

Original investigation

Space and habitat use of the African elephant in the Tarangire–Manyara ecosystem, Tanzania: Implications for conservation

By Valeria Galanti, D. Preatoni, A. Martinoli, L.A. Wauters and G. Tosi

Dipartimento Ambiente-Salute-Sicurezza, Università degli Studi dell'Insubria, Varese; and Istituto Oikos ONLUS, Milano, Italy

Receipt of Ms. 18.1.2005

Acceptance of Ms. 28.10.2005

Abstract

As migratory animals, sustainable management of African elephant populations, both within and around protected areas, is a major challenge in the conservation policy of many African countries. We captured seven female elephants, representative members of family groups, in different parts of Tarangire National Park (TNP), Tanzania, and used GPS satellite radio-tracking (November 1997–June 2000) to monitor their space and habitat use and seasonal migrations throughout wet and dry seasons. Patterns of home range overlap revealed the existence of two large clans that occupied the north-central and southern parts of TNP, respectively. At the end of the dry season, elephants from the southern clan migrated about 100 km southeast of the park boundary, those from the northern clan remained mostly inside the park, or used periodically wet-season core areas in the nearby Game Controlled Areas. No natural mortality occurred during the study, but two elephants were poached outside the park. Human disturbance also affected activity patterns, and elephants were less active at day outside than inside the park. Home range size varied from 477 to 1078 km² for the northern elephants, and from 1630 to 5060 km² for the southern elephants. Migration routes were characterised by higher cover (open and closed forest) than core areas. Our results indicate that elephant management must be considered across park boundaries and that migration corridors must be protected against human disturbance and land cultivation. Society problems linked to elephant conservation can be solved by creating alternative, sustainable, use of natural resources that enhance the livelihood of local communities.

© 2005 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Key words: *Loxodonta africana*, conservation, habitat-use, migration, GPS-collars

Introduction

Over the past decades, human population growth, immigration and land transformation (from natural habitats to cultivated areas) have strongly increased around protected areas in many parts of Africa, includ-

ing the Tarangire area (Mwalyosi 1991; Newmark et al. 1994; Codipietro 2002). As human populations expand and encroach upon natural habitats, many animal species, in particular large-bodied widely roaming

mammals, face increasing competition with people for space and resources (Pimm et al. 1995; Naughton-Treves 1998; Woodroffe and Ginsberg 1998; Balmford et al. 2001). Moreover, the resulting fragmentation of natural habitats can create local extinction of some species, and can also locally increase population sizes of other species, within the protected areas (Douglas-Hamilton 1972; Woodroffe and Ginsberg 1998). In the case of large herbivores, local overpopulation often produces high browsing or grazing pressure that can endanger the regeneration and even survival of sensitive habitat types (Bell 1971; Barnes 1982; Lewis 1986; du Toit and Owen-Smith 1989). A typical example is the African savannah elephant (*Loxodonta africana*), which for this and other reasons is a paradigm species for habitat and wildlife conservation and management in Africa (Armbruster and Lande 1993; O'Connell-Rodwell et al. 2000; Leader-Williams et al. 2001).

In most parts of their current range, African elephants occur within the boundaries of national parks where protection is guaranteed (Weir 1972; Leuthold and Sale 1973; Stokke and du Toit 2000, 2002). Therefore, elephant populations that move far from the Park boundary and spend much of their time outside a protected area pose several problems for wildlife conservation and management, leading to what is referred to as human–elephant conflict (HEC, Barnes 1996; Hoare and du Toit 1999; Hoare 2000; Sitati et al. 2003). HEC can take the form of crop raiding, infrastructural damage, disturbance of every-day human activity and even injury or death of people and elephants. Many of these conflicts occur along the traditional migration routes of large herbivores, in particular where conversion of savannah to agricultural land has occurred (Thouless 1994; Tchamba 1996; Hoare 2000; O'Connell-Rodwell et al. 2000; Blanc et al. 2003; Sitati et al. 2003). Consequently, some traditional migration routes have already been completely interrupted and the remaining corridors are essential for the long-term survival of migrating large herbivores (Borner 1985; Newmark 1996). Hence, because of migratory behaviour and large home ranges,

the management of elephant populations in and around protected areas is one of the greatest challenges of the modern principles of sustainable use of natural resources, that must look for livelihood activities of local people than can co-exist with the elephants (Brandon and Wells 1992; Walpole and Leader-Williams 2001; Ogotu 2002; Blanc et al. 2003).

The Tarangire–Manyara ecosystem, containing Tarangire National Park (TNP), hosts the largest population of savannah elephants in northern Tanzania, with 2334 animals counted in the dry season of 1995 (TWCM 1998a, b; Galanti et al. 2000). During the dry season (June–November) thousands of herbivores concentrate within the protected area because of the constant water supply of the Tarangire River, with zebra, *Equus burchelli*, wildebeest, *Connochaetes taurinus*, buffalo, *Syncerus caffer* and elephant as key species, both in numbers and biomass (Lamprey 1964; TWCM 1995, 1998a). During the rainy season (December–May), most of these herbivores leave TNP and spread into a wide area of the Tarangire–Manyara ecosystem. For more than 6 months they depend on the resources available in this area where communities of pastoralists and farmers live (Borner 1985; Newmark et al. 1994), and where there is growing demand to turn savannah into large-scale, intensively farmed agriculture land.

The aim of this study is to explore space and habitat use and migratory movements of Tarangire elephants marked with GPS satellite radio collars, and investigate how elephant behaviour and activity change seasonally. We further use our data to: (i) investigate the location and the availability of natural habitats of those areas outside the park that are of major importance during the wet season, (ii) determine and map the remaining migration routes still used by elephants, and (iii) apply data on elephant space use patterns and migration to suggest conservation strategies for the whole Tarangire–Manyara ecosystem. We consider 'migration' as a seasonal two-way movement, involving a return to the area originally vacated, usually following traditional pathways (Viljoen 1989).

Material and methods

Study area

The study area falls within an eastern limb of the East African Rift Valley, and includes TNP and the surrounding areas of the Tarangire–Manyara ecosystem, used by migratory wildlife, extending over 35 000 km² (Fig. 1). TNP (2642 km²) is located in Arusha Region, between 3°40'S and 4°35'S latitude and 35°50'E and 36°20'E longitude, at an

average altitude of 1200 m. The topography is predominantly that of a gently undulating plateau; the main soil type is the dark red sandy clay loam of the semi-arid plains. Within the depression where the drainage is impeded there is black clay known as Black Cotton soil (Kahurananga 1979). The most prevalent types of woody vegetation in TNP are *Acacia* woodlands in the drainage lines and *Commiphora–Combretum* deciduous woodlands on the uplands (Vesey-Fitzgerald 1973). Using standard spatial overlay operators provided

