The concept of home range in relation to elephants in Africa

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Abstract

The concept of home range has been a source of debate among ecologists, especially regarding animals such as elephants. Methods for determining home range that are widely reported in elephant literature are outdated and inaccurate. This paper outlines the concept of home range; it compares different methods that have been used to determine ranges and discusses their relevance to elephant ecology. Rainfall is used as a variable across elephant habitats to explain range variation.

Additional key words: *Loxodonta africana*, core areas, habitat destruction

Résumé

Le concept de domaine vital est une source de débats entre les écologistes, spécialement quand cela concerne des animaux tels que les éléphants. Les méthodes qui servent à déterminer le domaine vital et qui sont largement reprises dans la littérature sur les éléphants sont dépassées et inexactes. Cet article décrit le concept de domaine vital, il compare les différentes méthodes qui ont servi à déterminer les domaines et discute de leur adéquation avec l'écologie de l'éléphant. Les chutes de pluie servent de variables dans les habitats des éléphants pour expliquer les variations du domaine.

Mots clés supplémentaires : *Loxodonta africana*, aires centrales, destruction de l'habitat

Introduction

'One may wonder whether it is worthwhile to attempt to measure anything as indefinite and variable as home range' (Stickel 1954).

Elephants require large areas in which to roam. But the areas available to them are decreasing rapidly as humans clear and settle more of the elephants' habitat. The many organizations involved in wildlife conservation use the term 'home range' widely with reference to elephants. This review of the home range concept is made to illustrate the complexity of the concept when it is applied to the biological requirements of elephants, because of their unique ability to move vast distances and their long lifespan.

The definition of home range most often encountered in the literature was given by Burt (1943): it states that home range is 'the area traversed by the individual in its normal activities of food gathering, mating and caring for young'. The problem with this definition is the idea of 'normal'. He also notes that dispersal and 'occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range'. White and Garrott (1990) state that home range is not the entire area over which an animal moves but the area over which it *normally* moves. Again, the problem is that mammals exhibit widely diverse movement patterns that are influenced by the resources available, social behaviour, predator avoidance and human disturbance. Some animals may regularly shift their range in response to environmental conditions.

The idea of home range is of interest because the properties of an animal's range should have adaptive significance and be a predictable aspect of its feeding strategy (Schoener 1981). Jewell (1966) states that 'home range is an area with a certain productivity that meets the energy requirements of the individual that occupies it'. McNab (1963) found that home range size could be expressed as a function of body weight that was directly comparable with the function relating basal metabolic rate to body weight. The range of an animal is also affected by behavioural constraints, such as predator avoidance, territoriality and interspecific competition. It is important to remember Sanderson's (1966) caveat that the size and shape of an animal's home range has little significance in itself; rather, it is essential to concentrate on the ecological factors that affect it.

To help clarify the concept, Jewell (1966) suggested the term *lifetime range*, meaning the 'total area with which an animal has become familiar, including seasonal home ranges, excursions for mating and routes of movement'. It then follows from this baseline definition that the range assessments attained for relatively long-lived and highly mobile animals are 'snapshots' and do not represent all the places they have traversed in their lifetime. This is particularly important with regard to elephants, as they are both long-lived and extremely mobile. It is not unreasonable, therefore, to state that no accurate assessment of the lifetime range of a free-ranging elephant has been made.

The boundaries of a home range may shift and vary as use patterns change. Stickel (1954) notes that the edges of range should be seen as diffuse and as estimations rather than as being sharply defined. This attitude continues to frustrate efforts to make range estimation precise, as many of the decisions regarding key definitions are still surprisingly arbitrary. In their extensive review of radio telemetry and home range analysis, Harris et al. (1990) note that most authors do not state why they chose one method of analysing home range over another. The criterion on which they based their home range size estimation, the number of fixes, autocorrelation or determination of cores was also not consistently reported. However, it is generally believed that determining home range can be useful for a variety of reasons if the objectives are clearly defined and the techniques used are stated.

