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SHORT COMMUNICATION

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Movements and corridors of African elephants in relation to protected areas

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Abstract Understanding how mammals satisfy their need for space in fragmenting ecosystems is crucial for ecosystem conservation. Using state-of-the-art global positioning system (GPS) technology we tracked 11 focal African elephants (*Loxodonta africana*) in Kenya at 3-hourly fix intervals and collected between 34 and 406 days per individual. Our recordings gave a high spatio-temporal resolution compared to previous studies and allowed novel insights into range use. The actual ranges of the tracked elephants are smaller than usually represented. Moreover, the ranges in our sample were complex and not confined to officially designated protected areas, except where fenced. All the unfenced elephants in our sample had distinct 'home sectors' linked by 'travel' corridors. Within each home sector the elephants concentrated in favourite 'core zones'. Such core zones tended to lie in protected areas whereas corridors typically crossed unprotected range. Elephants moved significantly faster along corridors than elsewhere in their range, which suggests awareness of danger outside the protected area. We conclude that understanding the complex use of an animal's range is crucial for conservation planning aiming to balance animal interests with those of human beings that co-habit in their range.

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Introduction

Declining and fragmenting ranges—typically through the effect of pressure by human expansion—put special emphasis on understanding how wildlife uses ecosystems. This is especially true for large mammals such as elephants. Both in Asia and Africa elephants are ecologically important as landscape 'gardeners', and socio-politically as revenue earners for national economies and local communities, or as destroyers of crops. In many areas elephants are the key animals defining serious human wildlife conflict (Dublin et al. 1997; Hoare and DuToit 1999). A frequent solution is to fence them but this may accelerate habitat destruction by the elephants.

Consequently it is important to measure and analyse how individuals and populations use their range. In this task we are greatly helped by recent advances in radio tracking using global positioning system (GPS) technology (Douglas-Hamilton 1998; Blake et al. 2001). This methodology allows high spatio-temporal resolution in plotting animal movements. Not surprisingly, such fine-grained data require novel analysis methods, which call for a careful redefinition of range. Although our research focuses on elephants (which can carry large batteries needed for extended GPS radio tracking) our conclusions are of general interest for the use of 'protected' areas by animals with large home ranges. For an excellent and concise review of the concept of tracking and data analysis see Harris et al. (1990).

Previous accounts describe African elephants as making extensive seasonal movements in home ranges that can vary greatly in size. Individual elephants have been allocated range areas covering from 10 to 10,738 km^2 (Douglas-Hamilton 1971; Leuthold and Sale 1973; Lindeque and Lindeque 1991; Thouless 1995, 1996; Whyte 1996) Migration routes in Mali of up to 450 km are known (Blake et al. 2002). Such range estimates have typically been calculated from infrequent radio fixes by the minimum convex polygon (MCP) method by connecting all the outermost position fixes of a cluster and calculating the total area between these perimeter connections. Although this method is outdated and indeed often misleading, nevertheless it is still widely used in the elephant literature when comparing ranges, as reviewed by Sukumar (2003, Table 4.5). Until the advent of GPS tracking it was rarely possible to record large animal movements with sufficient temporal resolution to give a full picture of movement patterns. Moreover negative data (i.e. areas never visited) were not recorded, and by default these areas became part of an animal's range.

Materials and methods

Between December 1996 and November 1999 we tracked 11 elephants in Kenya (7 males and 4 females) in four separate regions (Fig. 1a) and assembled a database totalling over 2,000 elephant days. Collar lifetimes varied between 34 and 406 days with an average life of 270 days per elephant.

The elephants' home ranges varied in degree of effective protected status. In addition some were fenced, others were not. At the coast, the Shimba elephant population was ring-fenced within a largely forested protected area that also encompassed the Mwaluganji community reserve. In Meru National Park there was an elephant fence along the western boundary only, but the animals were free to move in and out of the park including into the adjacent Bisanadi conservation area and surrounding areas. In Amboseli elephants

