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Densities of mammals in partially protected areas: the Katavi ecosystem of western Tanzania

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Summary

1. In Africa the majority of conservation areas sanction some sort of human activities within their borders but few of them are part of community-based conservation schemes. The effectiveness of these state-owned, partially protected areas in conserving mammalian fauna is largely unknown.

2. Large and medium-sized mammal densities in three different sorts of partially protected area were compared to mammal densities in an adjacent national park in western Tanzania by driving 2953 km of strip transects over a 14-month period.

3. In a Game Controlled Area that permitted temporary settlement, cattle grazing and tourist big game hunting, mammal diversity and mammal densities were relatively high. In a Forest Reserve that permitted limited hardwood extraction and resident hunting, most large species were absent. In a third, Open Area that allowed settlement, cattle grazing, firewood collection and beekeeping activities, mammal diversity and densities were again low but some large ungulates still used the area seasonally.

4. The chief factors responsible for lowered mammal densities outside the Park were illegal hunting, especially in close proximity to town, and to a lesser extent, resident hunting quotas that were too high.

5. These data suggest that state-owned conservation areas permitting human activities within their borders cannot be relied upon as a means of conserving large and middle-sized mammals in Africa.

6. Two methods are being employed to ameliorate this problem in Africa: excluding people from conservation areas while upgrading ground protection effort, and initiation of community-based conservation schemes. As yet, however, very few quantitative data are available to evaluate the efficacy of these methods in enhancing mammal populations.

Key-words: human impact, mammal densities, miombo woodland, multiple-use areas, national park.

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Introduction

Africa boasts an impressive list of conservation areas but the number that sanction human activities and resource extraction within their boundaries, termed partially protected areas (IUCN categories IV and V), exceeds the number that are totally protected (IUCN categories I–III) by a factor of 1·42 : 1 (WRI/UNEP/UNDP/WB 1996). Recently, a great deal of attention has focused on a subset of these partially protected areas: Integrated Conservation and Development Projects (ICDPs). In ICDPs, local people are given rights to a legally protected area and maintain an economic interest in it through wildlife utilization (Noss 1998), leasing the land to big game hunting consortiums (Lewis, Kaweche & Mwenya 1990), through tourism (Western 1994) or extraction of other resources. Despite a growing number of papers extolling the benefits to people of these community-based conservation schemes in Africa (e.g. Kiss 1990; Lewis 1993; IIED 1994; Metcalfe 1994; Alpert 1996; Crowe *et al.* 1997), there are less than 25 such projects in operation on the continent (IIED 1994; Kremen, Merelender & Murphy 1994), most notably in Zimbabwe and Zambia, and the effectiveness of these schemes is

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the subject of much debate (e.g. Kremen, Merelender & Murphy 1994; Little 1994; Barrett & Arcese 1995; Marks 1996). The great majority of partially protected areas, and therefore of African conservation areas in general, are instead set aside at the governmental level, and schemes by which people benefit economically from them are either absent or are very indirect (see Hanna, Folke & Maler 1996). These sorts of conservation areas usually lack financial support from central government and economic interest locally, and are thus said to 'exist only on paper', as lines on a map.

How well do these types of conservation area protect large mammals in Africa? This is an important question as such a large proportion of African conservation areas are only partially protected. Unfortunately, there are virtually no data that bear on this issue since the vast majority of research is conducted in national parks (see Sinclair & Arcese 1995 for a recent example), the type of conservation area most likely to receive governmental support. In this paper, I examine mammal densities in three types of partially protected areas in Tanzania using a fully protected national park as a comparison. These areas are found throughout Tanzania (Caro *et al.* 1998a) and are similar to many partially protected areas across the continent (Stuart & Adams 1990). They consist of an area where tourist hunting is permitted, an area in which local people can hunt under licence and extract timber, and an area in which most human activities are uncontrolled. In the second part of the paper, I explore some of the factors that are responsible for the observed mammal densities in partially protected areas.

Methods

STUDY AREA

The study was conducted in and immediately adjacent to Katavi National Park (latitude 6°45′ to 7°05′S, longitude 30°45′ to 31°25′E) at the north end of the Rukwa Valley in Rukwa Region, western Tanzania between September 1995 and December 1996 (Fig. 1). This area has always had a low population density due to tsetse fly. The local economy was traditionally based on shifting agriculture with livestock rearing on only a minor scale. As a result, wildlife populations were widespread throughout the whole area (Moffett 1958; Serengeti Ecological Monitoring Programme 1989). The region was gazetted as a Game Reserve and as Forest Reserves by the German authorities before the First World War; the area to the east was designated a Game Controlled Area by the British in 1932; and the north-eastern part of this area became a National Park in 1974.

The study site consists of four legally designated areas (Fig. 1). Katavi National Park (NP) consists largely of miombo woodland, dry forest habitat characterized by *Acacia*, *Combretum*, *Commifora*, *Grewia*, *Kigelia*, *Pterocarpus* and *Terminalia* tree species (Rodgers 1996) but also encompasses two seasonally inundated floodplains, Lakes Katavi and Chada. These are connected by the meandering Katuma River that opens out into a third less inundated plain in the eastern third of the Park. No temporary or permanent settlements are allowed aside from Park headquarters and two outlying ranger posts; no livestock, beekeeping, hunting, fishing or timber extraction are tolerated (Table 1). These laws are enforced by Tanzania National Park wardens and rangers conducting vehicle and foot patrols.

