The elephant population of Samburu and Buffalo Springs National Reserves, Kenya

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Abstract

A 21-month individual identification project on the Samburu and Buffalo Springs National Reserves' elephant population was conducted between November 1997 and July 1999. The free ranging population, of at least 767 elephants, which relied heavily on areas outside the reserves, was individually identified. The numbers of elephants observed per day fluctuated but were greater during dry periods then wet. However, the sizes of aggregations were greater during wet periods. Preliminary investigation suggested that the population could be divided into two groups, which were designated resident and non-resident family units. The groups comprised approximately equal numbers of cows and calves, but temporally had different reserve use patterns and calving peaks. The daily numbers of males and must males were correlated with numbers of females. The reserves appeared to be a focal area for calving, indicating that the study area was of reproductive importance to the population. Demographic data indicated a female biased population sex ratio, with over twice the number of mature females to males. The observed sex skew was greatest for older age classes, and the density of musth bulls in the study area was low. The population was affected by poaching. Continued monitoring will assist conservation efforts by alerting authorities of major demographic or range use changes.

Key words: demographic structure, monitoring, range use

Résumé

Entre novembre 1997 et juillet 1999, on a mené un projet d'identification individuelle des populations d'éléphants des Réserves Nationales de Samburu et de Buffalo tion sauvage, qui compte au moins 767 éléphants, qui dépend fortement de zones extérieures aux Réserves. Le nombre d'éléphants observés chaque jour variait mais il était plus important en saison sèche qu'en saison des pluies. Cependant, la taille des groupes était supérieure durant la saison des pluies. Les premières recherches laissent penser qu'on peut diviser la population en deux groupes, que l'on a désignés comme les unités familiales résidentes et les non résidentes. Les groupes comprenaient à peu près le même nombre de femelles et de jeunes. mais leur mode d'utilisation de la réserve était différent de même que les périodes de mises bas. Chaque jour, le nombre de mâles et celui de mâles en musth étaient liés au nombre de femelles. Les réserves semblent être une région centrale pour les mises bas, ce qui indique que la région étudiée est importante pour la reproduction de la population. Les données démographiques indiquaient un sex-ratio biaisé en faveur des femelles adultes, cellesci étant plus de deux fois plus nombreuses que les mâles adultes. Cette différence était plus forte pour les classes d'âge supérieures, et la densité des mâles en musth dans la région était faible. La population subissait les effets du braconnage. Une surveillance régulière aidera à la conservation en alertant les autorités des changements démographiques ou d'utilisation de l'habitat majeurs.

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Introduction

The greater Laikipia-Samburu region has the largest population of elephants, *Loxodonta africana* (Blumenbach), primarily residing outside of protected areas in Kenya (Poole *et al.*, 1992). The Kenya Wildlife Service 1999 aerial census estimated the population at approximately 3400 individuals (Kahumbu *et al.*, 1999). Extensive poaching occurred during the 1970s and 1980s in Kenya (Douglas-Hamilton, 1987). Although poaching still

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occurs in the region (King et al., 1999), Samburu and Buffalo Springs National Reserves are safe havens for wildlife.

Wildlife tourism brings revenue and employment to the reserves and local communities. The elephants within the reserves are approachable, making them ideal for tourism, research and monitoring. A recent study of movement patterns suggested that the elephants using the reserves are part of a subpopulation, numbering around 800 individuals, of the greater Laikipia-Samburu population (Thouless, 1996). However, the status of the reserves' elephants was unclear as the study did not observe individuals from the subpopulation to enter the reserves, and detailed information on the use of the reserves was not undertaken (Thouless, 1993).

A 21-month individual identification study of the elephant population within these reserves was conducted between November 1997 and July 1999. Data on demography, social behaviour and ranging patterns were gathered. This paper describes observed population fluctuations and social structure of the reserves' elephant population.

Materials and methods

Study area

The Samburu and Buffalo Springs National Reserves study area is approximately $330\,\mathrm{km}^2$ and located just north of the Equator at a longitude of $37\,^\circ\mathrm{E}$ (Fig. 1). Topographically rugged hills and watercourses characterize the reserves, with an elevation range between $800\,\mathrm{and}$ $1200\,\mathrm{m}$.