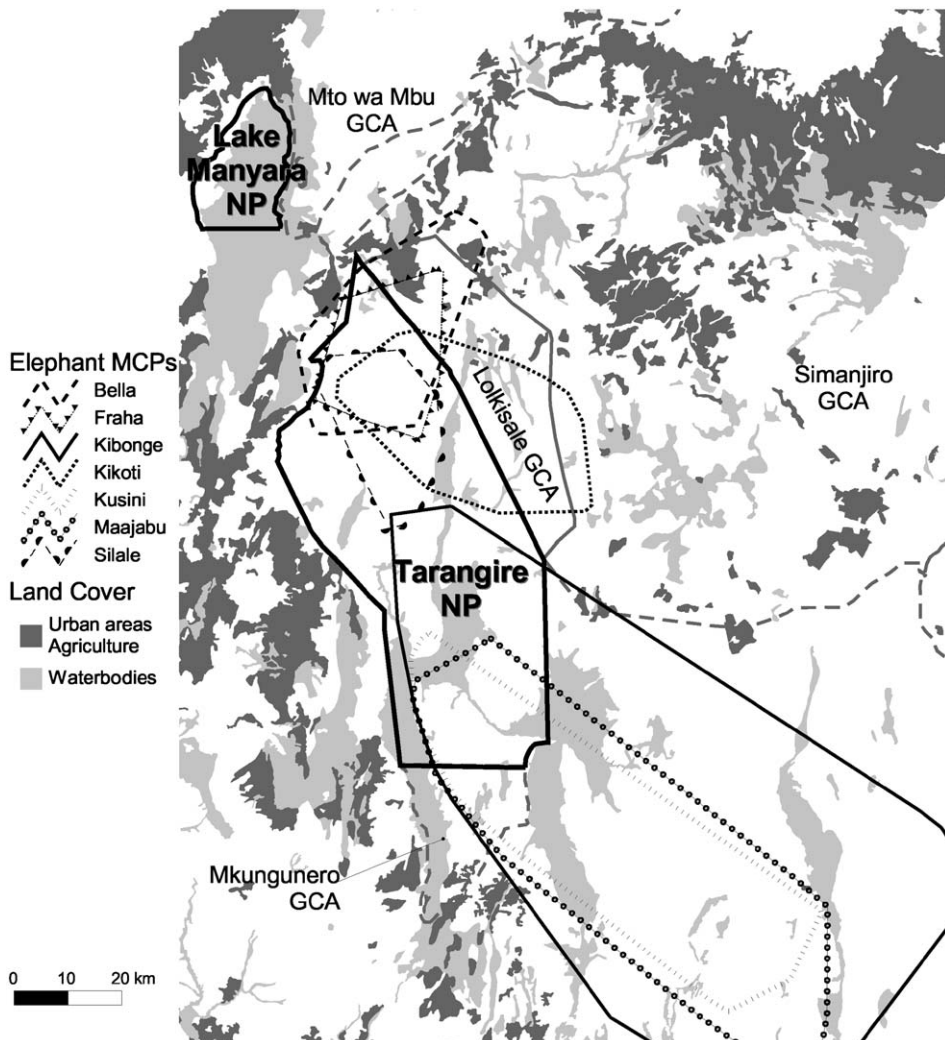


Fig. 1. Map of the Tarangire National Park (TNP) and surrounding areas of the Tarangire–Manyara ecosystem, and Minimum Convex Polygon (MCP) of the entire (year-round) home range of seven female elephants.

by ArcView GIS 3.2 (ESRI 1997) we constructed a 20 km buffer zone around the park boundaries (total size 16 959.68 km²) and used a preliminary draft of Africover Tanzania Multipurpose Land-cover Database (TMLD, FAO-Africover 2002) to map the different habitat types available to elephants. We re-classified the TMLD original land use categories according to the Land Cover Classification System (LCCS, Di Gregorio and Jansen 2000) into 11 major LCCS habitat types: agriculture areas including both large-scale intensive agriculture, small-scale herbaceous crops and fields, forest plantations and tree crops; closed forest, including woody closed vegetation; open to very open forest; savannah; closed shrubland; open shrubland, and open shrub with sparse trees; savannah with trees or shrubs; temporarily flooded herbaceous vegetation, shrubs or trees (water, non-permanent); permanently flooded herbaceous vegetation (water, permanent); waterbodies, including lakes, streams and river banks; and urban areas, including rural villages which only amounted to 1.49 km² less than 0.01% of the study area. This habitat type was never used by elephants and excluded from the analyses (Table 1). The entire study area is classified as ecological zones IV and V (Pratt et al. 1966) with a semi-arid climate. The average annual rainfall is 600–650 mm. There are two rainy seasons, the short rains from November to January, and the long rains from February to May.

Elephant numbers and legal status

The most recent estimates of the total number of elephants in Tanzania amount to about 109,700 animals (based on categories definite and probable counts in Blanc et al. 2003). Recent studies have revealed that during the dry season, maximum elephant numbers in the Tarangire NP vary between 1997 (total count in 1998) and 2334 (total count in 1995) (TWCM 1998a, b). Slightly lower numbers of elephants are present during the wet season, ranging from 1386 (1996) to 1631 (1998). Aerial counts and ground surveys also indicated that elephants in TNP occur in two distinct large groups (hereinafter called clans, Viljoen 1989): one using the northern and central section, the other the southern section (TWCM 1998a, b; Galanti et al. 2000). In the past, several migratory routes of elephants and other large herbivores have been described: the most important ones are to the east and northeast towards the Simanjiro and Lolikisale Game Controlled Areas (GCA), to the northwest along the Rift Valley to an area south of Lake Manyara, and towards the southeast and south into the Mkungunero GCA (Lamprey 1964;

Borner 1985). GCAs represent 8% of the total network of Protected Areas; in GCA wildlife utilisation is allowed, through tourism and resident hunting. In the Tarangire area, important concentrations of domestic animals (36% of regional stock) and cultivated land (18%) occur inside these GCAs. In Tanzania, elephants are protected, except for a limited harvest by safari hunting, and only the government can commercialise both raw and worked ivory (Government of Tanzania 1989). A limited export of elephant tusks as hunting trophies from Tanzania is permitted and in 2003 the government notified the CITES secretariat of a doubling in its export quota for legally acquired trophies from the previous 100 to 200 tusks (100 elephants, Blanc et al. 2003).

Capturing and marking elephants

Previous studies demonstrated that by marking adult female elephants, monitoring the locations of the radio-collar can be considered as representing the movements, space and habitat use of the entire family group (also called herd) to which the target elephants belong (Douglas-Hamilton 1972; Thouless 1996; Galanti et al. 2000). Therefore, we distributed our attempts to capture elephants over different areas of the Park, to obtain data of animals of several herds potentially belonging to different clans. Elephants from the northern and central sections of the park had access to water (Tarangire river, Silale swamp) throughout the year, but this was not the case for elephants living in the southern section, where during the dry season most water sources dried out. Five females were captured in November 1997 (Table 2, see also Galanti et al. 2000). Elephants were immobilised using gun-propelled syringes containing 12 mg of etorphine (Immobilon). While anaesthetised, vital signs, heart rate, respiration rate, body temperature and blood pressure, were monitored continuously. Each animal was fitted with a radio-collar, equipped with a 6 channel GPS receiver, a radio-modem for data communication, a non-volatile memory, and an independent VHF transmitter (GPS collar 1000, Lotek Engineering Inc., Canada). A detailed description of the GPS system is given by Galanti et al. (2000). After the collaring, the animals were given between 30 and 72 mg of diprenorphine as a reversal drug. In February 1999 two females from the north-central section of the Park (Bella and Kikoti) and another one from the southern area (Kibonge) were recaptured and their collars were replaced. Consecutively, two new female elephants were captured and radio-collared: one (Kusini) in the southern part of Tarangire, and one (Silale) in Silale swamp (Table 2).