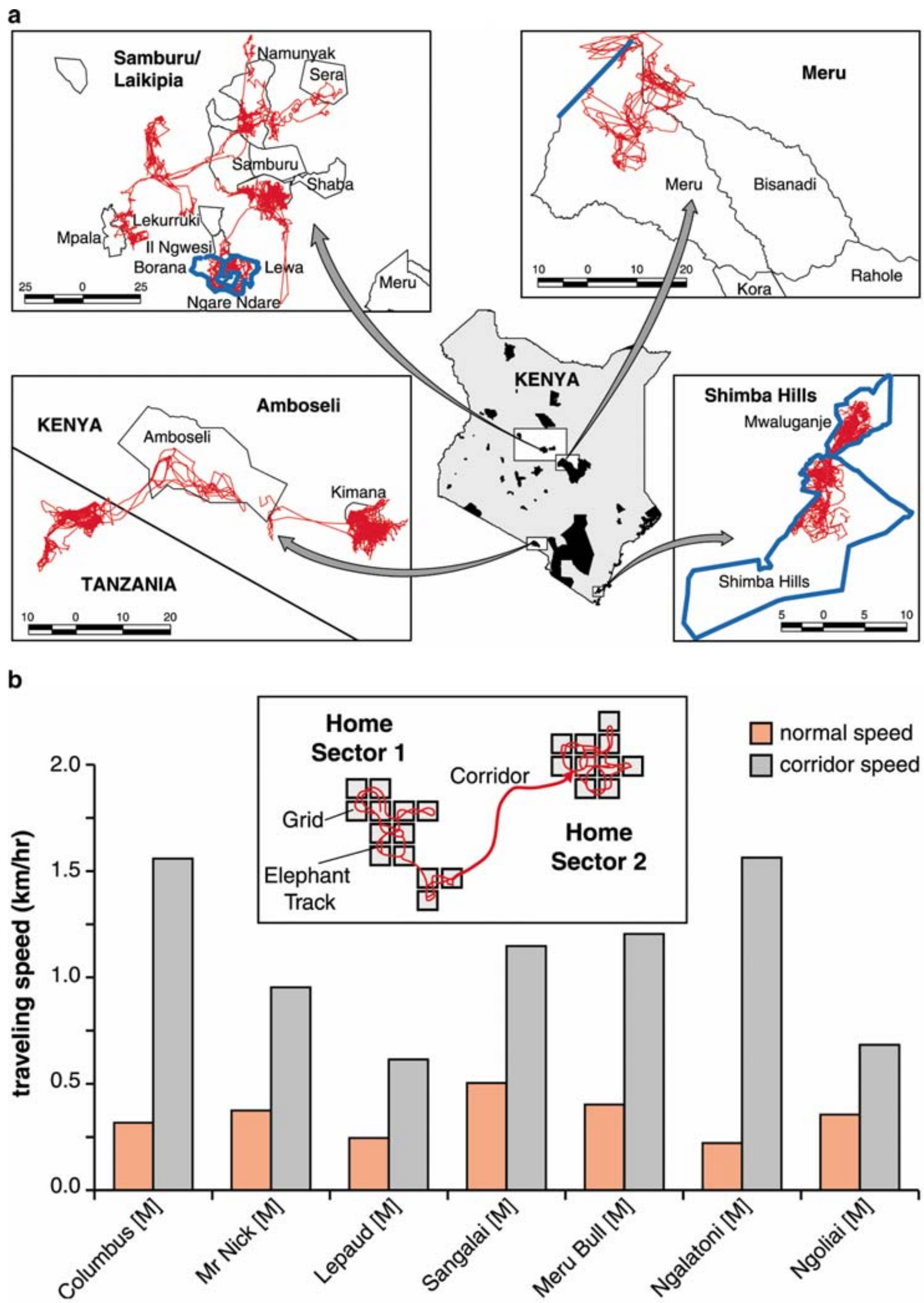

Fig. 1 **a** Four elephant ranges in Kenya, showing elephant movements (*red lines*), protected areas (*black outlines*), and fences (*blue lines*). Where elephants were unfenced they spent a significant proportion of their time outside protected areas. Distinct range sectors for each elephant were connected by narrow corridors (*scale in kilometres*). **b** Both male (M) and female (F) elephants tend to move much faster in corridors (1.1±0.4 km/h) than in non-corridor (or home) areas (0.35±0.1). This difference was significant (Student's *t*-test, paired test with the null hypothesis of equality in corridor and home zone speeds, n=7, P=0.0012). A corridor is defined as a path of continuous movement over at least 10 km distance, (connecting two home sectors by contiguous grid cells) and a home sector is defined as a set of contiguous grid squares with at least three observations per grid square (within 1 month with 3-h interval recording), which covers an area larger than 2 km^2

still ranged widely outside the national park, crossing the Kenya–Tanzania border to the Longido conservation area in the west, and going to the Kimana protected area in the east.