Core areas

Hayne (1949) observed that mammals do not use their entire home range with equal intensity but occupy certain areas with greater frequency than others do. Generally, researchers have been interested in the areas where animals spend *most* of their time. By definition, methods to estimate core areas identify areas of high animal activity and exclude occasional sallies.

For example, crop-raiding behaviour generally falls into the category of 'occasional sallies' and is therefore not easily incorporated into the present efforts to define home range structure. The sallies may be more important biologically than core areas. The core area may be over-represented as it will tend to be the location where an elephant is merely resting. In her study of home ranges of small mammals Stickel (1954) states that the 'extreme sallies of young animals may represent wandering or the dispersal of animals without an established range'. Some adults, however, make long trips that may be important for their orientation in their environment. Stickel (1954) also notes that males have 'a natural tendency for exploration that is important in the invasion of depopulated areas and in the extension of a species range'. Dispersal of young animals can be related either to behaviour such as competition for mates, or to finding new areas in response to lack of resources in an area. Dispersal in elephants is usually used in the context of wet-season movements. Young bull elephants leave family units and wander (Lee and Moss 1986), eventually associating with bull groups. The 'pioneering' phenomenon of bull elephants may be a more accurate description of this behaviour in certain cases. Bulls have been recorded preceding female herds into areas of traditional elephant range depleted of elephants. In areas where elephant habitat increased abruptly due to civil unrest (such as in Mozambique, Namibia), bull elephants often 'colonized' new areas from which people had moved before females came into them (Lindeque 1995). These factors are particularly important in connection with conflict with people.

Assessing home range

Kenward (1990) noted that there are at least six fundamentally different approaches for representing an animal's home range. A review of the literature on range analysis indicates that there is little agreement among authors about which technique is generally the most appropriate. Decision on which to use depends heavily on the questions being asked and the type of data being collected. Methods for calculating home range can be separated into those based on a statistical distribution of activity loci (Dixon and Chapman 1980) and non-statistical methods. Techniques for assessing range non-statistically involve either drawing polygons (convex, concave or restricted) around the outer fixes or overlaying grid cells (White and Garrott 1990). Probabilistic methods include drawing probabilistic circles or ellipses around all the fixes (Jennrich and Turner 1969) or using mathematical equations to draw contour lines around percentages of fixes (Dixon and Chapman 1980).

The simplest way to estimate the size of a home range is to draw a polygon that encloses all the points then estimate the area in the polygon. The *minimum convex polygon* (MCP) (Mohr 1947) is simple to calculate and is the most widely published estimate of range size. However, it is an unsatisfactory estimate because it has been shown that the range estimate continues to increase as more fixes are added (Jennrich and Turner 1969) or that the range estimate is a function of the number of locations used to generate the range (White and Garrott 1990). MCPs are also heavily influenced by 'outliers' and sample size (Schoener 1981). It is a common procedure to eliminate the outer 5% of fixes in the range. This technique has also been criticized because when two fixes are closely spaced but far from the majority of locations, the area contributed to the polygon by each of the outliers is small (Kenward 1987). Removing one fix may reduce the area of the polygon only slightly. The other limitation of this technique is that MCPs estimate the total area and give no indication of areas of intensive use.

Structure of core areas

It is not only the size and shape of a home range that is of interest, but also its *structure*. To determine the structure, one first determines the 'centre of activity' by using either the arithmetic mean (the mean of x and y coordinates) or a harmonic mean (inverse reciprocal mean of distances) for a set of fixes (Kenward and Holder 1995). One common approach to determining a 'core', is to draw an MCP around 50% or 60% of fixes farthest away from the 'centre of activity' (fig.1a). However, this technique encounters the same problems listed earlier for the MCP method (Clutton-Brock et al. 1982). Increasingly, non-parametric approaches are being used because no assumptions are made about the shape of the area used.