The Game Controlled Area (GCA) is a multiple use area to the east of the Park under the jurisdiction of the Department of Wildlife. It, too, consists of miombo woodland with scattered grassy plains; rivers near its western and southern borders prevent easy human access in the wet season. Four principal forms of human activity occur there (Table 1). To the east, Sukuma pastoralists maintain temporary settlements in the form of thorn stockades and earth-covered houses and graze large herds of cattle primarily during the dry season (July–October). On the western border, people from the small nearby town, Sitalike, and District headquarters, Mpanda, cut three species of hardwood tree under licences issued by the District Forest officer. They work slowly using hand-held saws and have not started to impact this area severely (Table 2). In addition, the GCA is leased to hunting companies by the Department of Wildlife that bring in tourist hunters between July and November. Resident hunting under licence is permitted in the area, but in practice little occurs as the GCA is too far from Mpanda, 40 km north of Sitalike, or the Regional headquarters (Sumbawanga), 170 km to the south, where most applicants live (J. Palangyo, personal communication). Very limited non-mechanized gold mining also occurs in the GCA.

The Forest Reserve (FR) to the north-east of the Park is also characterized by miombo woodland. Settlements, cattle grazing and tourist hunting are forbidden (Table 1) but hardwood extraction of three tree species is allowed under licence (Table 2). Although the latter is more advanced than in the GCA (Table 2), it occurs only in a limited area close to the road, and even there the forest is intact. To the casual observer, it does not appear to differ from the adjacent NP. Some gold mining occurs in the FR. In practice, people spend weeks or months camped in the forest cutting trees and mining. Resident hunting is carried out in the FR under licence and is more extensive than in the GCA owing to its proximity to Mpanda and Sitalike.

The Open Area (OA) to the south of the Park supports miombo woodland to the west of Mirumba (Fig. 1) but there is an open grassy plain to the north and east of this village. The OA allows for permanent settlement (notably three small villages: Mirumba, Manga and Kibaoni) and Sukuma also have a stock-

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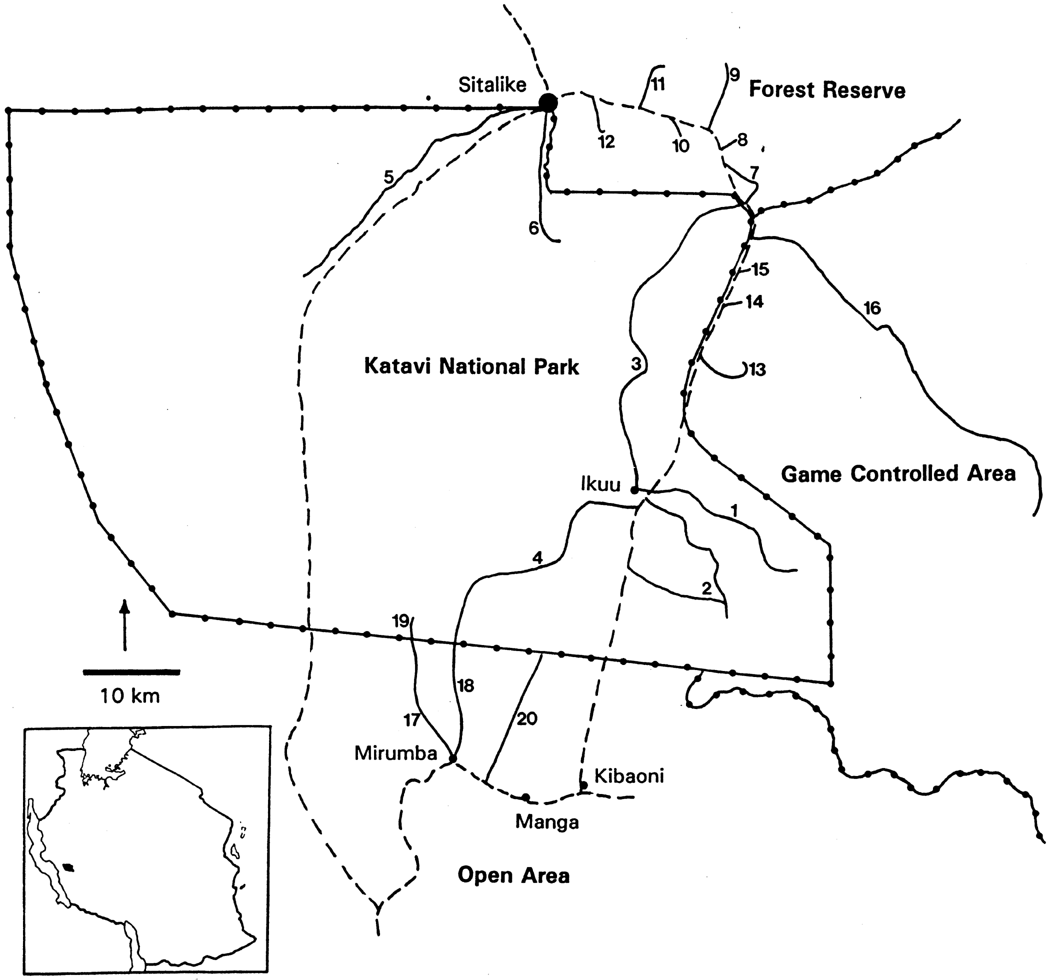

Fig. 1. The study area showing the location of Katavi National Park (NP), Msaginia Forest Reserve (FR), Mlele North Game Controlled Area (GCA), and Usevyia Open Area (OA). The small town of Sitalike and villages of Mirumba, Manga and Kibaoni are also shown, as well as basecamp at Ikuu. Mpanda is 40 km to the north of Sitalike by road, Sumbawanga is 130 km south of Mirumba by road. Conservation area boundaries are shown as solid lines with filled circles, gravel roads as dashed lines, approximate location of transects as solid lines. NP: nos. 1 (18·3 km in length), 2 (22·9), 3 (26·9) 4 (26·2) 5 (26·7) 6 (11·9) and 19 (1·8); GCA: 13 (5·9), 14 (1·8), 15 (0·9) and 16 (24·6); FR: 7 (4·7), 8 (2·5), 9 (6·4), 10 (2·3), 11 (5·9) and 12 (3·1); OA: 17 (11·7), 18 (7·1) and 20 (11·0). The location of Katavi National Park in Tanzania is shown in the insert at the bottom left.