The Ewaso Ngiro River, the largest semi-permanent river in this region, divides the reserves and is a focal area for wildlife. The river originates from tributaries on Mt Kenya and the Aberdares Range, draining northward through the Laikipia District. Rainfall is localized and highly variable in the region, with the majority falling during the long rains in March–May and the short rains in October–December. The study area is dry and hot throughout much of the year, receiving $360\pm170\,\mathrm{mm}$ (SD) of annual precipitation (Government of Kenya, 1997).

The distribution of vegetation in the study area largely depends upon the availability of water. The river acacia, *Acacia elatior*, and duom palm, *Hyphaene coriacea*, dominate the riverine woodland along the banks of the Ewaso Ngiro. Salt bush, *Salsola droides*, a low-growing shrub, is common on the saline soils of the low lying pans adjacent to the river. The two major vegetation communities in the study area are *Acacia-Commiphora* semiarid scrub woodland and *Acacia* wooded grassland, typically found in dry regions further from the river. Most of the plant species inhabiting these regions are ephemeral or shed their leaves during the dry season.

Data collection and analysis

Observations were made within the demarcated boundaries of the two reserves. A general transect following the study area water courses was used during each sampling day (Douglas-Hamilton, 1996). However, the location and densities of elephants affected the route taken and time spent per study area region. It was not possible to cover the entire study area each day of the study, and

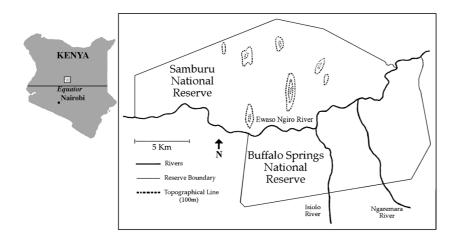


Fig 1 Map of the Samburu and Buffalo Springs National Reserves study area. The study area, 330 km², is located just north of the Equator and centred on the Ewaso Ngiro River, the major water source in the region

areas with greater elephant densities were more heavily sampled as a result of the method employed. Daily effort was consistent throughout the duration of the study. although numbers of observation days varied across months (the mean number of observation days per month \pm SD was 18 \pm 5). I conducted all identifications and successive data collection, excluding calving data after August 1999.

Each elephant within the study area was identified using sex, age and features unique to the individual, such as ear patterns (Douglas-Hamilton, 1972; Moss, 1988, 1996). Photographs and drawings of these features were used in the development of an identification dossier. When an elephant was located, the date, time and Global Positioning System (GPS) location were recorded as well as the identities of conspecifics present. All individual associations and behavioural interactions were recorded. Elephants observed within 1km of each other were defined as 'associating' (Douglas-Hamilton, 1972).

Family units consist of related breeding females (cows) and their offspring (Douglas-Hamilton, 1972; Moss, 1988). Family units were defined by quantifying association data of breeding females. Elephants associating at least two-thirds of the total number of observations for each female (median = 34, interquartile range 8-51observations; n = 203) were categorized as a family unit. This was designed to avoid errors caused by incomplete censusing, which can occur in thick bush. Using this definition, 86% of the identified elephants were assigned to a family unit. No individual was assigned to more than one family unit. The monthly frequency of family unit presence was plotted to assess usage patterns. The emergent bimodal distribution was used to delineate the population into resident and non-resident family units (cf.

Age estimates for individuals were conducted using shoulder height and physical appearance indices established through molar evaluation of culled individuals (Laws, 1966; Laws, Parker & Johnstone, 1975; Moss, 1996). A preparatory training course on ageing elephants was completed in Amboseli National Park with known age elephants. Error in estimates may increase for older age groups, as age-related differences are more pronounced in the younger age groups (Jachmann, 1985; Moss, 1996). Therefore, age structure analysis was presented in 5 year age classes for elephants up to the age of 20 years and 15 year age classes for elephants over the age of 20 years (Moss, 1996). Data on surviving calves

were from 26 months of known births in combination with age estimates of calves under 3 years at the onset of the study. Estimated calf ages were presented because calves under three are generally not weaned and in the early stages of tusk eruption (Moss, 1988), making them relatively easy to distinguish and age. Individuals of unknown age or sex were only included in analysis of family unit size.