The variability seen when examining the use of an area by an animal is generally referred to as *utilization distribution* (Worton 1989). A common method to measure home range was the arithmetic mean centre or the geographic centre of all points. However, this 'centre of activity' may not have any biological significance and certain home-range configurations may cause this point to lie outside an animal's actual home range (for example, a boomerang-shaped range) (Harris et al. 1990).

The *harmonic mean* (HM) has been widely used as a measure of animal activity centres (Dixon and Chapman 1980) (fig. 1b). The HM technique first calculates the harmonic centre of the fixes, which is the location where the inverse reciprocal mean distance to all other fixes is minimal (Spencer and Barrett 1984). Then isolines (contours) are drawn to predetermined percentages of fixes. The mathematics of contouring aims 'to define the fix density distribution and provide an ideal approach for identifying an activity centre' (Kenward 1990). However, the HM method has some drawbacks in that the contours that include all fixes tend to 'balloon' into areas never visited by an animal (Kenward and Holder 1995).

An approach that is effective at separating core from outlying fixes is the *cluster* method (fig. 1c). This technique identifies the densest cluster of fixes and then either adds fixes to it or starts a new cluster depending on distances of neighbouring fixes (Kenward 1987). This system is particularly useful for identifying patches of usage (Kenward 1990).

The *kernel* method proposed by Worton (1989) is similar to the HM method but uses the 'kernel fix estimator' instead of the HM centre and tends to give a more accurate representation of range. This method generates a grid using raw fixes and calculates the estimated probability of finding a location at any point in the study area (fig. 1d). The kernel method is preferable to the HM method because the output is the actual probability values. The HM method gives, for any given point on a map, a number that is the distance of that point from an 'activity centre' (R. Charif pers. comm.). Both methods, however, depend on contouring, which in turn depends on density estimation at intersections of an arbitrary grid imposed on the fixes. The kernel analysis described in Worton (1989) does minimize grid dependence by avoiding inverse reciprocal functions. Kenward (1990) states the 'density estimation is a smoothing process, so that even core isolines do not always conform well to the fixes'.

Figure 1 illustrates the differences between the four commonly used methods for home range estimation, using the same set of fixes. Table 1 shows the area enclosed by the different contours for the four methods. While the MCP is considered a poor estimate of home