Table 1. Summary of activities in the four conservation areas within the study area. NP denotes National Park; GCA, Game Controlled Area; FR, Forest Reserve; OA, Open Area

	NP	GCA	FR	OA
Settlements				
Temporary	–	+	–	–
Permanent	–	–	–	+
Cattle grazing	–	+	(–)	+
Timber				
Hardwood	–	(+)	+	(+)
Firewood	–	–	–	+
Hunting (legal)				
Tourist	–	+	–	–
Resident	–	(–)	+	(–)
Mining	–	(–)	(–)	–
Beekeeping	–	–	–	+

– denotes none, (–) little, (+) some, + common.

ades in the area. Pimbwe and Sukuma people practise cultivation although the majority of the OA is not cultivated intensively and fields are guarded only occasionally. They also graze cattle, collect firewood and grass, and put up beehives. Hardwood extraction is allowed but little occurs due to the distance from Mpanda; there is no mining (Table 2). Resident hunting is permitted under licence although in practice licences are never obtained. It should be noted that settlements, cultivation and grazing occur in close proximity to villages and are virtually absent within 5 km of the Park border.

Unlike the Park, there is virtually no on-site law enforcement in the GCA, FR or OA due to lack of funds from central offices for fuel and vehicle spare parts.

TRANSECTS

To determine densities of mammals and human activities in these four conservation areas, a total of 2953 km

Table 2. Percentage of cut hardwood trees in three conservation areas. GCA denotes Game Controlled Area; FR, Forest Reserve; OA, Open Area

Common name	Latin name	GCA	FR	OA
Mninga	*Pterocarpus angolensis* DC.	16·5	42·6	0
Msawala	*Sterculia quinqueloba* Sim	0·2	16·7	0
Mkola	*Swartzia madagascariensis* Desv.	0	4·8	0

Percentages were derived from counting cut and uncut trees along four transects in the GCA, six in the FR, and two in the OA, and taking an average of these for each area. There were no trees cut along National Park transects.

of transects were driven in a Landrover at <10 km hour^{-1} along the same established but minor tracks once during every month of the study except April and July 1996. Transects were chosen simply on accessibility since it was impossible to drive across country and cutting new tracks was not permitted (Fig. 1). Partially protected areas were sampled to equivalent extents (Fig. 1) but the NP was sampled four times as often as it was the focus of an additional study (Caro, in press, a).

Transects were conducted by one, two or three people sitting in the Landrover but there were no significant differences in the densities of any species comparing transects driven by a single observer to those driven by more than one. Data collection along each transect began at dawn, defined as the time that vehicle lights were not required for driving, or as soon as possible thereafter, and was halted at 10.30 hours even if the whole transect had not been completed: 10.30 hours was chosen as a cut-off time since many ungulates began their midday rest period then and hence became more difficult to observe. One transect in the OA that passed through cultivation was, however, sometimes completed after 10.30 hours.

During each transect a record was taken of all species of mammal seen that were larger than 0·2 kg. In total, 21 ungulates, 11 carnivores, two primates and two small mammal species were observed. As soon as a mammal was sighted, the vehicle was stopped and a record was made of the number of individuals within the group, defined as being within 50 m of the nearest neighbour. At each sighting, the behaviour of the individual or majority of individuals in the group was noted as feeding, moving, resting, vigilant, watching the observer, or fleeing.

To calculate the area of each transect, a nearly continuous record was made of the distance at which mammals could be seen on each side of it. Thus, at the start of the transect, the observer estimated the distance at which a hypothetical adult warthog *Phacochoerus aethiopicus* Pallas would still be visible and recorded this for each side of the track. A warthog was chosen as it fell at the low end of the weight distribution of mammals that could be observed, was small in stature, and therefore acted as a conservative marker. 500 m was set as the maximum distance visible on each side; estimated distances were repeatedly checked and revised using markers placed at known distances from base camp. If visible distance changed on either side of the transect after 0·2 km had been driven, a new record was made. This continued until the transect was completed. 200 m was chosen because sighting widths did not change dramatically over shorter distances. Subsequently, area was calculated by multiplying transect widths by lengths for each side of the transect and summing them (Burnham, Anderson & Laake 1980). For each species or constellation of species, density was calculated by adding the total number of individuals seen on a given transect and dividing by the area visible (Norton-Griffiths 1978; Mduma 1995). This method yields densities that are strongly correlated with those obtained using other ground based methods (Caro, in press, b).

In addition, a nearly continuous independent record was made of the vegetation type on each side of the vehicle by noting changes in vegetation structure. Following Pratt, Greenway & Gwynne (1966; see also Kikula 1980 for full details), vegetation was categorized into three types of woodland (defined as trees with canopy cover $>20\%$) dependent on canopy cover ($>70\%$, 50–69%, 20–49%), bushland (dense woody vegetation <6 m in height), bushed grassland (grassland with 2–20% bush canopy), wooded grassland (grassland with 2–20% tree cover), grassland (grass dominated), or cultivation (harrowed fields). By combining records of changes in vegetation with records of visibility, the area visible in each type of vegetation could be calculated (Caro, in press, b).

STATISTICAL ANALYSES

Following Schaller (1972), the units of biomass were taken as 0·75 of the female body weights given by Estes (1991); these figures were added together and divided by area to yield kg km^{-2}.

For each transect and for each species, average densities were first calculated across all 14 months over which data were collected. Mean densities for each transect were then compared across the four conservation areas using Kruskal–Wallis tests. For species or species constellations showing significant differences, data were further explored using Mann–Whitney *U* two-sample comparisons. Data were also examined separately by season by taking an average of dry season months (September–November 1995 and August–October 1996) when < 10 mm of rain fell before transects were conducted; an average of wet season months (January–March, and December 1996) when > 100 mm fell; and an average of transitional months (December 1995, May, June and November 1996), 1 month before and 2 months after the wet season. However, comparisons across conservation areas showed the same pattern of significant differences as did samples using all 14 months' data; consequently, only the latter are presented here. Non-parametric tests were used as there were many transects in which species were not seen by the observer, and the resulting large number of zeroes made use of parametric tests inappropriate. Tests were two-tailed with alpha set at 0·05.