Monthly rainfall data from 1957 to 1999 were provided by NRM³ (National Resource Monitoring, Management, and Modelling). Analyses across expected wet and dry seasons were partitioned using the long-term average monthly rainfall, March-May and October-December being wet season months (averaging $54.1 \pm 59.4 \, \text{mm}$ (SD) per month), and January-February and June-September being dry season months (averaging $7.0 \pm$ 18.3 mm (SD) per month). Analysis was also conducted according to actual monthly rainfall during the study. Wet months were defined as receiving more than 25 mm of precipitation (approximately one standard deviation more than the mean precipitation of dry season months) and dry months as receiving 25 mm or less.

Analysis of population fluctuations was conducted on actual numbers of elephants observed per day (N = 327 days). Repeated sightings of individuals were not included in daily totals. The number of associating individuals per observation was used to quantify group sizes for analysis. The first 3 months of data were spent identifying new elephants and becoming familiar with the study area. Therefore, they were not considered representative samples and excluded from analysis. Analyses were conducted using the SAS JMP IN statistical package. Nonparametric techniques were used for all tests.

Results

Individual identification

After 21 consecutive months of study, 744 elephants were identified. An additional 23 elephants were not fully identified. A minimum of 767 elephants used the study area during this period. New elephants, both cow/calf groups and males, entered and were identified in the study area throughout the project. No significant relationship was found between numbers of new elephants per month and numbers of days spent observing per month (Spearman rank correlation: $r_s = -0.0195$, n = 21, d.f. = 19, P = 0.9519). The monthly numbers of new elephants

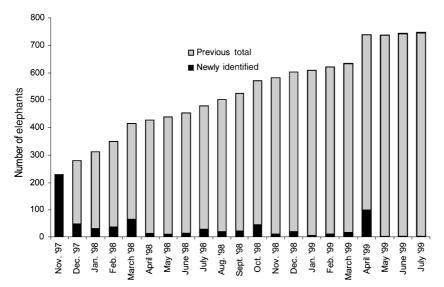


Fig 2 The number of elephants identified per month varied during the study. The combination of grey and black columns represents the total number of elephants identified in the population during that month. The greatest number of new individuals since the first month of the study was identified in April 1999. Few elephants were identified during the last 3 months of the study

declined over the study period, with over half of the population being identified in the first 5 months of the study (Fig. 2). The majority of the population, 76%, was identified during the expected wet season months. The median number of new elephants seen was 20 individuals per month (interquartile range 10-37 individuals; n=21). In April 1999 an unusual influx of 102 new elephants was observed, the greatest monthly number of elephants identified since the first month of the study.

Daily numbers of elephants recorded within the reserves fluctuated between 0 and 227 individuals, with

a median of 49 individuals (interquartile range 24–76 individuals; n=327). Daily numbers were significantly correlated with the observation day of the study ($r_s=0.3708, n=327, \text{d.f.}=325, P<0.0001$). However, this correlation was not present during the last 12 months of the study, which were relatively dry ($r_s=0.0742, n=222, \text{d.f.}=220, P=0.2710$). Daily numbers were negatively correlated with monthly rainfall ($r_s=-0.3597, n=327, \text{d.f.}=325, P<0.0001$), indicating that fewer elephants were observed in the study area during months with higher rainfall (Fig. 3).

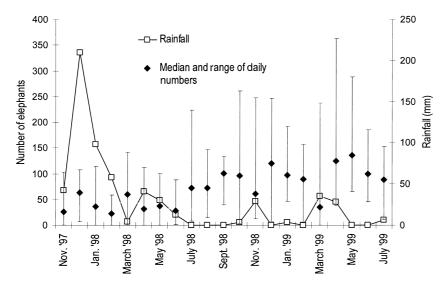


Fig 3 Monthly rainfall measurements (\square) were negatively correlated with daily number of individual elephants observed in the study area ($r_s = -0.3597$, n = 327, d.f. = 325, P < 0.0001). \spadesuit signify the median number of elephants observed per day. Errors bars represent the total range of the daily numbers for that month