In the north of Kenya, the Samburu/Laikipia elephant ranges (our main study area) straddled an archipelago of isolated protected 'islands' within a relatively insecure 'sea' of sparsely inhabited pastoral areas. Effectively protected islands included Samburu, Buffalo Springs, and Shaba National Reserves, the private conservancies, Lewa, Namunyak, and Kalama, and the ranches Borana, and Mpala, with large swathes of relatively unsafe range in adjacent areas of Samburu, Laikipia, Isiolo, and Meru districts. Lewa and Borana were the only protected areas that were fenced, but both land units had small gaps designed to allow elephant access and egress on their northern boundaries. They were also linked to each other in the south by the fenced corridor of the Ngare Ndare Forest (Fig. 1a).

The greater Laikipia–Samburu elephant population is estimated to number around 5,400 (Omondi et al 2002). This makes it the largest elephant population in Kenya existing primarily outside protected areas. It has been described as a continuous and freely intermixing population with several distinct and overlapping subpopulations (Thouless 1996). Since 1997 a research team set up by Save the Elephants has monitored elephant births, deaths, and social interactions in and around Samburu National Reserve (Wittemyer 2001; Wittemyer et al. 2005). By 2003 in this core area the number of known individuals had reached an asymptote of 910, which indicates that some 20% of the northern Kenyan Laikipia/Samburu elephant population uses this important area centred on the Samburu National Reserve in the Ewaso Ngiro watershed.

The collars we deployed were GPS 1000 models manufactured by Lotek Engineering of Newmarket, Canada (Douglas-Hamilton 1998). Sampling rates were programmable and were typically set for either 1-h or 3-h intervals. The collars on average gave positions within 50 m or less of the true position. Since May 2000, when the U.S. government removed "selective availability", fixes have become accurate to within 20 m or less. The collars were also fitted with standard radio beacons to facilitate location. Regular flights or visits on the ground allowed us to find the collars and communicate with them remotely in order to download the stored information and also to reprogram the collars, if required. Downloading was done approximately every 3 months.

To analyse the elephant movement data, Thiemo Krink designed and developed our GIS analysis program LoxoLab. To make all data sets comparable, a filter was applied to the data, to select only 3-h intervals between fixes. With this program we divided the landscape into a quarter-kilometre grid. This size of grid square was chosen to be as small as possible without swamping the computer and causing it to crash. Each grid square was scored according to how many times it was crossed by each elephant, and the total squares visited constituted that elephant's 'grid range'. The grid range was then compared with the range derived from an MCP.

After examining movement patterns it was evident that each elephant meandered in one or more 'home sectors' within its home range, where it spent time feeding. The elephants living in unfenced range had more than one sector each and at times moved rapidly down relatively narrow corridors from one sector to another. In some sectors elephants would spend much time in what we termed 'core zones'. To examine how movement patterns varied we selected objective criteria to quantify our intuitive notion of home sectors, corridors, core zones, and speeds.

– A *home sector* for an elephant was arbitrarily defined as an area larger than 2 km^2, in which neighbouring grid squares had been visited at least three times each by that elephant.
– A *corridor* was defined as a path of continuous movement over at least 10 km distance that connected two sectors.
– *Core zones* were defined by those grid squares that lay in the top 25% of all grid squares in term of visits by a particular elephant.
– *Speeds* were measured in kilometres per hour over 3-h time intervals.

Using these terms (see also inset in Fig. 1b for our grid square definitions) we quantified the underlying complexity of elephant ranges based on movement patterns as recorded through multiple daily fixes. The GPS data allowed a detailed analysis of speed of movement, and the amount of time spent in protected or unprotected areas.

Results

Our results indicate that nearly all elephant ranges studied over sufficient time have a highly complex structure (Figs. 1a and 2). Moreover elephants typically spent a substantial proportion of their time outside any sort of officially protected area. Our unfenced elephants had distinct 'home' sectors linked by 'travel' corridors. Corridors predominantly lay in unprotected areas and linked one safe haven with another.

Elephant ranges measured by the grid method averaged 225 km^2 (14–783 km^2) and were 4.3 times smaller than those estimated by MCPs that had a mean 968 km^2 (11–5,520 km^2). The larger the range the greater was the overestimate by the MCP method (Fig. 2 insert). The largest range was that of the female elephant, Ngoliai, in the Laikipia and Samburu districts where the grid method gave a range of 783 km^2 compared to 5,520 km^2 calculated by the MCP method, a sevenfold overestimate. In fact during 213 days of continuous tracking she only visited 14% of her so-called MCP range (See Fig. 2).