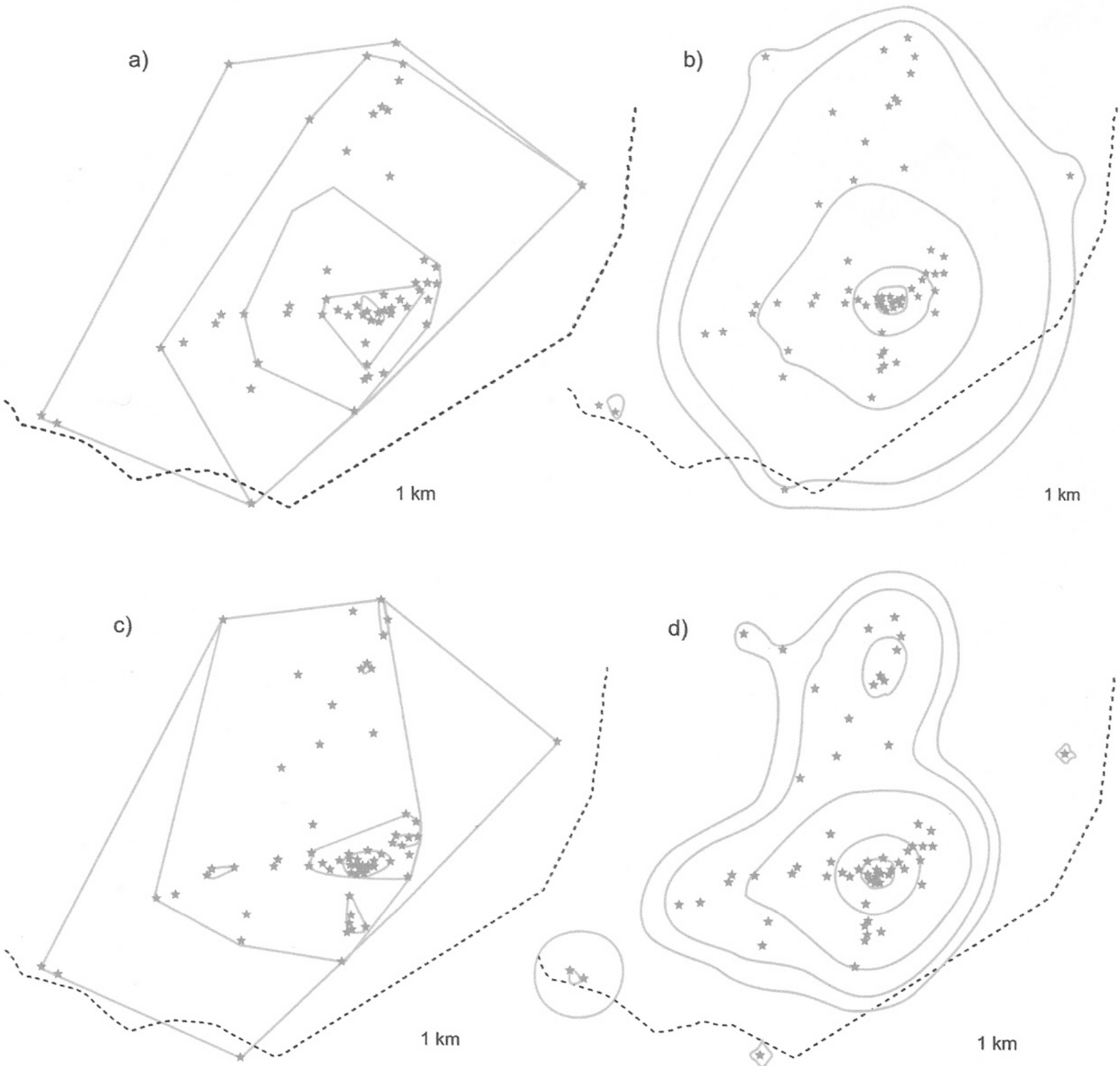

Figure 1. Four commonly used methods for estimating home range, using the same set of fixes: *a)* minimum convex polygon or MCP; *b)* harmonic mean; *c)* cluster; *d)* kernel.

range, it is still widely used. The kernel method, which appears to give the most accurate representation of the structure of an animal's range, is used for more precise estimates of total range and core area sizes.

Variation in range sizes

Comparing range size between elephant populations in different habitats is fraught with difficulty because the most widely used estimation of range is the MCP. As noted, MCPs are heavily influenced by outlying fixes although some trends are noticeable. Thouless (1996), in a review of the literature, points out that some elephant populations are 'sedentary' (for example, in Lake Manyara National Park, Douglas-Hamilton 1972) while others are nomadic or disperse in the wet season (Leuthold 1977; Viljoen 1989; Lindeque and Lindeque 1991). He demonstrates that home range sizes for el-

Table 1. Area included in different percentages of fixes by the four methods used in figure 1

Type of analysis	Percentage of fix and coverage in km^2 25%	50%	75%	95%	100%
MCP	0.39	3.95	24.73	79.91	121.34
Harmonic mean	0.79	4.26	34.94	125.17	162.19
Cluster	0.20	1.18	5.45	67.22	121.00
Kernel	0.77	5.10	29.64	71.43	101.39

ephants in Laikipia District in Kenya are inversely correlated with rainfall. Data obtained from the literature suggests that more factors may be influencing range size than just rainfall and primary productivity. These factors include the distribution of surface water, the topography of the landscape, and the diversity and quality of the soil and vegetation. There does, however, seem to be a relationship between rainfall and elephant range size. Using 100% MCPs, table 2 shows home range sizes for cows and bulls.