The average daily numbers during months with rainfall greater than 25 mm (median = 33.5, interquartile range 10.5–65.5; n = 102 days) were significantly less than numbers in months with rainfall 25 mm or less (median = 55, interquartile range 33–77; Z = 4.142, $n_1 = 102$, $n_2 = 225$, P < 0.0001). However, the group sizes during months with rainfall greater than 25 mm (median = 16, interquartile range 10–30; n = 175) were significantly greater than the group sizes during months with 25 mm or less of rainfall (median = 14, interquartile range 8-25; Z = 2.626, $n_1 = 175$, $n_2 = 673$, P = 0.0086). The daily numbers of elephants observed within the study area during the expected wet season (median = 50, interquartile range 24–84 individuals; n=170) were not significantly different from the expected dry season (median = 48, interquartile range 25-72; Normal Approximation Mann–Whitney Test: Z = 1.135, $n_1 = 170$, $n_2 = 157$, P = 0.2565). However, group sizes during the expected wet season (median = 19, interquartile range 10-30; n=395) were significantly greater than those recorded during the expected dry season (median = 12, interquartile range 7-20; Z = 5.943, $n_1 = 395$, $n_2 = 453$, P < 0.0001).

The daily numbers of elephants observed in the study area were more representative of cow/calf groups than independent males, because the numbers of cows observed per day (median = 18, interquartile range 9–28 individuals; n = 327 days) were significantly greater than the numbers of males (median = 2, interquartile range 1-4; Z = 17.69, $n_1 = 327$, $n_2 = 327$, P < 0.0001). The numbers of independent males per day

were correlated with the numbers of cows ($r_s = 0.4897$, n = 327, d.f. = 325, P < 0.0001). The numbers of musth males (Poole, 1987) per day (median = 0, range 0-3; n = 327) were also correlated with the numbers of cows $(r_s = 0.2039, n = 327, d.f. = 325, P = 0.0002)$, although the relationship was not as strong. This may be a result of the low density of musth males in the study area, as only 19 individuals were observed in musth during the study period.

Social structure

Identified cows and calves were grouped into 65 family units. Family unit monthly presence was bimodal, with modes of six family units present for 4 months and eight family units present for 11 months (Fig. 4). This pattern was used to delineate the population into two categories. The 39 family units using the parks for 9 months or more are referred to as 'resident' (56% of the identified cows and calves) and the 26 family units using the parks for 7 months or fewer are referred to as 'non-resident' (44%). Although every family unit left the study area, durations of absence varied. Males were generally more transient, and lacked a bimodal frequency distribution (Fig. 4).

The median family unit size was nine individuals (range 3–36; n = 65; Fig. 5). The numbers of individuals comprising resident family units (median = 8, range 3-36 individuals; n=39) were not significantly different from non-resident family units (median = 9, range 3-25individuals; Z = 0.194, $n_1 = 39$, $n_2 = 26$, P > 0.25).

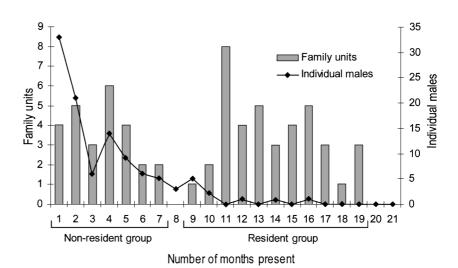


Fig 4 Columns represent the family unit monthly presence and lacktrianglerepresent male monthly presence. The bimodal distribution of family unit presence was used to delineate resident and non-resident family units. The distribution of males was not representative of distinct groups

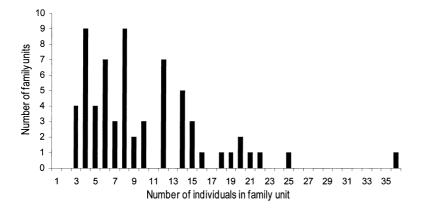


Fig 5 Distribution of core family unit size consisting of associating cows and their offspring. Breeding females associating greater than two-thirds of the total number of observations were categorized as a family unit

Table 1 The age and sex structure of the Samburu and Buffalo Springs National Reserve's elephant population

Age groups (years)	Males	Females	Sex ratio of aggregated ages M: F	Group population (%)
0–4.9	129	121		34
5-9.9	77	89	258:279	22
10-14.9	25	37	(1:1.1)	8
15-19.9	27	32		8
20-34.9	47	80		17
35-49.9	14	59	62:145	10
50+	1	6	(1:2.3)	1
Total	320	424		

The elephant birth sex ratio is 1:1 (Poole, 1996). In undisturbed populations, males have slightly higher rates of mortality than females (Laws *et al.*, 1975; Lee & Moss, 1986; Poole, 1989a). The demographic section of the Samburu population under 20 years old did not significantly differ from the 1:1 ratio ($\chi^2=1.134$, d.f. =1, P>0.20). However, the male: female sex ratio of elephants 20 years and older was 1:2.3, which significantly deviated from the expected sex ratio ($\chi^2=33.28$, d.f. =1, P<0.0001; Table 1).