Where elephants were unfenced, between 10 and 98% of their time was spent within officially protected areas (see Table 1). Overall, the animals spent more than half their time (55%) under protection although less than half their range (47%) was within protection. Three elephants were confined by fences within protected areas and never went out, but the seven unfenced, or partially fenced,

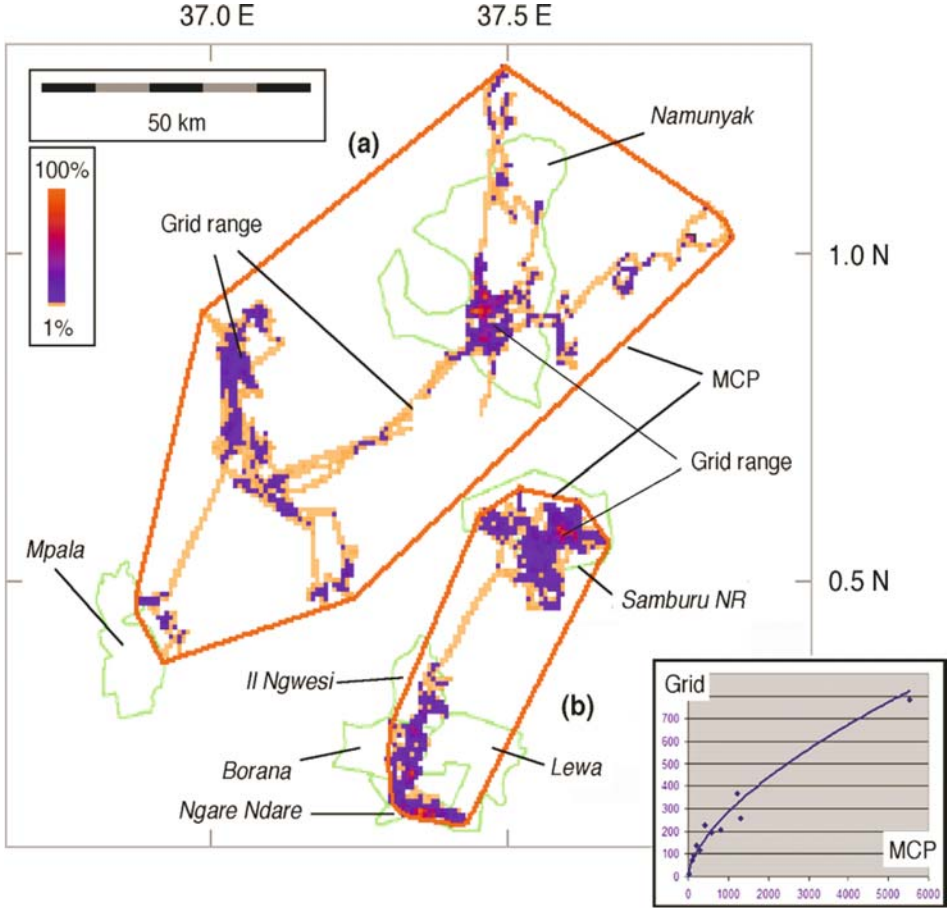

Fig. 2 Grid ranges and minimum convex polygons (MCPs) for two female elephants in northern Kenya. **a** Ngoliai, 18 February to 10 October 1998: grid range area = 783 km^2; MCP area = 5,520 km^2; **b** Ngalatoni, 2 February 1998 to 19 March 1999: grid range area = 370 km^2; MCP area = 1,240 km^2. *Lower right insert* shows for 11 elephants the observed ranges (*Grid*) by square quarter-kilometre grid squares and the traditional estimation (*MCP*) by minimum convex polygons, both in square kilometres. MCPs seriously overestimate the actual ranges in a non-linear way ($y=3.9547\times0.6194$; $r^2=0.964$; $n=11$)

Table 1 Elephant total tracking hours and grid ranges show on average that the unfenced elephants spent more than half their time under protection, though less than half their range was under protection