Figure 2 compares the mean annual rainfall and the ranges for the elephant populations listed in table 2. The relationship between rainfall and home range size does exist, but the trend is weak. It is not clear whether this is because home range was estimated inaccurately due to previously noted problems with

Table 2. Published home range sizes of male and female elephants based on 100% minimum convex polygon and the relationship to rainfall in different habitats

Location [a]	Home range size (km^2)	No. [b]	Annual rainfall (mm)	Reference
Female elephants				
Tsavo East NP	2380	8	300	Leuthold 1977
Namibia	5800–8700	7	315	Lindeque and Lindeque 1991
Amboseli NP	2756	6	350	Western and Lindsay 1984
Laikipia	600–800	14	400	Thouless 1996
Kruger NP	129–1255	21	550	Whyte 1993
Tsavo West NP	408	2	550	Leuthold 1977
Transvaal	115–465	11	600	De Villiers and Kok 1997
Hwange NP	1038–2544	11	632	Conybeare 1991
Waza NP	2484–3066	2	700	Tchamba et al. 1995
Laikipia	450–500	4	750	Thouless 1996
Zambezi Valley	156	11	800	Dunham 1986
Queen Elizabeth NP	363	6	900	Abe 1994
South India [c]	105–115	2	900	Sukumar 1989
Lake Manyara NP	10–57	2	1000	Douglas-Hamilton 1972
Male elephants				
Tsavo East NP	1035–1209	2	300	Leuthold and Sale 1973
Tsavo West NP	294–337	2	550	Leuthold and Sale 1973
Transvaal	157–342	21	600	De Villiers and Kok 1997
Hwange NP	1300–2981	7	632	Conybeare 1991
Sengwa	322	9	668	Osborn 1998
Queen Elizabeth NP	500	6	900	Abe 1994
South India [c]	170–320	2	900	Sukumar 1989
Malaysia [c]	32–60	4	2500	Olivier 1978

[a] Listed in ascending order of rainfall
[b] Number of elephants used in the analysis
[c] Asian elephants included for comparison
NP – national park

the MCP method or if other factors are influencing these results. Elephants in the Communal Lands of north-eastern Zimbabwe appear to have much larger ranges than those that are always in protected areas (Taylor 1983). The rainfall in the protected areas and in the Communal Lands in this part of Zimbabwe is similar. What is causing the variation in range? Perhaps it is caused by human settlement.

Human impact on elephant ranging patterns

Numerous authors indicate that human settlement patterns and illegal hunting have had a profound effect on ranging patterns of elephants. Rapidly expanding human populations maintained by a subsistence economy are changing land-use patterns in a way that constricts the habitat available to elephants. Human encroachment into elephant habitat cuts off the channels through which elephant populations responded to environmental fluctuations, such as emigration and dispersal (Watson and Bell 1969). For example, seasonal migration is affected by human pressures, primarily poaching, in the elephant wet-season range in Amboseli (Western and Lindsay 1984). Lewis (1986) noted a shift in elephant feeding patterns once the disturbance of poaching was relieved in the Luangwa Valley in Zambia. Human interference and harassment influences movement patterns of elephants in the forests of Central Africa (Ruggiero 1992; Barnes et al. 1992; Tchamba et al. 1995). Kangwana (1995) found that elephant movements are strongly affected by competition with pastoralists over livestock forage and access to water and by direct, targeted killing by warriors in Amboseli National Park.

