia huillensis, Pyranthus sepialis, and Aspilia mosambicens scences woody plants, which are major sources of elephant forage. The two water points on the further south of the park boundary are only used by livestock and humans during the dry season.
Fig 5 Spatial distributions of varying speeds of moving elephants from December 2005 to December 2007. (a) Below 0.2 km h$^{-1}$, associated with foraging or resting. (b) 0.2–1 km h$^{-1}$, associated with limited foraging or shifts from one habitat patch to another. (c) Spatial distributions of speeds of moving elephants (greater than 1 km h$^{-1}$) from December 2005 to December 2007, which is associated purely with high speed ‘transport’ movements between fragmented habitats. Consistent high speed (greater than 1 km h$^{-1}$) is associated with movements from drinking water points to foraging habitats through corridors.
bushy forest edge and drinking water points inside the forest (Fig. 5b and c).

Discussion

Speed of movement and herds’ composition

In this study we have observed that bachelor and female family herds of elephants moved at almost the same speed (fig. 2). However, bachelor herds (mean speed = about 0.30 km h\(^{-1}\)) moved slightly faster than female family herds (mean speed = about 0.25 km h\(^{-1}\); fig. 2) which could be due to the social organization of the elephants. Collared female family herds contain young elephants (KWS [KENYA WILDLIFE SERVICE], 2006), who cannot move fast (Estes, 1991; Moss, 1996). Conversely, the collared bulls were individuals, or in a bachelor herds (KWS [KENYA WILDLIFE SERVICE], 2006), without young individuals to retard their speed. These observations are in line with already existing observations on the social organization of elephants (Moss, 1996).

During the intermediate season, the elephants moved from the wet season habitats (lowland shrubs) to the dry season ones (Marsabit forest and adjacent shrubland) and vice versa. The female family and bachelor herds appear to be minimising their time on the slippery volcanic soils of the forest mountain during the wet season. However, during the onset of dry season, scarcity of drinking water on the lowland shrubs forces the elephants to move back to the areas around the forested mountain, where they remain until the end of the dry season. The higher speed of female family herds during the intermediate season compared with the dry season may be attributed to their long distance movements. Before the female family herd enter the volcanic lava area, the average speed was about 2 km h\(^{-1}\), but it was reduced to about 1 km h\(^{-1}\) on entering the lava area. This indicates that the speed of moving elephants during their migration depends on the nature of the ground surface they are migrating through. Within the noncorridor areas, the speed of moving elephants was less than 1 km h\(^{-1}\); elephants move faster in corridors than noncorridor areas as also reported by Douglas-Hamilton et al. (2005). Similar seasonal movement patterns and varying speeds of movements by elephant have been observed in Zokouma National Park, Chad (Dolmia et al., 2007), Chope National Park, north-east Botswana (Cushman, Chase & Griffin, 2005), Tarangire National Park, Tanzania (Galanti et al., 2000), Maputo elephant reserve, Mozambique (Boer et al., 2000), protected forest, West Africa (Blom et al., 2005), Kunene region northwest Namibia (Leggett, 2006), and northern Namib desert region of Kaokoveld, Namibia (Viljoen, 1989).

Our results on the maximal speed of moving elephants (about 19 km h\(^{-1}\)) are in line with available literature (Famini & Hutchinson, 2003; Hutchinson et al., 2003; Douglas-Hamilton et al., 2005; Hutchinson et al., 2006). In addition, Estes (1991) reported that the normal speed of a walking elephant is about 6–8 km h\(^{-1}\), which may be increased to about 10–13 km h\(^{-1}\) by taking longer, quicker strides, and can reach about 30 km h\(^{-1}\) at top speed. Hutchinson et al. (2006) reported that the near maximal speed of an African elephant is less than 25 km h\(^{-1}\). The near maximal speed of moving elephants could have been reached due to two reasons. First, at night, elephants move from the highland forest to the lowlands shrubs but get back to the forest during the early morning hours as the lowlands are used by livestock herdsmen during the day (Ngene et al., 2009). However, cases of elephants returning to the forest between 8:00 a.m. and 9:00 a.m. have been observed. This is the time livestock herdsmen take their animals out to graze and browse. It therefore implies that the elephants have to move faster, even approaching maximal speed. Secondly, poaching of elephants in Marsabit is common (Thouless et al., 2008) and one of the collared female elephants was poached in April 2006 (KWS [KENYA WILDLIFE SERVICE], 2006). As such, we expect the elephants to escape from the poachers at near maximal speed.