Table 1. Habitat availability and seasonal habitat use of radio-tracked elephants in and around the Tarangire National Park, Tanzania. Habitat use was investigated seasonally (wet vs. dry season) and for each elephant separately, both at the level of total home range (95% kernel range) and the core area (70% kernel range). The utilisation of each habitat type (mean $\pm$ SD) is expressed as a percentage of total habitat use, and selection examined with the selection index (w_i). A (+) or a (–) after w_i indicates that w_i is significantly larger (selection) or smaller than 1.0 (avoidance), respectively

Habitat type (% available)	Wet season habitat use			Dry season habitat use		
	% Use		w_i	% Use		w_i
	Home range	Core area		Home range	Core area	
Agriculture (7.6)	0.8 $\pm$ 2.0	0.3 $\pm$ 0.9	0.05 (–)	2.2 $\pm$ 3.9	0.1 $\pm$ 0.3	0.02 (–)
Forest, closed (5.3)	1.4 $\pm$ 1.9	0.7 $\pm$ 1.6	0.14 (–)	1.7 $\pm$ 2.4	1.5 $\pm$ 3.1	0.28 (–)
Forest, open (21.5)	26.3 $\pm$ 17.7	24.0 $\pm$ 20.5	1.11	17.8 $\pm$ 6.8	6.9 $\pm$ 6.3	0.32 (–)
Savannah (5.6)	6.9 $\pm$ 6.3	9.5 $\pm$ 12.1	1.70	7.4 $\pm$ 5.3	10.0 $\pm$ 7.5	1.79
Shrubland, closed (5.3)	8.2 $\pm$ 6.8	13.4 $\pm$ 16.7	2.53	6.0 $\pm$ 8.5	14.0 $\pm$ 18.9	2.64
Shrubland, open (29.1)	34.0 $\pm$ 14.9	31.7 $\pm$ 16.8	1.09	32.6 $\pm$ 17.5	34.6 $\pm$ 20.9	1.19
Savannah with trees or shrubs (8.9)	15.1 $\pm$ 11.7	13.6 $\pm$ 13.7	1.53	17.9 $\pm$ 13.3	17.5 $\pm$ 17.1	1.96
Waterbodies (1.5)	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.01 (–)	0	0	—
Water, non-permanent (14.6)	6.8 $\pm$ 8.4	6.7 $\pm$ 12.4	0.46	13.3 $\pm$ 12.2	14.5 $\pm$ 12.7	0.99
Water, permanent (0.5)	0.3 $\pm$ 0.6	0.1 $\pm$ 0.2	0.13 (–)	0.9 $\pm$ 1.9	0.9 $\pm$ 2.0	1.78

Table 2. Niche breadth (proportional similarity index), home range size (100% MCP, 95% kernel) and core-area size (70% kernel) estimates of wet and dry season home ranges, and home range (HR) and core area (CA) overlap between the wet and dry season ranges (% overlap) of elephants in the Tarangire area, northern Tanzania

Elephant (n_w , n_d)	Niche breadth		MCP (km ²)		95% kernel (km ²)		70% kernel (km ²)		% Overlap	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	HR	CA
Bella (1679, 654) N	0.64	0.55	853	545	672	332	268	114	38	24
Fraha (847, 159) N	0.60	0.59	451	224	219	126	57	43	42	18
Kikoti (2266, 1144) C	0.64	0.53	1078	531	564	243	84	66	33	26
Silale (528, 0) C	0.63	—	477	—	527	—	141	—	—	—
Kibonge (1861, 1113) S	0.63	0.68	5994	5627	2716	1531	636	385	25	4
Maajabu (990, 162) S	0.42	0.39	1459	3235	622	977	237	260	11	0
Kusini (573, 0) S	0.39	—	2002	—	1073	—	233	—	—	—
Mean	0.56	0.55	1759	2032	913	642	237	174		
SD	0.11	0.11	1946	2350	833	597	194	145		

(n_w = number of fixes wet season, n_d = number of fixes dry season, N = captured in northern part of Tarangire NP, C = central part, S = southern part).

These capture locations had been chosen to target elephants from herds that could be using different migration routes than those used by the other radio-collared animals. Based on tooth wear, age of the captured elephants was determined to range between 15 and 30 years old; hence all were adults. By June 2000, all GPS collars were successfully removed from all the elephants.

Data analyses

The GPS radio-collars were scheduled to record geographical coordinates (25m spatial accuracy) every 4 h, recording also date, time, air temperature, and animal activity in terms of head movements. For downloading the recorded data, radio-tracking, to locate the VHF transmitters,

was carried out from an aeroplane or by car (Galanti et al. 2000).

All data on home range size, home range use, and overlap of home ranges were analysed using the Animal Movement SA 2.0 extension (Hooge and Eichenlaub 2000) in an ArcView GIS 3.2 environment (ESRI 1997). For each elephant, in each period (wet season, dry season), the following parameters were calculated: (1) total home range size (100% of the point fixes) using the minimum convex polygon method (MCP), (2) kernel home range estimator using 95% of all locations (fixed kernel method, Silverman 1986), (3) core area estimate based on the 70% kernel density estimator (the inflection point in the slope of the utilisation distribution indicated that the 70% core area best described an animal's activity centre), (4) home range overlap between wet and dry season ranges (using the 95% kernel estimates) for the five elephants monitored in both seasons, (5) core area overlap between wet and dry season ranges (using the 70% kernel estimates) for the five elephants monitored in both seasons, (6) home range (95% kernel estimates) and core area (70% kernel estimates) overlap between different elephants, expressed as percentage of overlap of an elephant's home range (core area) with the home range (core area) of all other elephants. Bandwidth for the fixed kernel method was set at 250 m, corresponding with the spatial resolution of 250 m characterising the land cover data set.

Habitat selection was investigated for each habitat type comparing proportion use with its availability in the study area, and niche breadth and niche overlap were calculated for each single elephant. The availability of each habitat type i (a_i) was calculated by dividing the area of that habitat in the study area by total study area size (Table 1). For each elephant, the utilisation of each habitat type i (u_i) was calculated dividing the area of that habitat type comprised in the total home range (95% kernel estimator) and that comprised in the core area (70% kernel estimator) by, respectively, total home range size and core area size (Table 1). Habitat utilisation was analysed for wet and dry season ranges separately. Habitat utilisation at the level of the total home range was strongly positively correlated with habitat utilisation at the core area level (Spearman rank correlation of average percentage utilisation per habitat type: wet season $r_s = 1.0$, $df = 8$, $P < 0.001$; dry season $r_s = 0.88$, $df = 8$, $P < 0.001$). Since core areas represented the areas most intensively used by elephants, we used habitat utilisation at the core area level in further analyses.

Niche breadth and overlap were estimated using Czekanowski's Index as proposed in Feinsinger

et al. (1981), i.e.

$$PS = 1 - \frac{1}{2} \sum_i |u_i - a_i|,$$

where u_i is – as in the case above – the proportion of habitat i in the elephant's core area (habitat utilised), and a_i is the proportion of habitat i available in the study area, or, in the case PS is used to evaluate the extent of the intersection between the utilisation frequency distribution of two elephants, u_i is the proportion of habitat used by one elephant and a_i is the proportion of the same habitat used by the other. PS index ranges from the minimum found value for a_i to 1, indicating, respectively, a narrow niche (or a minimal niche overlap) or a broadest possible niche (or complete overlap).

We also examined levels of selection for each habitat type (i) by elephants in wet and dry season, respectively. The selection index (w_i) was derived from $w_i = u_i/a_i$, where u_i is the proportion of habitat i in the elephant's core area (habitat utilised), and a_i is the proportion of habitat i available in the study area. The null hypothesis, that elephants were randomly selecting habitats in proportion to availability, was tested using a log-likelihood χ^2 statistic. A value of $w_i = 1$ indicates no selection, a value > 1 indicates preference and a value < 1 indicates avoidance. Each w_i value has been tested to see if it is significantly different from 1.0 by computing a χ^2 statistic from $(w_i - 1)/SE(w_i)^2$ with $df = 1$, and with a Bonferroni adjustment, i.e. here the significance level $\alpha = (0.05/10) = 0.005$ (Manly et al. 1993). A (+) or a (–) after w_i indicates that w_i is significantly larger (selection) or smaller than 1.0 (avoidance), respectively.

Migratory movements were defined as directional movements between successive locations outside the 70% core areas. Subsequently, habitat use during migration was estimated based on habitat types at these locations.