Three aerial censuses have been conducted recently in the Katavi ecosystem: in December 1988 (Serengeti Ecological Monitoring Programme 1989), November 1991 (Tanzania Wildlife Conservation Monitoring 1992) and December 1995 (B. Woodworth, unpublished data), each of which covered areas outside the Park. Surveys were carried out using radar altimeter equipped Cessna 182 and 185 aircraft with a front and two rear seat observers flying at 200 kph at a target height of 350 feet (120 m). Survey methodology followed Norton-Griffiths (1978) for systematic reconnaissance flights (Campbell & Borner 1995). Flight lines were spaced 5 km apart, and the beginning, end and direction marked on 1 : 250 000 scale flight maps on which planned transect lines were drawn. Strip widths were defined by parallel fibreglass rods attached to wing struts and averaged ≈ 300 m; this resulted in ≈ 6% of the area being sampled. The method used to calculate population estimates followed that of Jolly (1969). Densities of mammals seen in these censuses within the Park and to the north-east, east and south of it were averaged across the three surveys and are used as a comparison to ground counts. It should be noted that these censuses encompassed a wider area outside the Park than that covered by ground transects and that aerial censuses are poor at detecting rare or cryptic species (see Caro *et al.* 1998a).

Results

DENSITIES IN PARTIALLY PROTECTED AREAS

Game Controlled Area

Out of 24 species or species constellations seen in the NP, 16 were seen in the GCA (Table 3). Wild mammal biomass km^{-2} in the GCA was approximately one-third of that in the NP, although not significantly lower (Table 3). Nevertheless, compared to the Park, the GCA contained significantly lower densities of elephant *Loxondata africana* Blumenbach, hippopotamus *Hippopotamus amphibius* Linnaeus, eland *Taurotragus oryx* Pallas, impala *Aepyceros melampus* Lichenstein and spotted hyena *Crocuta crocuta* Erxleben. In comparison to the FR, total wild mammal biomass km^{-2} in the GCA was significantly greater, as were densities of giraffe *Giraffa camelopardalis* Linnaeus, buffalo *Synercus caffer* Sparrman, zebra *Equus burchelli* Gray and warthog. Both mammal biomass and buffalo densities were significantly greater in the GCA than in the OA.

In the GCA, human presence (people, livestock and their activities km^{-2}; Table 3) was greater than in the Park but not significantly so. The density of people and their activities was far lower in the GCA than in the OA however; similarly, density of human activity was significantly lower in the GCA than in the FR.

Forest Reserve

Out of the 24 species seen in the NP, only eight were seen in the FR (Table 3). There, mammalian biomass km^{-2} was significantly lower than in the Park, primarily because buffalo and elephant densities were significantly lower, as were many other large species: hippopotamus, giraffe, eland, zebra and waterbuck *Kobus ellipsiprymnus* Ogilby (Table 3). Densities of topi *Damaliscus korrigum* Burchell, bushpig *Potamochoerus porcus* Linnaeus, warthog, impala, lion *Panthera leo* Linnaeus, spotted hyaena, and small carnivores such as side-striped jackal *Canis adustus* Sundervall were lower too. In addition, giraffe and impala densities were significantly lower than in the OA.

Densities of people and human activities were higher than in the Park; human and livestock densities were significantly lower than in the OA.

Open Area

Of the 24 species of mammals seen in the Park, eight were seen in the OA. Mammalian biomass km^{-2} in the OA was significantly lower than in the NP, owing primarily to significantly lower densities of elephant and buffalo (Table 3). Eland, waterbuck, topi, warthog and spotted hyena were also found at significantly lower densities. As mentioned, impala densities were significantly higher here than in either of the other partially protected areas and giraffe densities were significantly higher than in the FR.

In the OA, people, their livestock and their activities were all found at significantly greater densities than any of the other areas, with the exception of livestock in the GCA and activities in the FR.

COMPARISON OF GROUND AND AERIAL CENSUSES

Wild mammal biomass km^{-2} and densities of many mammals derived from aerial censuses were generally

Table 3. Mean densities km^{-2} over 14 months of mammals, people, livestock and human activities in four conservation areas in the Katavi ecosystem taken from ground transects. NP denotes National Park; GCA, Game Controlled Area; FR, Forest Reserve; OA, Open Area

	A NP ($n = 7$)	B GCA ($n = 4$)		C FR ($n = 6$)		D OA ($n = 3$)	
Biomass	22526	7106		152	Ab	705	ab
Mammals							
Elephant	1·96	0·10	a	0	A	0	a
Hippopotamus	5·15	0	a	0	a	0	
Giraffe	2·17	1·78		0	AB	0·55	c
Buffalo	21·15	12·30		0·05	AB	0·03	ab
Eland	1·45	0·03	a	0	A	0	a
Roan	0·19	0·04		0·13		0	
Sable	0	0		0		0	
Zebra	5·64	1·65		0	Ab	1·33	
Waterbuck	4·28	0·58		0	A	0	a
Greater kudu	0·01	0·07		0		0	
Hartebeest	0·35	1·30		1·04		0·08	
Topi	2·13	0·26		0	A	0·05	a
Bushpig	0·07	0		0	a	0	
Warthog	1·34	1·82		0	Ab	0	a
Reedbuck	0·39	0·26		0		0	
Impala	3·72	0	a	0	A	5·12	bC
Bushbuck	0·04	0		0·07		0	
Small antelope*	0·06	0·91		0·35	a	0·09	
Lion	0·73	0		0	a	0	
Spotted hyaena	0·19	0	A	0	A	0	a
Small carnivore†	0·04	0		0	a	0	
Mongoose‡	0·21	0·11		0·21		0	
Baboon	0·01	0·06		0·12		0	
Vervet	0·47	0·06		0·05		0·24	
Small mammal§	0·01	0		0		0	
Human presence							
Human	0·01	1·33		1·52	A	14·65	Abc
Livestock¶	0	6·12		0		69·05	AC
Human activity**	0	0·03		1·92	Ab	5·14	Ab

Mammals are arranged in order of descending body weight and taxonomic affiliation. Factors showing significant differences between ground transects comparing A, B, C and D using a Kruskal–Wallis test are in bold type. Suffixes refer to significant differences between that column and earlier ones using Mann–Whitney *U*-tests; upper case denotes $P < 0{\cdot}01$, lower case $P < 0{\cdot}05$. *n* refers to the number of transects driven per month. Biomass is measured in kg km^{-2} (see Methods).

