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 Methods for determining home range that are widely reported in elephant literature are outdated and inaccurate.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 il s’agit de l’éléphant. Les méthodes qui servent à déterminer le domaine vital et qui sont largement reprises dans la littérature sur les éléphants sont dépassées etincorrectes. 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, zones 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, moving and caring for young’. The problem with this definition is the idea of ‘normal’. He also notes that ‘dispersal and occasional sojourns 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

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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 have 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 within 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, Hazen 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**

Havre (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 de-populated 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 re-
stricted) around the outer fixes or overlaying grid cells (White and Garrott 1990). Probabilistic methods in- clude drawing probabilistic circles or ellipses around all the fixes (Kenrich and Turner 1969) or using math- ematical equations to draw contour lines around per- centages 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 cal- culate 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 (Kenrich and Turner 1969) or that the range estimate is a func- tion of the number of locations used to generate the range (White and Garrott 1990). MCPs are also heav- ily 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 con- tributed 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 limita- tion 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 re- ciprocal mean of distances) for a set of fixes (Kenward and Holder 1995). One common approach to deter- mining 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-para- metric approaches are being used because no assump- tions 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 utiliza- tion distribution (Worton 1989). A common method to measure home range was the arithmetic mean cen- tre 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 dis- tance to all other fixes is minimal (Spencer and Barrett 1984). Then isolines (contours) are drawn to prede- terminate percentages of fixes. The mathematics of contouring aims 'to define the fix density distribu- tion 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 vis- ited by an animal (Kenward and Holder 1995).

An approach that is effective at separating core from outlier 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 pref- erable 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 dis- tance of that point from an 'activity centre' (R. Charif pers. comm.). Both methods, however, depend on contouring, which in turn depends on density estimations 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 horse range estimation, using the same set of fixes. Table 1 shows the area en- closed by the different contours for the four methods. While the MCP is considered a poor estimate of home range
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. Thoslees (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 Lindke 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

<table>
<thead>
<tr>
<th>Type of analysis</th>
<th>Percentage of fix and coverage in km²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>25%</td>
</tr>
<tr>
<td>MCP</td>
<td>0.39</td>
</tr>
<tr>
<td>Harmonic mean</td>
<td>0.79</td>
</tr>
<tr>
<td>Cluster</td>
<td>0.20</td>
</tr>
<tr>
<td>Kernel</td>
<td>0.77</td>
</tr>
</tbody>
</table>

Elephants 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 convex polygon and the relationship to rainfall in different habitats.

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

<table>
<thead>
<tr>
<th>Location</th>
<th>Home range size (km²)</th>
<th>No.</th>
<th>Annual rainfall (mm)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female elephants</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tsavo East NP</td>
<td>2380</td>
<td>8</td>
<td>300</td>
<td>Leuthold 1977</td>
</tr>
<tr>
<td>Amboseli NP</td>
<td>5800–8700</td>
<td>7</td>
<td>315</td>
<td>Lindeque and Lindeque 1991</td>
</tr>
<tr>
<td>Laikipia</td>
<td>600–800</td>
<td>14</td>
<td>400</td>
<td>Tholess 1996</td>
</tr>
<tr>
<td>Kruger NP</td>
<td>129–1255</td>
<td>21</td>
<td>550</td>
<td>Whyte 1993</td>
</tr>
<tr>
<td>Tsavo West NP</td>
<td>408</td>
<td>2</td>
<td>550</td>
<td>Leuthold 1977</td>
</tr>
<tr>
<td>Transvaal</td>
<td>115–465</td>
<td>11</td>
<td>600</td>
<td>De Villiers and Koë 1997</td>
</tr>
<tr>
<td>Hwange NP</td>
<td>1038–2544</td>
<td>11</td>
<td>632</td>
<td>Cornbread 1991</td>
</tr>
<tr>
<td>Waza NP</td>
<td>2484–3066</td>
<td>2</td>
<td>700</td>
<td>Tshomba et al. 1995</td>
</tr>
<tr>
<td>Laikipia</td>
<td>450–550</td>
<td>4</td>
<td>750</td>
<td>Tholess 1996</td>
</tr>
<tr>
<td>Zambesi Valley</td>
<td>156</td>
<td>11</td>
<td>800</td>
<td>Dunham 1986</td>
</tr>
<tr>
<td>Queen Elizabeth NP</td>
<td>363</td>
<td>6</td>
<td>900</td>
<td>Abe 1994</td>
</tr>
<tr>
<td>South India</td>
<td>105–115</td>
<td>2</td>
<td>900</td>
<td>Sukumar 1989</td>
</tr>
<tr>
<td>Lake Manyara NP</td>
<td>10–67</td>
<td>2</td>
<td>1000</td>
<td>Douglas-Hamilton 1972</td>
</tr>
<tr>
<td>Male elephants</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tsavo East NP</td>
<td>1035–1209</td>
<td>2</td>
<td>300</td>
<td>Leuthold and Sale 1973</td>
</tr>
<tr>
<td>Tsavo West NP</td>
<td>294–337</td>
<td>2</td>
<td>550</td>
<td>Leuthold and Sale 1973</td>
</tr>
<tr>
<td>Transvaal</td>
<td>157–342</td>
<td>21</td>
<td>600</td>
<td>De Villiers and Koë 1997</td>
</tr>
<tr>
<td>Hwange NP</td>
<td>1300–2581</td>
<td>7</td>
<td>670</td>
<td>Cornbread 1991</td>
</tr>
<tr>
<td>Senguwa</td>
<td>322</td>
<td>9</td>
<td>668</td>
<td>Osborn 1998</td>
</tr>
<tr>
<td>Queen Elizabeth NP</td>
<td>500</td>
<td>6</td>
<td>900</td>
<td>Abe 1994</td>
</tr>
<tr>
<td>South India</td>
<td>170–320</td>
<td>2</td>
<td>900</td>
<td>Sukumar 1989</td>
</tr>
<tr>
<td>Malaysia</td>
<td>32–40</td>
<td>4</td>
<td>2500</td>
<td>Olivier 1978</td>
</tr>
</tbody>
</table>

* Listed in ascending order of rainfall
* Number of elephants used in the analysis
* Asian elephants included for comparison
NP — national park

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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 constrains 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 w orriors 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. Merx (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 km² (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.

![Graph](image)

**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.

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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, unharrassed, 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 tech-niques to measure it. The importance of understand-ing core areas and linking their relevance to elephant conservation is noted. The influences that dictate range size are related to rainfall, but human influ-ences may now play a larger role in determining where elephants can roam.

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References
Lewis, D.M. 1986. Disturbance effects on elephant feed-