Results

Habitat use

During the wet season, elephant females were found in all ten habitat types, whereas in the dry season they used nine of them (Table 1). Elephants avoided cultivated areas, closed forest, and water bodies in both seasons, and also permanently flooded shrub in the wet season (Table 1). The latter habitat was used in the dry season, but only by one elephant (Kikoti) that used the central area of the

Park. The use of cultivated areas, while still minor, did increase from 0.8% in the wet to 2.2% in the dry season due to occurrence of some elephant herds raiding crops that mature in the beginning of the dry season. There was large individual variation in the use of ephemeral pans (temporary flooded shrub), but each individual elephant included more of this habitat in its core area in the dry than in the wet season, when fresh grazing became available. Elephants avoided open forest in the dry season, but this was not the case during the wet season. The remaining habitats were used according to their availability. Thus, in both seasons, elephants were mainly found in savannah, savannah with trees, open and closed shrub (Table 1). The mean percentages of habitat utilisation in wet and dry season were significantly correlated (Spearman rank correlation $r_s = 0.83$, $df = 8$, $P = 0.003$), suggesting that there were no major changes in habitat use between the two seasons.

Niche breadth varied little between wet and dry season (Table 2). Niche overlap between wet and dry season was high for the two elephants captured in the north (0.78 and 0.80), lower for the others (Kikote 0.67, Kibonge 0.62 and Maajabu 0.37).

Home ranges and core areas

The number of fixes per animal ranged from 528 to 2266 in the wet season and 159 to 1144 in the dry season (seasons combined 528–3410, Table 2). Total home range size (MCP) varied strongly, between 477 and 7648 km² (Fig. 1). It was larger for elephants from the southern section (2002, 4587 and 7648 km²) than for those captured in the northern (515 and 865 km²) and central sections (477 and 1078 km²). The different range estimators, in both wet and dry season ($n = 12$), were strongly correlated (MCP with 95% kernel: $r_s = 0.95$; MCP with 70% core area $r_s = 0.86$; 95% kernel with 70% core area $r_s = 0.93$; all $P < 0.001$). Thus, elephants with larger wet or dry season home ranges also had larger core areas than those with smaller home ranges (Table 2). Individual variation in home range and core area size of elephants was large: from 527 to 2716 km² in

the wet season, and from 126 to 1531 km² in the dry season for the 95% kernel estimator. We tested whether the number of fixes that differed between animals and seasons affected the different home range estimators by calculating a generalised linear model (GLM-models) with season as class, number of fixes as independent variable, and home range estimator (see above) as dependent variable. Variation in the seasonal home range estimators, wet and dry season MCP, 95% kernel home range, and 70% kernel core area, were not significantly affected by season or by number of fixes (GLM-model on MCP: season $F_{1,8} = 0.08$; fixes $F_{1,8} = 0.75$; season $\times$ fixes interaction $F_{1,8} = 0.01$; GLM-model on 95% kernel: season $F_{1,8} = 0.00$; fixes $F_{1,8} = 0.62$; season $\times$ fixes interaction $F_{1,8} = 0.01$; GLM-model on core area: season $F_{1,8} = 0.00$; fixes $F_{1,8} = 0.50$; season $\times$ fixes interaction $F_{1,8} = 0.01$; all $P > 0.4$). Thus differences in home range and core area size among elephants, in wet and dry season, were not caused by differences in the number of fixes. This was confirmed if single correlation coefficients between range estimators and number of fixes were calculated (non-parametric Spearman rank-correlation: MCP $r_s = 0.36$; 95% kernel $r_s = 0.33$; core area $r_s = 0.32$, $n = 12$, $P > 0.2$ in all cases).

In four out of five cases wet season ranges were larger than dry season ranges (Table 2). During the wet season, home range sizes of the three female elephants using the southern section of the park were larger than those of females using the northern and central areas (Mann–Whitney U -test on MCP: $U = 0$, $n_1 = 3$, $n_2 = 4$, $P = 0.028$). Also during the dry season, home ranges of elephants using the southern part of TNP (977 and 1531 km² using 95% kernel estimator, Table 2) were 3 to more than 10 times larger than those using the northern-central parts (126–332 km², Table 2). The elephants captured in the northern and central parts of Tarangire NP had the highest overlap between wet and dry season home ranges (and core areas), suggesting they made less and/or shorter migratory movements than those from the southern part (Table 2). The percentage seasonal home range overlap was, for all

elephants, larger than seasonal core area overlap (Table 2, Wilcoxon matched-pairs signed ranks test: $n = 5$, $T = 0$, $P = 0.043$), suggesting they used different high-quality habitat patches according to season.

Core areas (70% kernel contours) were much smaller than total home ranges. In the wet season core areas were between 15% and 40% of home range size. In the dry season core areas ranged from 25% to 34% of home range size (Table 2). For the seven wet, and five dry season ranges combined, variation in core area size was positively correlated with the amount of core area overlap ($r_s = 0.65$; $P = 0.02$). We investigated whether variation in core area size, core area overlap and season (wet vs. dry) affected variation in home range size between elephants, combining wet and dry season range estimates, using a GLM-model with stepwise backward selection ($P > 0.05$ as selection criteria for eliminating non-significant variables). Effects of the season $\times$ core area interaction, season and core area overlap were not significant (all $P > 0.6$). Variation in core area size explained 93% of variation in total home range size (Selected model $F_{1,10} = 148.6$, $P < 0.0001$; $R^2 = 0.93$; 95% kernel home range size = $-66 (\pm 90) + 4.1 (\pm 0.3)$ core area size).

During the wet season, there was between 18% and 33% of home range overlap (95% kernel contours) among the three elephants captured in the southern part of the park, and only Kibonge and Maajabu shared 30% of their core areas (70% contours). There was no home range overlap between these three elephants and the other females that were monitored. Elephants captured in the northern and central sections showed marked home range overlap (8–26%), but limited core area overlap in the wet season (0.3–13%, Fig. 2), suggesting that they belonged to herds that sometimes joined and sometimes segregated. In the dry season, only Kibonge and Maajabu, two elephants captured in the southern part, showed extensive core area overlap (46%), while core areas of the other animals monitored during the dry season did not show any overlap (Fig. 2). Total home range overlap (based on 95% kernel contours) between these two animals was also high, 30%. Maajabu showed only marginal dry-season range overlap with Fraha and Bella (0.5 and 2.5%) captured in the northern part of the park, and none with Kikoti, captured in the central part of the Park. Overall, these home range overlap patterns indicated the existence of two clans (Fig. 2). A northern clan using the northern and

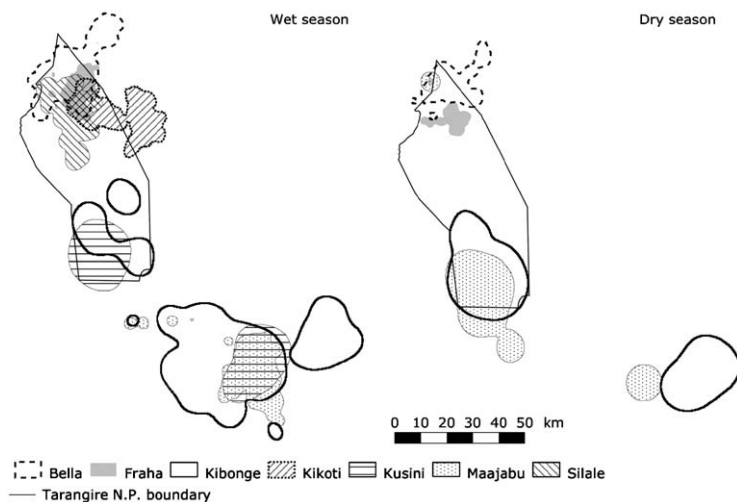


Fig. 2. Core area overlap between radio-collared female elephants in Tarangire National Park, in both seasons.

central areas of the park during the wet season, splitting up in smaller herds that showed limited overlap during the dry season (overlap Bella-Fraha 1%, Bella-Kikoti 0%, Fraha-Kikoti 7%); and a southern clan, also consisting of several herds that tended to have separate core areas (Fig. 2).