Birth and mortality

The birthing cycles of the two social categories, estimated from numbers of surviving calves, appeared distinct across a 5 year sample. The number of surviving calves born to resident family units peaked in 1999, whereas those born to non-resident family units peaked in 1998 (Fig. 6). The number of births in 1999 was exceptional, with 93 recorded in the population. Over 85% (n = 64) of the calves observed within 1 month of their birth were

born during the wet seasons of that year (Kahindi, 1999; Wittemyer, 1999).

Recorded mortality rates were low. Of the seven confirmed deaths within the reserves, four were calves less

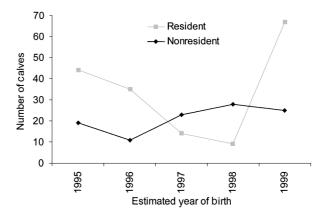


Fig 6 The number of surviving calves was indicative of a staggered calving interval between resident and non-resident family units. Ages were estimated for calves born in 1995, 1996 and early 1997

than 2 months of age. Because these elephants were free ranging, it was difficult to distinguish between absent and dead elephants. It is probable that more elephants died during the study period than were recorded. Although no instances of poaching occurred within the study area, at least six elephants were illegally killed within a 20 km radius of the reserves in February (4), May (1) 1998 and June (1) 1999. Other instances of poaching occurred in areas that were probably used by the study population.

Discussion

The elephant population of Samburu and Buffalo Springs National Reserves inhabits an unconfined semi-arid ecosystem. The number of elephants identified exceeded previous estimates of the reserves' population. As indicated by fluctuations in daily numbers, the population regularly used regions outside the protected area. The data presented in this paper represent minimum population figures, because not all individuals entering the reserves were observed.

The monthly number of elephants identified progressively decreased during the study. During the final 3 months, monthly identifications averaged 2.7 individuals. Follow-up monitoring had not identified any new cow/calf groups through July 2000, although occasionally young, unidentified males (younger than 25 years) were observed (O. Kahindi, pers. coms.), indicating that the majority of the population had been identified by July 1999.

The daily numbers of elephants observed were positively correlated with the observation day, although the correlation weakened as the study progressed. My monitoring capacity may have induced this trend. However, daily numbers were negatively correlated with monthly rainfall totals, indicating that the population was increasingly outside the reserves during wet periods, when they were less reliant on the river. The exceptional 'El Nino'induced rainfall, which connected the short and long rains during the first year of the study, may have depressed the numbers of elephants using the reserves through June 1998 by enhancing the ecological conditions in the region. As food and water surpluses outside the reserves gradually declined or became less accessible, portions of the population may have been pushed into the reserves where permanent water and little human competition occur. Daily numbers were not correlated

with the observation day during the last 12 months, when monthly wet season rainfall was below average. Additionally, poor security during the initial 12 months of the study may have caused elephants to avoid the region.

Daily numbers were significantly lower in months with rainfall greater than 25 mm but aggregations tended to be larger during these intervals. Larger aggregations during wet periods have been observed in other ecosystems, where researchers suggested that aggregations are ecologically dependent (Douglas-Hamilton, 1972; Moss & Poole, 1983; Moss, 1988). Ranges of daily numbers were wider during wet months, when the maximum daily numbers were observed within the study area. Increased ranges reflect the mobility of the population, indicating greater daily variation in the numbers moving in and out of the reserves. Additionally, the majority of identification events occurred during the expected wet season months. During the rains, normally dry regions contain temporary water sources, allowing dispersal that is water limited during the dry season. The observed population fluctuations and increase in identification events may have been related to this 'opening' of dry regions, inducing elephant migrations (Western & Lindsay, 1984; Thouless, 1995). Additionally, aggregations were greater during expected wet season months, although daily numbers did not differ across season, indicating that elephants may have amassed in anticipation of the rains. This may have been related to social factors such as seasonal peaks in reproduction, as signified by monthly numbers of