Name	Location	Sex	Tracking time (h)	Time in protected areas (%)	Grid range (km^2)	Range in protected areas (%)
Unfenced or partially fenced elephants						
Columbus	Amboseli area (west)	M	4,023	40	119	21
Mr Nick	Amboseli area (east)	M	3,264	10	196	38
Esidai	Samburu/Laikipia area	M	816	98	94	94
Lepaus	Samburu/Laikipia area	M	3,705	39	260	38
Sangalai	Samburu/Laikipia area	M	924	68	205	41
Ngalatoni	Samburu/Laikipia area	F	9,744	92	370	77
Ngoliai	Samburu/Laikipia area	F	5,127	37	783	24
Meru Bull	Meru National Park area	M	1,701	57	228	52
Mean			3,943	55	290	47
Fenced elephants[a]						
Lewa family	Samburu/Laikipia area	F	2,577	100	139	100
Justina	Shimba Hills area	F	6,690	100	72	100
Ted	Shimba Hills area	M	1,353	100	14	100
Mean			3,540	100	75	100

[a] The fenced elephants were effectively protected throughout their fenced range

elephants still had a choice and travelled from one sector to another through corridors. The corridors in most cases joined protected areas, although in the case of the western Amboseli bull, Mr Nick, his corridor linked Amboseli National Park with an area of better woody vegetation that lay across the border in Tanzania. However this is known as the Longido Game Controlled Area and probably should be classified as a protected area. There was only one unfenced elephant, Esidai, that did not exhibit corridor behaviour, but this was because his data only covered

1 month during the study period. Over a longer period he has since exhibited corridor ranging behaviour like the others and has spent significant times in unprotected areas (showing the importance of long-term data collection).

On average the unfenced elephants had 47% of their range inside protected areas. Furthermore, each elephant had areas of intense concentration that we defined as ‘core zones’. In our sample the elephants tended to focus their core zones within protected areas, with significantly more core-zone grid squares found within protected than unprotected areas (79 vs 21%, Student’s t-test, one tailed, null hypothesis: percentage of core zones within protected areas = 50%, n=11, P=0.016). Despite the high intensity of visits to core zones, they occupied on average less than 1% of the grid range.

Speed of movement in corridors differed compared to non-corridor areas (Fig. 1b). In the strip-like corridor zones the elephants averaged speeds of movement of 1.1 km/h compared to 0.35 km/h in the home zones. This difference was significant (Student’s t-test, paired test with the null hypothesis of equality in corridor and home zone speeds, n=7, P=0.0012).

Discussion

Our data on elephant movements were acquired at greater accuracy than before and revealed the complexity of range use by male and female African elephants. Range use is less homogeneous than has previously been implied. We show the uneven way in which elephants make use of their range, the areas where they never go, and how elephants cross unprotected areas swiftly down travel corridors, a behaviour we are tempted to name ‘streaking’. This may minimise the time spent in dangerous areas, as well as to access new feeding and watering grounds. These movements are often made under cover of darkness (unpublished observations).

Within protected areas, on the other hand, elephants tend to have preferred areas where they linger. In these core zones, often in riverine vegetation, the damage to trees can be intense (Laws 1970; Ben-Shahar 1993; van Wyk and Fairall 1969; Kahumbu 2002). Core zones and corridors make up a very small fraction of the whole grid range yet in terms of conservation value both are disproportionately important. High-resolution tracking coupled with appropriate analysis can later be combined with other data layers such as vegetation, rainfall, forage quality, human population, livestock densities, and land use. Clearly, the complex inter-relationships between these environmental features and elephant needs must be taken into account to plan for conservation. After all, elephants are pro-active key species and their future will, to a large extent, determine the future of whole ecosystems.

The large proportion of elephant range lying outside the reserves shows the importance of these ‘unprotected’ areas to elephants. This land they share with people, mainly pastoralists in our study. The areas required by elephants are so large that it would often be unsustainable to plan for their conservation solely within officially protected areas. It underscores the importance of reducing conflict and planning human–elephant coexistence. Using local perceptions and cultural perceptions of elephants can improve elephant conservation, especially in pastoral areas (Kuriyan 2002), as can fine-grained knowledge of the geographical location of corridors.

Poole (1996) predicted that increased human settlement in elephant dispersal areas around parks and reserves will result in increased conflict between elephant and human. She suggested migration routes will be restricted or blocked completely. Our observations contend that conservation planning could be greatly improved by catering for elephant space needs. A relatively small investment in keeping open crucial corridors identified by high-resolution radio tracking would allow elephants to spread their impact between different segments of their potential range.

The viability of many mammalian metapopulations may depend on linkages provided by corridors. For ‘our’ Samburu/Laikipia elephants we have now begun to identify such crucial pathways using the techniques outlined in this article. And we expect that not only elephants, but also other wildlife will benefit if the pachyderm corridors are not only recognised but also protected.

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