* Bush duiker, klipspringer, oribi and dik-dik combined.

† Leopard, wild dog, ratel, serval, and side-striped jackal combined.

‡ Banded, dwarf, black-tipped and marsh mongoose combined.

§ Hare and squirrel combined.

¶ Cow, goat and donkey combined.

** Beehive, treecutters' camp, firewood pile, sawpit, grass pile, and pile of bricks combined.

lower than those based on ground transects (compare Tables 3 and 4; see also Caro, in press, b). Nevertheless, for some species such as eland, zebra and livestock, densities were higher in aerial than in ground censuses in the GCA and FR, and for many species in the OA such as buffalo and impala. Factors that could explain these discrepancies include aerial censuses covering a greater and perhaps more representative area than ground counts, and a tendency for aerial censuses to avoid areas of human habitation.

Given only three aerial censuses, it was not possible to use them to compare conservation areas statistically. Instead, significant differences derived from ground transects were examined (Table 3) and verification by eye using mean aerial census figures was attempted. Broadly, densities derived from aerial censuses showed similar trends to the significant ground transect results with the exception of the GCA vs. NP comparison for eland and impala; significant differences here should therefore be treated with caution.

Table 4. Mean densities km^{-2} of mammals, livestock and human activities in four conservation areas in the Katavi ecosystem taken from three aerial censuses. NP denotes National Park; GCA, Game Controlled Area; FR, Forest Reserve; OA, Open Area

	A NP	B GCA	C FR	D OA
Biomass	12067	3858	220	394
Mammals				
Elephant	0·97	0	0	0·04
Hippopotamus	0·33	0·09	0	0
Giraffe	0·56	0·68	0·15	0·23
Buffalo	15·14	5·09	0·09	0·26
Eland	0·82	0·71	0·06	0
Roan/sable*	0·24	0·18	0·14	0·08
Zebra	3·20	4·72	0·10	0·14
Waterbuck	0·49	0·44	0·06	0
Greater kudu	0	0	0·02	0
Hartebeest	0·04	0·39	0·29	0·29
Topi	1·68	0·36	0	0
Bushpig	0	0·05	0	0
Warthog	0·38	0·73	0·15	0·16
Reedbuck	0·12	0·05	0·05	0·01
Impala	0·20	0·99	0·05	0·10
Bushbuck	0·02	0·01	0	0·01
Duiker†	0	0·02	0·02	0
Spotted hyaena	0	0	0	0
Baboon	0	0	0	0
Human presence				
Livestock‡	0	19·44	3·70	67·59
Human activity§	0·05	0·35	1·44	8·78¶

Mammals are arranged in order of descending body weight and taxonomic affiliation. Biomass is measured in kg km^{-2}.
* Roan and sable antelope combined.
† Bush duiker, klipspringer, oribi and dik-dik combined.
‡ Cow, goat and donkey combined.
§ Beehive, treecutters' camp, firewood pile, sawpit, grass pile, and pile of bricks combined.
¶ Activities as recorded from the air are not strictly comparable to those recorded on the ground.

CAUSES OF REDUCED DENSITIES IN PARTIALLY PROTECTED AREAS

To determine whether mammal densities outside the Park resulted from human disturbance or ecological factors, three sets of additional analyses were carried out. First, I compared the percentage area of each of the eight vegetation types that were visible from transects in the four conservation areas. There was no significant difference between conservation areas (Friedman test, $\chi^2 = 11{\cdot}250$, d.f. = 7, NS), thus, a priori, differences in vegetation seemed unlikely to account for differences in densities across conservation areas. Second, for each mammal species and measure of human presence, I noted the vegetation type in which less than 5% of sightings fell. The visible area constituted by these vegetation types was then excluded from the denominator used to calculate densities in order to remove vegetation that was avoided by each species. Comparisons of mammal and human presence densities calculated thus were remarkably similar to comparisons using the total visible area method. Of the 45 significant differences reported in Table 3 (excluding biomass comparisons), 44 were significant when vegetation that was avoided by each species was dropped from analysis.

Third, the original analyses were repeated but restricted to three park transects that ran close to the Park boundary (Nos 1, 6 and 19, Fig. 1) and compared with the 12 GCA, FR and OA transects that also ran close to the border (Nos 7–15, 17, 18 and 20); all these transects traversed thick woodland for the greater part of their lengths. Results still showed significantly lower densities of biomass km^{-2} outside the Park than inside ($\bar{X}s = 2464$, 21 051 kg km^{-2}, respectively, Mann–Whitney U-test, $z = -2{\cdot}165$, $P = 0{\cdot}030$). Densities of 13 species were significantly lower outside than inside the Park. These were elephant ($\bar{X}s = 0{\cdot}02$, $2{\cdot}13$ km^{-2}, respectively, $z = -2{\cdot}373$, $P = 0{\cdot}018$), hippopotamus ($\bar{X}s = 0$, $3{\cdot}40$ km^{-2}, $z = -2{\cdot}000$, $P =$