The 1:2.3 (male: female) sex ratio of elephants 20 years and older is relevant to the management of this population, as it may affect population dynamics (Lewis, 1984; Poole, 1989a; Barnes & Kapela, 1991). The strength of sex ratio skew increased exponentially across age classes. The sex ratio may have been caused by study area biases, such that areas of high cow/calf concentrations were sampled more heavily than areas with equal or higher concentrations of male densities. However, there was no evidence of sexually distinct areas (e.g. Moss & Poole, 1983). In contrast to undisturbed populations that have only slightly skewed sex ratios, similar degrees of skew to that of the Samburu population were observed in elephant populations that have experienced high levels of poaching (Poole, 1989a). The skewed sex ratio was most probably caused by selective poaching, as mature males are more likely than females to be killed for ivory, due to their larger tusks (Pilgram & Western, 1986; Poole,

1989a). The observed sex ratio indicated that the population had not recovered from past poaching pressures and may be subject to a current level of poaching sufficient to maintain the skew. Daily numbers were more representative of breeding females than males as a result of the population differences, and the number of musth males, which are the oldest males in a population (Poole, 1987; Poole, 1989b), was low.

The reserves are a focal area for calving, which peaked during the wet season months of 1999. This peak occurred 2 years after the exceptional rains of 1997, signifying increased breeding activity during that wet year. Additionally, the daily numbers of males, both total and musth individuals, were correlated with the numbers of cows, indicating that male density may have been partially motivated by cow presence. It is likely that musth males excluded other competitors from the study area during their periods of dominance (Poole, 1989b), resulting in little variation in the number of musth males present during the study. The low number of mature males in the population probably also contributed to this trend.

Preliminary analysis was indicative of two distinct social sets, categorized into resident and non-resident families. These groups utilized the reserves differently, which may reflect distinct movement patterns and ranges. Additionally, their breeding cycles varied, indicated by ages of surviving calves, and calving peaks occurred during different years. The two groups may have been affected by different stimuli in relation to fecundity, such as reaction to localized ecological conditions, mobility of the family unit, or insecurity. The age structures of both groups were indicative of high levels of recruitment and the family unit structure was similar across groups. Mature males were largely independent as has been found in other studies (Douglas-Hamilton, 1972; Moss, 1988).

In April 1999 a major influx of unidentified elephants into the reserves was observed. The number of new elephants identified this month was in the 95th percentile of the identification numbers' range, second only to the initial month of the study. Although not analysed, these elephants were behaviourally distinct from other elephants in the study area, tending to be more nervous and, in some cases, highly aggressive. Range shifts may be related to ecological, social or security factors. This unusual influx occurred during the wet season and may have been in response to seasonal variations in range use. However, this month's numbers exceeded any prior

seasonal peak and the behavioural abnormalities of these individuals were rarely experienced in the study area. Considering the security situation in the region and the behaviour of these elephants, it is likely that human disturbance caused this influx.

This study was set up with the aim of providing information on the elephant population and creating an 'early warning system' for wildlife authorities regarding marked changes in poaching levels or elephant population shifts. Ecological conditions appeared to be a driving factor of the Samburu population's social behaviour and movements. It was clear the population was dependent on areas exterior to the reserves' boundaries. Although the study area was physically unconfined, it may have been constricted by security factors. Ground observations and calving events suggested that elephants identified the reserves as a 'safe haven'. If human pressures reduce the elephant range, the numbers using the reserves may increase. This could have negative ecological effects. Additionally, if stresses on the population increase, the viability of the population may be affected.

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References

Barnes, R.F.A. & Kapela, E.B. (1991) Changes in the Ruaha elephant population caused by poaching. *Afr. J. Ecol.* 29, 289–294. Douglas-Hamilton, I. (1972) *On the Ecology and Behaviour of the African Elephant: Elephants of Lake Manyara*. DPhil Thesis, University of Oxford, Oxford.

Douglas-Hamilton, I. (1987) African elephants population trends and their causes. *Oryx* 21, 11–24.