Speed

Speed was measured to detect the impact of the threat posed by human settlements outside the park on elephants. Elephant speed was calculated by dividing linear distance between subsequent locations by the time in which they were bridged (m s^{-1}). The calculated speed was further categorised as speed by day or speed at night, considering average sunrise and sunset time (06.30 and 18.30, respectively) as published by the US Naval Astronomical Observatory (USNO 2003). The generalised linear model with speed as dependent variable had no significant season by night/day by inside/outside park interaction (3-way interaction term $F_{1,35} = 0.001$, $P = 0.99$), and none of the two-factor interactions with season (all $P > 0.7$), or the season effect were significant ($F_{1,35} = 0.62$, $P = 0.44$). There was however a significant period (day vs. night) by area (inside vs.

outside park) interaction ($F_{1,35} = 6.06$, $P = 0.02$). Therefore, data were pooled over seasons, but the period effect (day or night speed) was investigated for movements inside and outside the park separately. Inside the park, speed was significantly higher during the day than at night (Table 3, $F_{1,20} = 5.37$, $P = 0.031$), indicating that elephants, when undisturbed, were mainly day-active. In contrast, outside the park speed at day was much lower inside the park, and there was no significant difference between speed at day and speed at night ($F_{1,19} = 1.47$, $P = 0.24$). The latter was on average even slightly higher than speed at day (Table 3). Thus, outside the park boundaries, elephants rested more during the day and were more active at night than when they were foraging or travelling inside the park.

Migration

Only the three elephants captured in the southern part of the Park showed real migratory movements that coincided with the end of the dry season, leaving the park, and with the end of the wet season, returning to TNP. To investigate whether different habitats were selected for migrating than for other activities, we compared the proportion

Table 3. Average and maximum speed (km h^{-1}) traveled by the GPS-collared elephants in the course of the research period (1997–1999). Values are expressed as mean $\pm$ standard deviation. Maximum speed is enclosed in square brackets. *N*: number of bridging segments

Elephant	Inside park		Outside park	
	Day	Night	Day	Night
Bella	0.14 ± 0.12 [0.87] (<i>n</i> = 752)	0.09 ± 0.08 [0.84] (<i>n</i> = 617)	0.13 ± 0.09 [0.76] (<i>n</i> = 421)	0.12 ± 0.10 [0.56] (<i>n</i> = 541)
Fraha	0.12 ± 0.11 [0.67] (<i>n</i> = 492)	0.07 ± 0.08 [0.91] (<i>n</i> = 466)	0.09 ± 0.08 [0.33] (<i>n</i> = 23)	0.13 ± 0.18 [0.70] (<i>n</i> = 23)
Kibonge	0.17 ± 0.16 [1.28] (<i>n</i> = 462)	0.18 ± 0.18 [1.29] (<i>n</i> = 495)	0.11 ± 0.11 [1.50] (<i>n</i> = 976)	0.13 ± 0.13 [0.85] (<i>n</i> = 1039)
Kikoti	0.12 ± 0.10 [0.79] (<i>n</i> = 1104)	0.09 ± 0.08 [0.55] (<i>n</i> = 1021)	0.10 ± 0.08 [0.55] (<i>n</i> = 644)	0.09 ± 0.08 [0.55] (<i>n</i> = 639)
Kusini	0.17 ± 0.13 [1.03] (<i>n</i> = 186)	0.09 ± 0.13 [0.83] (<i>n</i> = 166)	0.13 ± 0.12 [0.66] (<i>n</i> = 112)	0.16 ± 0.25 [1.45] (<i>n</i> = 108)
Maajabu	0.19 ± 0.21 [1.20] (<i>n</i> = 52)	0.17 ± 0.19 [0.76] (<i>n</i> = 56)	0.09 ± 0.13 [2.38] (<i>n</i> = 495)	0.09 ± 0.10 [0.58] (<i>n</i> = 547)
Silale	0.19 ± 0.15 [0.84] (<i>n</i> = 266)	0.08 ± 0.12 [0.65] (<i>n</i> = 261)	—	—

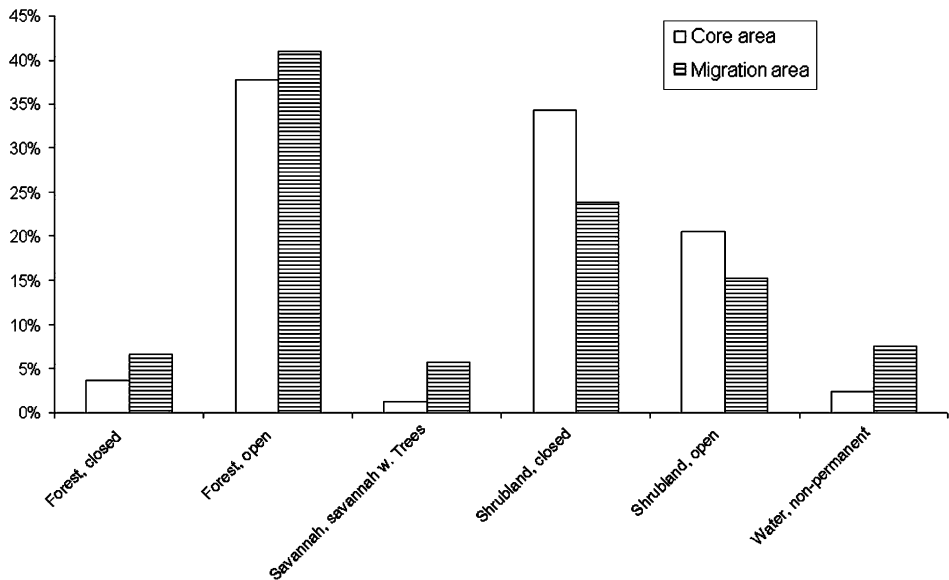


Fig. 3. Habitat utilisation in wet and dry season core areas and during migration.

of migration locations in each habitat type with those included within these elephants' core areas. The relative proportions of habitat types along the migration routes differed significantly from those within the core areas ($\chi^2 = 30.7$, $df = 5$, $P = 0.0002$). During migration, human settlements, agriculture land, and permanently flooded vegetation and water bodies were not crossed or used. Elephants used open and closed forests and temporarily flooded areas more during migration than in their core areas, while open and closed shrub was used less during migration than in the core areas (Fig. 3). However, open forest and open and closed shrub were the most intensively used habitat types both within core areas and during migration (Fig. 3).

Although Bella showed high fidelity using always the same route during its wet season movements outside the Park, its movement patterns could not be considered a true migration. Still other herds (elephant Kikoti) moved between the central regions of the Park and the south and central areas of Lolkisale GCA, east of the Park (Fig. 4), in both wet and dry season. The herds of Kikoti and Bella met only once in the area they had

in common in their wet season home ranges, remaining at more than 600 m from one another. Also Bella and Fraha tended to use their strongly overlapping areas at different times, suggesting different family groups of the northern clan avoided each other in time. Because of the lack of regular migration, elephants of the northern clan did not show a clear distinction between dry and wet season range (seasonal range overlap > 33%).

The mortality switch of the radio-collars of two elephants (Kibonge and Kusini) indicated that they had been poached while outside the park. Hence, two of our seven radio-collared elephants died during the 32 months the study lasted, an average annual mortality rate of 12%.