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0·046), giraffe ($\bar{X}s = 0{\cdot}62$, $1{\cdot}18\ \text{km}^{-2}$, $z = -2{\cdot}035$, $P = 0{\cdot}042$), buffalo ($\bar{X}s = 4{\cdot}08$, $23{\cdot}23\ \text{km}^{-2}$, $z = -2{\cdot}130$, $P = 0{\cdot}033$), eland ($\bar{X}s = 0{\cdot}01$, $0{\cdot}19\ \text{km}^{-2}$, $z = -2{\cdot}373$, $P = 0{\cdot}018$), topi ($\bar{X}s = 0{\cdot}09$, $2{\cdot}75\ \text{km}^{-2}$, $z = -2{\cdot}038$, $P = 0{\cdot}042$), waterbuck ($\bar{X}s = 0$, $3{\cdot}81\ \text{km}^{-2}$, $z = -2{\cdot}928$, $P = 0{\cdot}003$), bushbuck *Tragelaphus scriptus* Pallas ($\bar{X}s = 0{\cdot}04$, $0{\cdot}07\ \text{km}^{-2}$, $z = -1{\cdot}960$, $P = 0{\cdot}050$), warthog ($\bar{X}s = 0{\cdot}53$, $1{\cdot}79\ \text{km}^{-2}$, $z = -2{\cdot}234$, $P = 0{\cdot}026$), bushpig ($\bar{X}s = 0$, $0{\cdot}09\ \text{km}^{-2}$, $z = -2{\cdot}000$, $P = 0{\cdot}046$), lion ($\bar{X}s = 0$, $0{\cdot}08\ \text{km}^{-2}$, $z = -2{\cdot}000$, $P = 0{\cdot}046$), spotted hyaena ($\bar{X}s = 0$, $0{\cdot}22\ \text{km}^{-2}$, $z = -3{\cdot}714$, $P < 0{\cdot}001$) and small carnivores ($\bar{X}s = 0$, $0{\cdot}01\ \text{km}^{-2}$, $z = -2{\cdot}000$, $P = 0{\cdot}046$). No mammal densities were higher outside the Park. This clear pattern suggested that human disturbance, virtually absent from inside the Park, played the prominent role in producing low mammal densities outside the Park as the border did not run along significant ecological boundaries. In summary, it was difficult to attribute low mammal densities outside the Park to differences in vegetation or to any attraction of mammals to water sources or high-quality forage in the Park centre.

HUNTING PRESSURE

What aspects of human disturbance might result in low densities of large and middle-sized mammals? Two lines of evidence suggested that hunting was important. First, I ranked ungulates (species prized as meat) according to body size and then density (as determined from mean NP densities). Preferences of illegal hunters have been found to be affected by both of these factors elsewhere in Tanzania (Arcese, Hando & Campbell 1995). Species that were larger than the median ungulate body weight and that lived at higher than median densities in the NP were marginally more likely to be found at lower densities outside the Park than inside (Fisher exact test, $P = 0{\cdot}054$; Table 5). Furthermore, they were found at significantly lower densities in one or more conservation areas compared to the Park than other smaller species found at lower densities (Fisher exact test, $P = 0{\cdot}01$). Thus initially numerous, large species were differentially lost in the absence of protection.

Second, patterns of species' behaviour were examined in relation to observers inside and outside Park boundaries. Four species were more likely to flee from the vehicle when encountered outside than inside: giraffe (44·4% fled at sightings outside vs. 8·2% inside, $\chi^2 = 22{\cdot}923$, d.f. = 1, $P < 0{\cdot}001$), buffalo (55·6% vs. 17·6%, $\chi^2 = 5{\cdot}872$, d.f. = 1, $P = 0{\cdot}015$), zebra (36·4% vs. 10·7%, $\chi^2 = 4{\cdot}340$, d.f. = 1, $P = 0{\cdot}037$) and reedbuck *Redunca redunca* Pallas (100% vs. 0%, $\chi^2 = 11{\cdot}245$, d.f. = 1, $P < 0{\cdot}001$). Two others were more likely to observe the vehicle intently when outside the Park: waterbuck (66·7% vs. 27·8%, $\chi^2 = 6{\cdot}633$, d.f. = 1, $P < 0{\cdot}01$) and warthog (50·0% vs. 17·3%, $\chi^2 = 5{\cdot}922$, d.f. = 1, $P = 0{\cdot}015$). Most of these species occurred at significantly lower densities outside Park boundaries suggesting they were subject to hunting.

Hunting outside the Park took two forms: legal hunting by tourist hunters in the GCA and by resident hunters in the FR; and illegal hunting in many places. Which type of hunting may have been responsible for low mammal densities? In the GCA hunting block, the average number of mammals legally hunted by tourists per annum was low, never exceeding an average of five individuals per species per year, with the exception of buffalo (Table 6); moreover, tourist hunters are required to take males of most of these species (see Greene *et al.* 1998). Compared with estimated population sizes taken over $\approx 1000\ \text{km}^2$ of hunting block, legal offtake might only affect population growth rates for a few trophy ungulates: eland, roan *Hippotragus equinus* Desmarest, sable *Hippotragus niger* Harris, greater kudu *Tragelaphus strepsiceros*

Table 5. Ungulates separated according to differences in density from the National Park (NP), by body weight and density

		Did species show significantly lower densities outside the NP than inside? YES	NO
Are species greater than median body weight and also living at greater than median densities?	YES	Elephant Hippopotamus Giraffe Buffalo Eland Zebra Waterbuck	
	NO	Roan Topi Bushbuck Warthog Impala Bushbuck	Sable Kudu Hartebeest Reedbuck Duiker

Table 6. Mammal offtake per annum by tourists and residents in Mpanda District and estimated total population sizes in the Forest Reserve and Game Controlled Area bordering Katavi National Park. Population sizes were calculated by multiplying mean densities km^{-2} from ground counts or average densities km^{-2} over 3 aerial censuses, by 1000 (i.e. the 20 km boundary × 50 km in from the road) for the Game Controlled Area; and by 402 (i.e. the 20·1 km boundary × 20 km in from the East of the road) for the Forest Reserve