- DOUGLAS-HAMILTON, I. (1996) Counting elephants from the airtotal counts. In: Studying Elephants, AWF Technical Handbook Series 7 (Ed. K. KANGWANA). African Wildlife Foundation, Kenya.
- Government of Kenya (1997) Isiolo District Development Plan 1997-2001. Rural Planning Department Office of the President and Ministry of Planning and National Development, Kenya.
- JACHMANN, H. (1985) Estimating age in African elephants. Afr. J. Ecol. 23, 199-202.
- Kahindi, O. (1999) Save the Elephants Monthly Reports: Samburu Elephant Project. Save the Elephants Report, Kenya.
- KAHUMBU, P., OMONDI, P., KING, J., MURIUKI, G., GEDDES, C. & HIGGINBOTTOM, J. (1999) Total Aerial Count of Elephants in Samburu/Laikipia. Kenya Wildlife Service Report, Kenya.
- King, J., Kahumbu, P., Omondi, P. & Douglas-Hamilton, I. (1999) The Status of Kenya's Elephant Populations, September 1999. Kenya Wildlife Service Report, Kenya.
- LAWS, R.M., PARKER, I.S.C. & JOHNSTONE, R.B.C. (1975) Elephants and Their Habitats: the Ecology of Elephants in North Bonyoro, Uganda. Clarendon Press, Oxford.
- LAWS, R.M. (1966) Age criteria for the African elephant, Loxodonta a. africana. E. Afr. Wildl. J. 4, 1-37.
- LEE, P.C. & Moss, C.J. (1995) Statural growth in known-age African elephants (Loxodonta africana). J. Zool, Lond. 236, 29-41.
- LEE, P.C. & Moss, C.J. (1986) Early maternal investment in male and female African elephant calves. Behav. Ecol. Sociobiol. 18,
- LEWIS, D.M. (1984) Demographic changes in the Luangwa Valley elephants. Biol. Conserv. 29, 7-14.
- Moss, C.J. (1996) Getting to know a population. In: Studying Elephants, AWF Technical Handbook Series 7 (Ed. K. KANGWANA). African Wildlife Foundation, Kenya.
- Moss, C.J. (1988) Elephant Memories: Thirteen Years in the Life of an Elephant Family. William and Morrow, New York.

- Moss, C.J. & Poole, J. (1983) Relationships and social structure in African elephants. In: Primate Social Relationships an Integrated Approach (Ed. R. A. HINDE). Blackwell Scientific Publications, Oxford.
- PILGRAM, T. & WESTERN, D. (1986) Inferring hunting patterns on African elephants from tusks in the international ivory trade. J. app. Ecol. 23, 503-514.
- POOLE, J.H. (1996) The African Elephant. In: Studying Elephants, AWF Technical Handbook Series 7 (Ed. K. KANGWANA). African Wildlife Foundation, Kenya.
- POOL, J.H., AGGEAWAL, N., SINANGE, R., NGANGA, S., BROTEN, M. & Douglas-Hamilton, I. (1992) The Status of Kenya's Elephants 1992. Kenya Wildlife Service Department of Resource Surveys and Remote Sensing Report, Kenya.
- POOLE, J.H. (1989a) Elephants are not beetles. Oryx 23, 188-199. POOLE, J.H. (1989b) Mate guarding, reproductive success and female choice in African elephants. Anim. Behav. 37, 842-849.
- POOLE, J.H. (1987) Rutting behaviour in African elephants: the phenomenon of musth. Behaviour 102, 283-316.
- THOULESS, C.R. (1996) Home ranges and social organization of female elephants in northern Kenya. Afr. J. Ecol. 34, 284-297.
- THOULESS, C.R. (1995) Long distance movements of elephants in northern Kenya. Afr. J. Ecol. 33, 321-334.
- THOULESS, C.R. (1993) Laikipia Elephant Project Final Report. Kenya Wildlife Service Report, Kenya.
- WESTERN, D. & LINDSAY, W.K. (1984) Seasonal herd dynamics of a savannah elephant population. Afr. J. Ecol. 22, 229-244.
- WITTEMYER, G. (1999) Samburu Elephant Project Final Report. Kenya Wildlife Service Report, Kenya.

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