Discussion

One of the most important results of this study was that elephants using the TNP could be subdivided into two clans (Douglas-Hamilton 1972; Viljoen 1989), hereinafter called the northern and the southern clan, that had no home range overlap during the wet season, and very little overlap during the

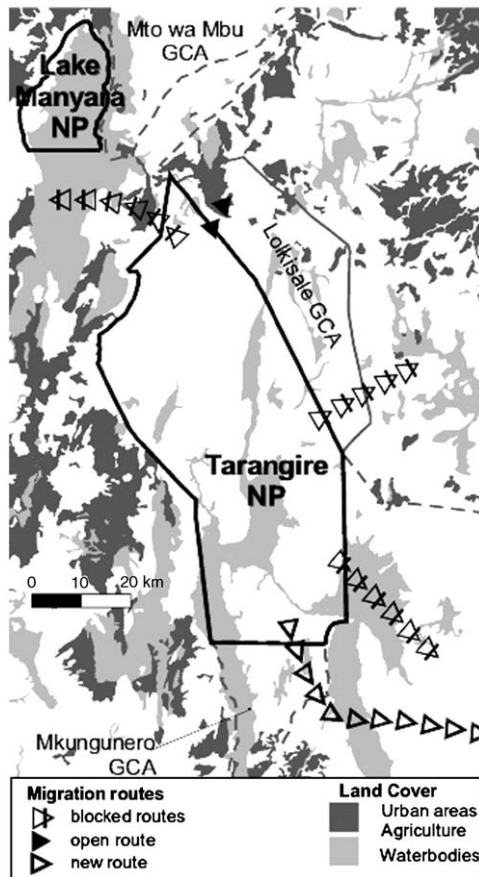


Fig. 4. Migration corridors used by elephants and other large herbivore populations of the Tarangire National Park. Past and current status of the wildlife migratory routes in the Tarangire–Manyara Area (1964–2001).

dry season. Also, core area overlap and occasional observations of radio-collared females within each clan showed they belonged to different smaller herds, that foraged and moved separately during most of time, but joined-up temporarily, especially during migratory movements and during the mating season (March–April). The northern clan, with more than 300 individuals, included 32 distinct family groups (Foley et al. 2001). This global social structure agreed with other studies on elephant populations occurring in similar habitats of Kenya and northern Tanzania (Douglas-Hamilton 1972; Leuthold and Sale 1973; Thouless 1995, 1996). African elephants can move over long

distances, but there is a great deal of variation, with some populations being very sedentary (Leuthold and Sale 1973; Caughley and Goddard 1975), while others are nomadic or migrate seasonally (Leuthold and Sale 1973; Leuthold 1977; Viljoen 1989; Lindeque and Lindeque 1991; Thouless 1995; Tchamba et al. 1995). This variation seems to be related to habitat heterogeneity, the spatio-temporal distribution of water as a primary resource, sexual segregation between female family groups and groups of non-mating adult males, and intra-sexual avoidance between dominant and subordinate bulls (Poole and Moss 1981; Stokke 1999; Stokke and du Toit 2000, 2002). Mean home ranges of bulls and

cows in different habitats in Kenya varied between 350 and 1580 km² (Tsavo National Park) and 102–5527 km² (Laikipia-Samburu region) and were linked with spatio-temporal rainfall patterns that determined food availability (Leuthold and Sale 1973; Thouless 1996). Home ranges of clans were smaller when group size was small and evergreen vegetation was available, and strongly increased when considerable movements were made between wet and dry season foraging grounds (Thouless 1996).

Similarly, total home ranges of female elephants from TNP varied greatly among individual animals, from a minimum of 477 km² to a maximum of 5060 km². Thus some elephants roamed over an area 2 times the size of the Park. Wet season home ranges (527–2716 km²) and core areas were larger than those in the dry season (126–1531 km²), when elephants tended to concentrate more around perennial water sources, and elephants from the southern clan had larger ranges than those from the northern clan. Variation in core area size was positively correlated with the amount of core area overlap suggesting that also the Tarangire elephants used larger foraging areas (core areas) when the habitat had to be shared with (more) other family groups (higher core area overlap). Finally, the lack of perennial water sources in the southern part of TNP resulted in water (and food) availability being insufficient to support the dry-season concentration of elephant herds throughout the year. Consequently, elephants of the southern clan roamed widely over a 4500 km² area south-southeast of TNP.

Radio-collared elephants did not show any marked habitat selection, consistent with elephants being food generalists that tend to change habitat use through time, selecting habitats with progressively more abundant but less digestible forage (Field 1971; Western and Lindsay 1984). Habitats offering good feeding and/or cover, that covered most of the Tarangire area (highest percentage availability), such as open forest, open shrub and savannah with or without trees, were also used most frequently.

The elephants of the southern clan, that spend many months of the year in the Kiteto

district about 20–100 km southeast of the Park, appeared to change their daily movement patterns to avoid conflicts with humans. They tended to hide in denser vegetation (closed shrub and open forest) during most daylight hours, and were more active at night. Inside the park, elephants had no artificial restrictions on foraging and movements and were most active during the day. Similar disturbance effects were recorded for elephants crossing park boundaries in Zambia (Lewis 1986). The elephants from the southern clan showed a distinct clumped distribution pattern, representing wet and dry season home ranges that had little overlap (<25%). The three elephants used the same dry and wet season areas, as indicated by the high degree of home range overlap and were regularly located in a single large group of up to 300 animals. The dry season area was concentrated around two big waterholes known as Mkungunero pools. The wet season range mainly extended over partly sheltered habitats, such as open and closed shrub and savannah with trees, in Kiteto District, between Makami and Ndedo villages, occupied also by few Maasai pastoralists. During most of the wet season, Kusini frequented a herd that foraged separately from the 'Maajabu-Kibonge' herd as indicated by the lack of core area overlap.

The northern clan consisted of several herds with different spatio-temporal spacing patterns, and different preferred feeding patches, as indicated by the small amount of core area overlap between individuals. The 'Fraha' herd remained inside TNP, and close to the Tarangire river, most of the time and its home range strongly overlapped with that of the 'Bella' herd during most of the wet season. However, the latter herd also moved, periodically during the wet season (December–May), northwards to the northern section of Lolkisale GCA, at a maximum distance from the park boundary of only 20 km.

The movements of elephants of the southern clan could be defined as a regular migration. Patterns of movement from the dry season to wet season ranges were strikingly similar in the 2 years, with elephants returning to the same areas in the south after the onset of the

rains, and following the same routes in both years. At the end of the dry season, most of these elephants migrated in a southeasterly direction for about 100 km from the park boundary, to Kiteto Region, moving in a straight line, at night and at a sustained speed of almost 15 km in 10 h (Galanti *et al.* 2000). During migration, elephants avoided human settlements and agriculture land, moving mainly in open forest and open and closed shrub, and regularly used cover of dense bush during daylight hours.