	Game Controlled Area		Forest Reserve	
	Tourist hunting year^{-1} (1992–96)	Est. pop. in 1000 km^2 of hunting block	Resident hunting year^{-1} (1993–96)	Est. pop. within 20 km of road
Elephant	–	0–100	–	0
Hippopotamus	1·0	0–90	–	0
Giraffe	–	680–1780	–	0–60
Buffalo	7·2	5090–12300	32·0	20–36
Eland	1·2	30–71	4·8	0–24
Roan	2·0	40–90*	–	28–52*
Sable	2·2	0–90*	–	0–28*
Zebra	4·4	1650–4720	–	0–40
Waterbuck	3·4	440–580	–	0–24
Greater kudu	1·0	0–70	–	0–8
Hartebeest	4·2	390–1300	16·3	117–418
Topi	1·4	260–360	7·5	0
Bushpig	0·6	0–50	7·5	0
Warthog	2·2	730–1820	10.0	0–60
Reedbuck	2·4	50–260	10.0	0–20
Impala	1·4	0–990	13·8	0–20
Bushbuck	1·4	0–10	6·3	0–28
Duiker	1·2	20–670	5·0	8–141
Klipspringer	0·2	176†	–	0†
Dik-dik	–	0†	5.0	0†
Lion	2·4	0†	–	0†
Leopard	2·2	0†	–	0†
Spotted hyaena	0·4	0	–	0
Jackal	0·2	0†	–	0†
Baboon	0·4	0–60	–	0–48
Hyrax	–	0†	5·0	0†
Hare	–	0†	12·5	0†

* Aerial censuses combined roan and sable antelope, thus mean densities were divided by 2 in calculating population sizes for each species.
† Not recorded in aerial censuses.

Pallas and bushbuck (assuming each species produces one offspring per year). Lion and leopard *Panthera pardalis* Linnaeus populations might also be adversely affected by such offtake; spotted hyaena and side-striped jackal population sizes were probably underestimates. Since tourist hunters took no elephants in the GCA, legal hunting could not account for low elephant densities compared to the NP.

With regard to the FR, residents who apply to the District Game officer for hunting licences usually hunt on the borders of the Park, including part of the FR in the study area (J. Palangyo, personal communication). The average number of hunting licences issued per year therefore represents a maximum *legal* offtake. Although offtake is higher than through tourist hunting, and in practice both sexes are taken, legal numbers never exceeded a total of 15 individuals per species per year except in the cases of hartebeest *Alcelaphus lichtensteinii* Peters and buffalo. Nevertheless, Table 6 shows that legal offtake of buffalo, eland, topi, bushpig, warthog, reedbuck, impala and bushbuck might adversely affect local population sizes within 20 km of the road, the distance a resident might enter the FR in a vehicle. This is because offtake constituted well over 25% of the median of the two population estimates and most of these species produce only one offspring per year. Even if resident hunters used their licences elsewhere on half the occasions, these species' populations were under threat. Yet, it is clear that legal resident hunting could not account for low densities of elephant, hippopotamus, giraffe, zebra, waterbuck, lion, spotted hyaena, and small carnivores since licences were not issued for these species.

These crude calculations suggest that legal hunting by tourists in the GCA and by residents from Sitalike and Mpanda in the FR could, at best, only partially account for the low densities of mammals seen in conservation areas outside the Park. This points to the importance of illegal hunting. Unfortunately, it is extremely difficult to obtain accurate information on illegal hunting. Nevertheless, when species' densities in the GCA and FR were reanalysed with respect to distance from Sitalike, known to be a centre of illegal hunting, density of wild mammal biomass km^{-2} in each of the FR and GCA transects increased significantly with the distance from the town as measured from the point at which that transect joined the main road to Sitalike (Fig. 1) ($n = 10$ transects, $r_s = 0{\cdot}733$, $P = 0{\cdot}016$). More specifically, densities of giraffe, buffalo, and zebra increased significantly with transect distance from Sitalike ($n = 10$, $r_s = 0{\cdot}694$, $P = 0{\cdot}026$; $r_s = 0{\cdot}821$, $P = 0{\cdot}004$; $r_s = 0{\cdot}738$, $P = 0{\cdot}014$, respectively). Again, these species were large and numerous as measured by Park standards, and hence likely to be favoured first by poachers, who typically carry guns in the area and can thus target their prey selectively.

Discussion

None of the partially protected areas contained as high a density of mammals as the NP despite being adjacent to it. Prior analyses showed that this was not the result of differential sampling in different seasons when mammals might have moved from one area to another; furthermore, it was only in exceptional circumstances that a transect was not driven every month. In addition, vegetation structure could not account for the observed differences between conservation areas since vegetation did not differ significantly between conservation areas, results were unaffected by omitting least preferred vegetation from analyses, and comparisons of transects inside and outside but close to the Park boundary confirmed that partially protected areas contained lower mammal densities. These results mirror many case studies in other partially protected areas in Africa (e.g. Lindsay 1987; FitzGibbon, Mogaka & Fanshawe 1995; Hofer *et al.* 1996; Jachmann & Billouw 1997; Verlinden 1997).

Game Controlled Area

Human presence was greater in the GCA than in the NP but was far lower than in the OA. Nevertheless, livestock densities in the GCA were relatively high, as measured by ground and aerial counts; Sukuma pastoralists move their livestock into the area during the dry season.

The GCA contained the greatest number of mammal species and highest wild mammal biomass km^{-2} after the NP. Densities of most species were greater than zero, in contrast to the FR and OA (Table 3), and for only a few species were densities significantly lower than in the Park. Absence of hippopotamus from the GCA was due to setting transects far from watercourses (to avoid vehicles getting stuck) and aerial census data suggest that, by chance, ground transects were situated in areas avoided by eland and impala. Giraffe, buffalo, zebra and warthog densities were all higher in the GCA than in the FR.