In dry areas, the general trend for elephants is to move large distances in search of food and water. In wet areas, elephants tend to have smaller home ranges because both food and water are more available. However, this trend is not always seen in the rainforest. Merz (1986) reports that forest elephants (*Loxodonta africana cyclotis*) can move considerable distances in the wet season. The home range of forest elephants in Cameroon varies between 224 and 315 km^2 (Powell 1997). I suggest that rainfall may once have had a strong impact on the size of elephant home range, but now the major influence in many areas is the size of the area in which elephants are allowed to move

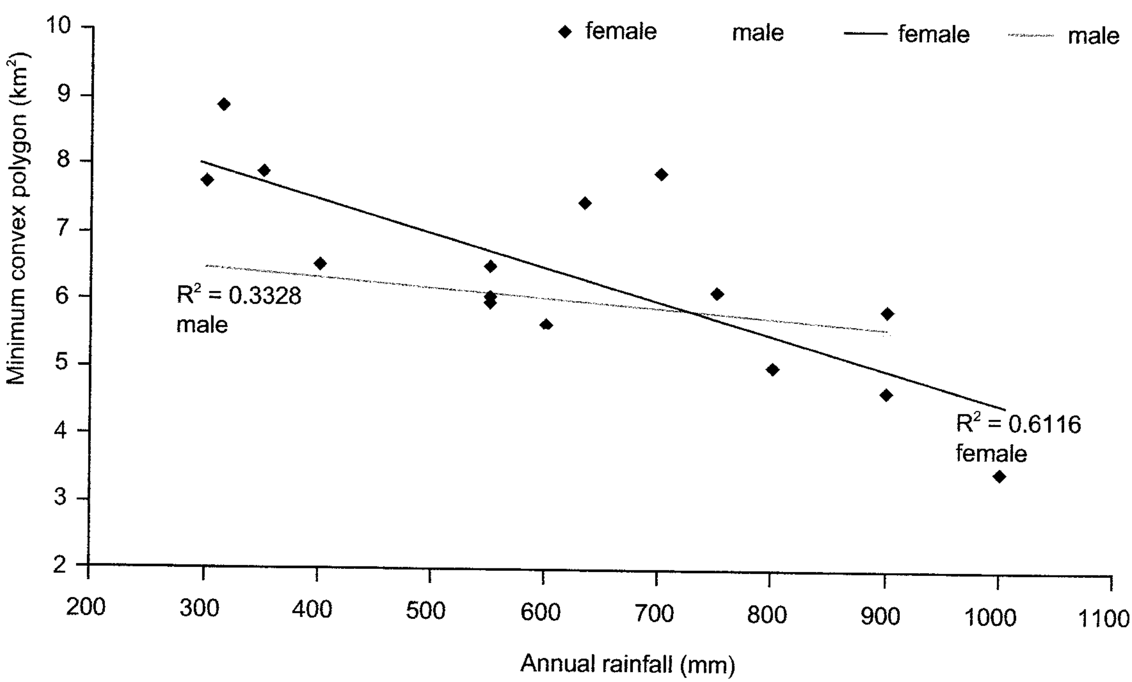

Figure 2. Home range size (100% minimum convex polygon (MCP)) for male and female elephants from across Africa and Asia, compared with the mean annual rainfall. See table 2 for sources of information on other populations.

unimpeded. From the data in table 2, it appears that the estimated ranges relate more closely to the size of the area in which the elephants are free to roam, unharassed, than to rainfall patterns. In dry areas, there tends to be little agriculture, thus elephants are able to range over much larger distances. In wet areas, agriculture is far more intensive and the elephant home range is correspondingly restricted. For example, the range that Douglas-Hamilton (1972) found for the Lake Manyara National Park elephants is almost exactly the size of the protected area available to them. In Namibia, at the other extreme, there are almost no restrictions to the east–west movement of elephants and they use the available habitat fully (Lindeque and Lindeque 1991).

Conclusion

This review outlines the concept of home range with regard to elephants and different commonly used techniques to measure it. The importance of understanding core areas and linking their relevance to elephant conservation is noted. The influences that dictate range size are related to rainfall, but human influences may now play a larger role in determining where elephants can roam.

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