The large home ranges and migration patterns of elephants in the Tarangire–Manyara ecosystem have important implications for habitat and species conservation management. By the late dry season, resources (water and food) become limited and elephants need to spend about 75–80% of their active time foraging and feeding (Field 1971; Wyatt and Eltringham 1974; Barnes 1982, 1983; Lewis 1986; Viljoen 1989), thus becoming more sensitive to the intensity and duration of disturbance. Tarangire herds spent most the critical dry season period inside the park, often near perennial water sources, thus avoiding conflict with humans. However, the considerable time spent outside the park during the wet season implies the need for a global elephant management plan that crosses park boundaries. In northern Tanzania, there have been no legal quota for elephant-trophy hunting and no culling for damage prevention since 1990 (TANAPA, pers. comm.). However, the age structure of elephant herds and of adult males (Foley *et al.* 2001) and our data indicate that poaching is a serious problem, which might be mitigated by providing better protection to elephants through a closer collaboration between TANAPA and Wildlife Division anti-poaching units, and sensibilisation of Hunting Safari Companies operating in the blocks surrounding TNP. Efficient elephant conservation, as well as that of other migratory herbivores, depends on safeguarding the natural habitat structure of the existing migration corridors, threatened by continuous extension of cultivated areas. Only urgent and rigid land use planning that prohibits any further cultivation of natural habitats can save the remaining migration

corridors and wet-season ranges. A first step in this direction has been made by Wildlife Division changing the Mkungunero GCA into a Game Reserve. This should improve habitat and wildlife protection measures along the migration corridor and wet season range of the southern elephant clan, since in the reserves all human activities, except tourist hunting and safaries, are prohibited. However, such land use planning must be compatible with enhanced livelihood of local communities of maasai and farmers, involving them as stakeholders in the decision making process of landscape/wildlife planning and management (e.g. Brandon and Wells 1992; Gibson and Marks 1995; Levine 2002). In Tanzania, the recently initiated Local Government Reform Project will link up with the recent developments in the environmental policy framework, such as the development of Wildlife Management Areas (WMAs), to solve existing socio-economic problems of habitat destruction and create an alternative, sustainable, use of animal (and plant) populations.

Acknowledgements

Tarangire Conservation Project was a joint project between University of Insubria—Varese, Istituto Oikos NGO and Tanzania National Parks (TANAPA) funded by the European Union (B7-6200/94-18/VIII/ENV) and, as Tarangire–Manyara Conservation Project, by US Agency for International Development (Award No. 623-A-00-98-0064-00) through WWF Tanzania Program Office. Elephant captures were conducted in co-operation with TANAPA, Wildlife Division, Zoological Society of London and Tarangire Elephant Project. We are grateful to Rossella Rossi, Paola Codipietro and Malcolm Ryen and the Oikos, University of Insubria and TNP staff, to Richard Kock, Phil Mathew, Charles and Lara Foley, John Simonson, FAO Africover East Africa, and the Frankfurt Zoological Society, for their help. The opinions expressed in this publication are those of the authors and not necessarily reflect the views of the EU and the USAID.

Zusammenfassung

Raum- und Habitat-Nutzung des afrikanischen Elefanten im Tarangire–Manyara Ökosystem, Tansania: Folgerungen für den Artenschutz

Für die Erhaltung von Populationen des Afrikanischen Elefanten als wandernde Tierart ist das Management sowohl innerhalb als auch um geschützte Gebiete herum eine Hauptherausforderung für den Artenschutz vieler afrikanischer Länder. Wir untersuchten sieben weibliche Elefanten, jeweils stellvertretend für Familiengruppen, in verschiedenen Teilen des Tarangire National Parks (TNP), Tansania. Mittels GPS Satellitentelemetrie (vom Juni 1997 bis November 2000) beobachteten wir die Raum- und Habitat-Nutzung, sowie die Saisonwanderungen zwischen den Regen- und Trockenzeiten. Die erhaltenen Muster der Home-Range-Analysen ergaben Hinweise auf die Existenz von zwei großen Clans, die einerseits den zentral-nördlichen und andererseits den südlichen Teil von TNP besetzten. Am Ende der Trockenzeit wanderten die Elefanten des südlichen Clans ungefähr 100 km in südöstlicher Richtung aus dem Park heraus. Der nördliche Clan blieb hingegen größtenteils innerhalb des Parks, oder verwendete regelmäßig Kerngebiete innerhalb des kontrollierten Bereichs (Game-Controlled-Area), die schon während der Regenzeit genutzt wurden. Während der Studie kam keine natürliche Sterblichkeit vor, zwei Elefanten wurden hingegen außerhalb des Parks durch Wilderer getötet. Menschliche Störungen beeinflussten auch die täglichen Aktivitätsmuster. Elefanten waren außerhalb des Parks weniger tagaktiv als innerhalb des Parks. Die Home-Range Größen variierten von 477 bis 1078 km² für den nördlichen Clan, und von 1630 bis 5060 km² für die südliche Elefantengruppe. Die Wanderwege führten durch offenen oder geschlossenen Wald und zeigten damit einen höheren Deckungsgrad im Vergleich zu den Kerngebieten. Unsere Ergebnisse zeigen, dass das Management der Elefantenpopulationen über die Park-Grenzen betrachtet werden muss. Wichtig ist auch, dass Wanderwege gegen menschliche Störungen und gegen die Zerschneidung durch Landkultivierung geschützt werden müssen. Gesellschaftliche Probleme, die mit dem Schutz der Elefanten in Zusammenhang stehen, können beispielsweise durch die nachhaltige Nutzung von Bodenschätzen, die den Lebensunterhalt der lokalen Bevölkerung erhöhen können, gelöst werden.

© 2005 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

References

- Armbruster, P.; Lande, R. (1993): A population viability analysis for African elephant (*Loxodonta africana*): how big should reserves be? *Conserv. Biol.* **7**, 602–610.
- Balmford, A.; Moore, J. L.; Brooks, T.; Burgess, N.; Hansen, L. A.; Williams, P.; Rahbek, C. (2001): Conservation conflicts across Africa. *Science* **291**, 2616–2619.
- Barnes, R. F. W. (1982): Elephant feeding behaviour in Ruaha National Park, Tanzania. *Afr. J. Ecol.* **20**, 123–136.
- Barnes, R. F. W. (1983): Elephant behaviour in a semi-arid environment. *Afr. J. Ecol.* **21**, 185–196.
- Barnes, R. F. W. (1996): The conflict between humans and elephants in the central African forests. *Mammal Rev.* **26**, 67–80.
- Bell, R. H. V. (1971): A grazing ecosystem in the Serengeti. *Sci. Am.* **225**, 86–93.
- Blanc, J. J.; Thouless, C. R.; Hart, J. A.; Dublin, H. T.; Douglas-Hamilton, I.; Craig, C. G.; Barnes, R. F. W. (2003): African Elephant Status Report 2002: An Update from the African Elephant Database. IUCN/SSC African Elephant Specialist Group. IUCN, Gland, Switzerland, Cambridge, UK.
- Borner, M. (1985): The increasing isolation of Tarangire National Park. *Oryx* **19**, 91–96.
- Brandon, K. E.; Wells, M. (1992): People and Parks: Linking Protected Area Management with Local Communities. Washington, DC: World Bank, World Wildlife Fund, USAID.
- Codipietro, P. (2002): Tarangire–Manyara Conservation Project Final Report—Technical Reports and Maps: Land Cover. Istituto Oikos, TANAPA, University of Insubria.
- Di Gregorio, A.; Jansen, L. (2000): Land Cover Classification System, Classification Concepts and User Manual. Rome: Food and Agriculture Organization of the United Nations.
- Douglas-Hamilton, I. (1972): On the ecology and behaviour of the African elephant. Diss. Thesis, Oxford University.
- du Toit, J. T.; Owen-Smith, N. (1989): Body size, population metabolism and habitat