Long distance movement, seasonal elephant range and seed dispersal

Mammals move to place themselves in optimum conditions for as long as possible (Sinclair, 1983). This enables them to build body reserves, which are important for enhancing their breeding success including walking and foraging (Sinclair, 1983). The Marsabit elephants exhibit a seasonal movement pattern. They move from the Marsabit forested mountain to the lowland shrubland during the wet season and vice versa during the dry season. The reasons for the seasonal movements are threefold. First, the relatively high rainfall at the mountain results in lower quality forage, compared to the drier lowland shrublands (Pomeroy & Service, 1992). Second, the presence of adequate dry season water supplies trapped in shallow lava troughs within.
the volcanic lowlands. Third, the steep slopes and wet conditions make the volcanic soils in the mountain area slippery, therefore increasing the possibility of injuries if elephants slip and fall. As the dry season approaches, lowland water points dry up and the lowland shrubs start to shed their leaves. In contrast, drinking water is available year round on the mountain. The mountain shrubs and grasses are greener during the dry season, owing to the high water table around the forest and clay rich soils, which are able to retain water for a longer period (Ayien, 2005; Oroda et al., 2005). As a result, the elephants migrate from the lowlands shrubland to the mountain shrubland and forest. Our findings are in line with other studies in Meru, Mount Kenya, and the Samburu areas (Douglas-Hamilton et al., 2005), northern Namib Desert, Namibia (Viljoen, 1989), and Kunene region, northwest Namibia (Leggett, 2006). The data confirms that elephants tend to move much faster in corridors than noncorridor areas because of lack of adequate forage and drinking water as well as disturbances from humans including farms, fences and settlements (Douglas-Hamilton et al., 2005).

The maximum speed of migrating elephants depends on the morphology of the ground surface they encounter. In Marsabit, the presence of rock boulders and outcrops at a section covered with lava along the north eastern migratory routes significantly slowed elephants’ speed of movement.

The wet season elephant range is dominated by Acacia spp., Vangueria madagascariensis, Bauhinia tomentosa, Pyrantthus sepialis, Aspilia mosambiscences, and a few Croton megalocarpus woody plants, which are major sources of elephant forage (Ngene & Omondi, 2005; Githae et al., 2007). The dry season elephant range cover Marsabit forest and the shrubs on its periphery. The peripheral shrubs are dominated by B. tomentosa, P. sepialis, A. mosambiscences, and a few Croton dichogamus (Ngene & Omondi, 2005). In addition, during the dry season, at night, elephants use riverine vegetations extending to about 10 km from the forest boundary (Ngene et al., in press). The riverine vegetation is dominated by C. megalocarpus, Acacia spp., B. tomentosa, V. madagascariensis, P. sepialis, and A. mosambiscences. The area is the only source of drinking water during the dry season (Loitome, 2005).

Avoidance of intra-specific and inter-specific competition is an important strategy for animals using the same ecosystem (Pomeroy & Service, 1992). One strategy used by the animals to avoid intra-specific and inter-specific competition is to partition resource use in space and time (Estes, 1991; Pomeroy & Service, 1992). The Marsabit elephants portrayed avoidance of intra-specific and inter-specific competition by using different sites at the same time or using the same sites at different times. For example, during the day in the dry season, elephants were not using the lowlands on the western side of the forest due to presence of livestock in the area (Loitome, 2005), thereby avoiding inter-specific competition. The use of the same site on the lowlands on the southern and south eastern parts of Marsabit forest by different elephant herds at different periods was a demonstration of avoidance of intra-specific competition. Such avoidance of intra-specific and inter-specific competitions are also recorded in Samburu (Douglas-Hamilton et al., 2005), northern Namib Desert, Namibia (Viljoen, 1989), and Kunene region, northwest Namibia (Leggett, 2006).

Although this research did not focus on phytogeography of plants foraged by elephants, it is possible that elephants play a major role in the distribution of seeds of different plants. For example, C. megalocarpus is browsed more by elephants during the dry season, a period when their seeds are mature (Ngene & Omondi, 2005). This plant species is distributed throughout the entire mosaic of forest and savannah, although it is most common in the forest and along riverbeds (Ngene & Omondi, 2005; Githae et al., 2007). It is possible that elephants are responsible for distributing the C. megalocarpus seeds. Elephants have been reported to be good agents of seed dispersal in other areas including Kibale National Park, Uganda (Cochrane, 2001), Kwango National park, Zimbabwe (Dudley, 2000), Ruaha National Park, Tanzania (Barnes, 1982), Banyang-Mbo wildlife sanctuary, south-western Cameroon (Nchanji & Plumptre, 2003), and Tarangire National Park, Tanzania (Gonthier, 2007).

Spatial distribution of varying speed and corridors

Different travelling speeds are associated with different types of behaviour (Douglas-Hamilton et al., 2005). Hence the spatial distribution of hourly speeds can act as a crude guide to the activities in an area. Speeds below 0.2 km h⁻¹ are normally associated with foraging, resting and comfort behaviour around water sources, whereas speeds from about 0.2 to 1.0 km h⁻¹ are associated with limited foraging and gentle shifting between foraging patches (Famini & Hutchinson, 2003; Douglas-Hamilton et al., 2005; Hutchinson et al., 2006). At speeds above 1.0 km h⁻¹ elephant do not forage but movements are
associated with shifts between foraging and drinking, or travelling along corridors (Famini & Hutchinson, 2003; Douglas-Hamilton et al., 2005; Hutchinson et al., 2006).

The slow speeds associated with foraging (and resting) did not occur within the mountain forest except around the few water sources where reduced speed was associated with drinking and bathing. This is because the foliage of the forest is largely in the canopy (>20 m) making the foliage to be out of reach to elephant. Moreover, the few tree seedlings (e.g., C. megalocarpus, Strombosia schlefferi, Diospyros abyssinica, Olea africana, and O. capensis) available for browsing by the elephants are of low nutritional value (Ngene & Omondi, 2005). However, few shrubby patches dominated by B. tomentosa, P. sepialis, A. mosambicensis, Glewia similis and young C. megalocarpus occur within the forest, especially along riverbeds. These shrubby patches are utilized by elephants as feeding sites, resulting to speeds of less than 0.2 km h⁻¹ therein.

Slow movements are observed at forest edges. This is attributed to feeding behavior, due to the presence of preferred plant species (e.g., P. sepialis, B. tomentosa, V. madagascariensis, a variety of Acacia species, and Aspilia mossambicensis; Estes, 1991; Ngene & Omondi, 2005; Githae et al., 2007). In addition, the areas are also near

Fig 6 A map showing areas proposed for protection from development, area available for settlements, and proposed boundary of Marsabit National Park. Marsabit forest and corridor areas between Karare and Kituruni are proposed to be inside the park. This portion is critical for movement of elephants to the southern part of Marsabit forest. The area proposed for protection from development matches the range of elephants during the dry and wet seasons. The names are the town and villages around the Marsabit mountain forest.
water sources (Loltome, 2005; Ngene et al., 2009). Elephants moved slowly where preferred food plants were plenty in Maputo elephant reserve, Mozambique (Boer et al., 2000), Manovo-Gounda-St Floris National Park, Central African Republic (Ruggiero, 1992), Northern Namib Desert, Namibia (Viljoen, 1989), and Lake Manyara National Park, Tanzania (Kalemera, 1989).

Effect of human development on elephants in Marsabit

Settlements and large arable farms occur around the Marsabit forest, specifically at Marsabit town, Hula Hula, Kijiji, Karare, Lpus, Kituruni, Songa, Leyai, Badassa, Gabbra Scheme, Sagante and Dirib Gombo. However, some agricultural areas have vegetation patches, which connect the forest and lowlands and are currently used as migratory or dispersal routes by the elephants. Conversely, in heavily settled areas like Sagante, Dirib Gombo, Gabbra Scheme and Badassa, patches of shrub-lands occur within the settlement areas, and along the riverine vegetation. These patches are used by the elephants to migrate between the mountain forest and the plain shrubland. However, an increasing human population may result in conversion of these interspersed shrub-lands into farms and residential areas (Oroda et al., 2005), fragmenting the corridors between seasonal habitats. Therefore, we expect the population of Marsabit elephants to decline due to fragmenting landscape. We recommend an area of about 1,300 km² to be protected from developments like construction of new settlements and establishment of new farms (Fig. 6). We propose that the expansion of settlements and farms from Karare to Hula Hula, Karare to Kituruni and from Kituruni to Badassa should be regulated through land-use zoning, delineation of improved corridors, and through appropriate legislation. Gazetting the seasonal migratory corridors including the entire Marsabit forest (about 150 km², Fig. 6) as part of Marsabit National Park is also suggested.

Conclusion

In this study we describe and explain the ranging patterns of elephants in (and around) the Marsabit protected area. Bachelor herds moved significantly faster than female family herds. We conclude that the presence of young elephants in female family herds forces them to move at a slower speed than bachelor herds. During migration, rock boulders and outcrops along migratory routes reduce the speed of migrating elephants. The Marsabit elephants seem to stay at forest edges longer than in forests. During the intermediate season, the speed of moving elephants was significantly higher than during the dry and wet seasons. The speed of moving elephants was significantly higher in corridor areas than noncorridor areas. The elephants used corridors to migrate from the forested mountain to the lowlands and vice versa. Loss of current migratory corridors due to continued expansion of settlements and crop farms are plausible. Controlled expansion of settlements and farms from Karare to Hula Hula, Karare to Kituruni and from Kituruni to Badassa is vital for preservation of the corridors. This could be achieved either through land-use zoning, enacting of appropriate legislation and gazetting the corridors as part of Marsabit protected area or both.

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