- specialisation among large African herbivores. *Am. Nat.* **133**, 736–740.
- ESRI (1997): Using ArcView GIS Version 3.2. Environmental Systems Research Institute, Inc. Redlands, CA.
- FAO-Africover (2002): Tanzania Multipurpose Landcover Database (digital map data set). Available on-line "<http://www.africover.org>"
- Feinsinger, P.; Spears, E. E.; Poole, R. W. (1981): A simple measure of niche breadth. *Ecology* **62**, 27–32.
- Field, C. R. (1971): Elephant ecology in the Queen Elizabeth National Park, Uganda. *East Afr. Wildl. J.* **9**, 99–123.
- Foley, C. A. H.; Papageorge, S.; Wasser, S. K. (2001): Non-invasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. *Conserv. Biol.* **15**, 1134–1142.
- Galanti, V.; Tosi, G.; Rossi, R.; Foley, C. (2000): The use of GPS radio-collars to track elephants (*Loxodonta africana*) in the Tarangire National park (Tanzania). *Hystrix* **11**, 27–37.
- Gibson, C. C.; Marks, S. A. (1995): Transforming rural hunters into conservationists: an assessment of community-based wildlife management programs in Africa. *World Dev.* **23**, 941–957.
- Hoare, R. (2000): African elephants and humans in conflict: the outlook for coexistence. *Oryx* **34**, 34–38.
- Hoare, R.; du Toit, J. T. (1999): Coexistence between people and elephants in African savannas. *Conserv. Biol.* **13**, 633–639.
- Hooge, P. N.; Eichenlaub, B. (2000): Animal Movement Extension to ArcView, version 2.0. Anchorage, AK, USA: Alaska Science Center – Biological Science Office, US Geological Survey.
- Kahurananga, J. M. N. (1979): The vegetation of the Simanjiro Plains, Northern Tanzania. *East Afr. J. Ecol.* **17**, 65–83.
- Lamprey, H. F. (1964): Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. *Afr. J. Ecol.* **2**, 1–46.
- Leader-Williams, N.; Smith, R. J.; Walpole, M. J. (2001): Elephant hunting and conservation. *Science* **293**, 2203.
- Leuthold, W. (1977): Spatial organization and strategy of habitat utilisation of elephants in Tsavo National Park, Kenya. *Z. Säugetierkunde* **42**, 258–379.
- Leuthold, W.; Sale, J. B. (1973): Movements and patterns of habitat utilisation of elephants in Tsavo National Park, Kenya. *East Afr. Wildl. J.* **11**, 369–384.
- Levine, A. (2002): Convergence or convenience? International conservation NGOs and development assistance in Tanzania. *World Dev.* **30**, 1043–1055.
- Lewis, D. M. (1986): Disturbance effects on elephant feeding: evidence for compression in Luangwa Valley, Zambia. *Afr. J. Ecol.* **24**, 227–241.
- Lindeque, M.; Lindeque, P. M. (1991): Satellite tracking of elephants in northwestern Namibia. *Afr. J. Ecol.* **29**, 196–206.
- Manly, B. F. J.; McDonald, L. L.; Thomas, D. L. (1993): Resource selection by animals: statistical design and analysis for field studies. London: Chapman & Hall.
- Mwalyosi, R. B. B. (1991): Ecological evaluation for wildlife corridors and buffer zones for Lake Manyara National Park, Tanzania, and its immediate environment. *Biol. Conserv.* **57**, 171–186.
- Naughton-Treves, L. (1998): Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conserv. Biol.* **12**, 156–168.
- Newmark, W. D. (1996): Insularization of Tanzanian parks and the local extinction of large mammals. *Conserv. Biol.* **10**, 1549–1556.
- Newmark, W. D.; Manyanza, D. N.; Gamassa, D. G. M.; Sariko, H. I. (1994): The conflict between wildlife and local people living adjacent to protected areas in Tanzania: human density as a predictor. *Conserv. Biol.* **8**, 249–255.
- O'Connell-Rodwell, C. E.; Rodwell, T.; Rice, M.; Hart, L. A. (2000): Living with the modern conservation paradigm: can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. *Biol. Conserv.* **93**, 381–391.
- Ogutu, Z. A. (2002): The impact of ecotourism on livelihood and natural resource management in Eselenkei, Amboseli ecosystem, Kenya. *Land Degradation Dev.* **13**, 251–256.
- Pimm, S. L.; Russell, G. J.; Gittleman, J. L.; Brooks, T. M. (1995): The future of biodiversity. *Science* **269**, 347–350.
- Poole, J. H.; Moss, C. J. (1981): Musth in the African elephant *Loxodonta africana*. *Nature* **292**, 830–831.
- Pratt, D. J.; Greenway, P. J.; Gwynne, M. D. (1966): A classification of East African rangeland. *J. Appl. Ecol.* **3**, 369–382.
- Silverman, B. W. (1986): Density Estimation for Statistics and Data Analysis. 1st edition. London: Chapman & Hall 175pp.
- Sitati, N. W.; Walpole, M. J.; Smith, R.; Leader-Williams, N. (2003): Predicting spatial aspects of human–elephant conflict. *J. Appl. Ecol.* **40**, 667–677.

- Stokke, S. (1999): Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. *Can. J. Zool.* **77**, 1723–1732.
- Stokke, S.; du Toit, J. T. (2000): Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* **23**, 70–80.
- Stokke, S.; du Toit, J. T. (2002): Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *Afr. J. Ecol.* **40**, 360–371.
- Tchamba, C. R. (1996): History and present status of the human/elephant conflict in the Waza-Logone region Cameroon, West Africa. *Biol. Conserv.* **75**, 35–41.
- Tchamba, M. N.; Bauer, H.; De Jongh, H. H. (1995): Application of VHF-radio and satellite telemetry techniques on elephants in northern Cameroon. *Afr. J. Ecol.* **33**, 321–334.
- Thouless, C. R. (1994): Conflict between humans and elephants on private land in northern Kenya. *Oryx* **28**, 119–127.
- Thouless, C. R. (1995): Long-distance movements of elephants in northern Kenya. *Afr. J. Ecol.* **33**, 321–334.
- Thouless, C. R. (1996): Home ranges and social organization of female elephants in northern Kenya. *Afr. J. Ecol.* **34**, 284–297.
- TWCM (1995): Aerial Wildlife Census of Tarangire National Park, Wet and Dry Season 1994. Arusha, Tanzania: Frankfurt Zoological Society.
- TWCM (1998a): Aerial Wildlife Census of Tarangire National Park, Wet Season 1998. Arusha, Tanzania: Frankfurt Zoological Society.
- TWCM (1998b): Aerial Wildlife Census of Tarangire National Park, Dry Season 1998. Arusha, Tanzania: Frankfurt Zoological Society.
- USNO (US Naval Observatory), Astronomical Applications Department (2003): Tables of Sunrise/Sunset, Moonrise/Moonset, or Twilight Times for an entire Year. Available on-line at http://aa.usno.navy.mil/data/docs/RS_OneYear.html.
- Vesey-Fitzgerald, D. (1973): Browse production and utilisation in Tarangire National Park. *East Afr. Wildl. J.* **11**, 291–305.
- Viljoen, P. J. (1989): Habitat selection and preferred food plants of a desert-dwelling elephant population in the Northern Namib desert, South West Africa/Namibia. *Afr. J. Ecol.* **27**, 227–240.
- Walpole, M. J.; Leader-Williams, N. (2001): Masai Mara tourism reveals partnership benefits. *Nature* **413**, 771.
- Weir, J. S. (1972): Spatial distribution of elephants in an African National Park in relation to environmental sodium. *Oikos* **23**, 1–13.
- Western, D.; Lindsay, W. K. (1984): Seasonal herd dynamics of a savannah elephant population. *Afr. J. Ecol.* **22**, 229–244.
- Woodroffe, R.; Ginsberg, J. R. (1998): Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128.
- Wyatt, J. R.; Eltringham, S. K. (1974): The daily activity of the elephant in the Rwenzori National Park, Uganda. *East Afr. Wildl. J.* **12**, 273–289.

Authors' addresses:

Valeria Galanti, Istituto Oikos ONLUS, via Crescen-
zago 1, I-20134 Milano, Italy
Damiano Preatoni, Adriano Martinoli, Lucas A.
Wauters, Guido Tosi, Dipartimento Ambiente-Salute-
Sicurezza, Università degli Studi dell'Insubria, via J.H.
Dunant 3, I-21100 Varese, Italy
(e-mail: adriano.martinoli@uninsubria.it)