Compared to the other GCAs in Tanzania, this one undoubtedly exhibited high mammal densities. In a similar analysis of aerial census data across the country in which GCAs and OAs were combined and compared with NPs and Game Reserves combined (Caro *et al.* 1998a), densities of hippopotamus, buffalo, giraffe, eland, roan, waterbuck, hartebeest, zebra and bushbuck were significantly lower in the former, unprotected areas. Yet these findings were not replicated in the GCA vs. NP comparisons in this study. This particular GCA is located far from Mpanda and Sumbawanga and therefore from resident legal hunting and, to a lesser extent, from Sitalike and hence from illegal hunting.

Forest Reserve

Densities of people and their activities were higher in the FR than in the NP. These activities were primarily tree cutting and transects were all conducted along logging roads, abandoned or in use, which undoubtedly inflated measures of human disturbance. Nevertheless, aerial censuses taken over a wider area showed that people used the FR and also indicated that livestock are grazed deep inside it.

In the FR, mean wild mammal biomass km^{-2} was less than 1% of that in the Park and was significantly lower than in the GCA. With the exception of buffalo and roan, most of the larger species were never observed over 14 months and many species showed significantly lower densities than in the Park. In contrast, small antelope, principally bush duiker *Sylvicapra grimmia* Linnaeus, were regularly seen in the FR, possibly because hunters refrained from targetting them on account of their small body size. A high density of hartebeest in the FR is enigmatic but this species may be attracted to burnt areas (P. Coppolillo, personal communication) or seasonally long grass (S. Creel, personal communication). From a mammalian perspective, the FR conforms to the picture of an empty forest said to cover many parts of the neotropics (Redford 1992); namely, a relatively uncut forest with few large mammals left in it.

Open Area

Densities of people, their livestock and activities (especially beekeeping) were significantly greater in the OA than in the NP, and for most comparisons, greater than in the GCA and FR. This was not surprising as transects were driven from the Park boundary into the centre of the village or to a main road.

Wild mammal biomass km^{-2} in the OA was significantly lower than in the NP or GCA. Many species were never observed in the OA or else showed significantly lower densities than the Park. Nonetheless, species such as giraffe and impala did visit the large floodplain south of the Park especially in transitional months. In addition, elephants caused problems in the fields around the villages in the wet season when they ate maize, bananas and papayas; and bushpigs raided maize fields. It is possible that harassment of wild mammals in the cultivated parts of the OA may have been responsible for reduced densities of some species in the OA but I have no data on this. Compared to other OAs in Tanzania, this one seemed fairly typical with the density of many species far lower than in protected areas (Caro *et al.* 1998a).

CAUSES OF REDUCED DENSITIES IN PARTIALLY PROTECTED AREAS

The principal factor responsible for low mammal populations outside the Park was illegal hunting by local people. Although few data could be obtained on poaching, wild biomass km^{-2} and densities of giraffe, buffalo (prized meat species) and zebra increased with distance from Sitalike. Illegal hunters come on foot from Sitalike where a number of men own muzzle loaders. In addition, anecdotal accounts from Park wardens indicated that poaching was heavy in the FR, common in the OA, and that poachers moved into the GCA in the wet season. Six elephants were poached in the GCA just outside the Park boundary during the course of the study. To a lesser extent, poachers also come from timber cutting camps in the forest itself, where woodcutters supplement their diet of maize meal with game meat.

Based on crude calculations, resident hunting quotas also appeared to be high in the FR. Data presented here suggest that local quotas for buffalo should be reduced to a quarter, while those for topi, bushpig, warthog, reedbuck and impala should be reduced to zero. Instead, quotas for hartebeest and duiker could be increased.

The fact that high livestock densities and tourist hunting occurred in the GCA where mammal densities were still high suggests that neither of these factors greatly reduced mammal densities. Indeed, Caro *et al.* (1998b) found that, across the country, tourist hunting adversely affected only populations of eland and perhaps small antelope, bushbuck, kudu, reedbuck, lion and leopard.

EMERGING SOLUTIONS TO THE PROBLEM OF PARTIALLY PROTECTED AREAS

In conclusion, this study indicates that absence of active on-ground protection in partially protected areas, either by a central authority or through local participation, results in low mammal densities (see also Leader-Williams, Albon & Berry 1990) particularly of large meat species. Nevertheless, partially protected areas that are remote from local towns and villages may still hold substantial densities of wild mammals since poaching using snares, arrows and guns is usually conducted on foot. As most partially protected conservation areas in Africa are not actively patrolled or under the jurisdiction of local people, the prospects for large mammals in such areas look grim. Clearly, managers cannot rely on state-owned conservation areas that permit human activities within their boundaries.

The problem of declining mammal populations in partially protected areas has been recognized informally in Tanzania and elsewhere for some time although few studies have examined it explicitly. Two methods are being employed to tackle the problem: development of community-based conservation schemes (e.g. Lewis, Kaweche & Mwenya 1990; Wilkie *et al.* 1998) and upgrading protection. For example, in Tanzania, community-based conservation schemes are being employed by Tanzania National Parks authorities to increase cooperation with people living adjacent to park borders (Bergin 1996), by the German Development Agency (GTZ) which has initiated community-based hunting programmes around Selous Game Reserve (Krishke, Lyamuya & Ndunguru 1996), and the Cullman Wildlife Project which is providing funding for schools and clinics to villages adjacent to its hunting concessions (Robin Hurt Safaris 1996). Unfortunately, the efficacy of these schemes measured in terms of increasing wildlife populations has yet to be evaluated, nor are they likely to be since few baseline measures of animal populations were taken beforehand. Nevertheless, despite an absence of evidence of their benefits for wildlife, these projects are becoming increasingly popular in Tanzania (Leader-Williams, Kayera & Overton 1996) and many African countries (e.g. Kiss 1990; Kock 1996) since they benefit local communities.

The other method being used to prevent mammal population decline in Tanzania is to reclassify partially protected areas into National Parks and Game Reserves (e.g. Tanzania Wildlife Conservation Monitoring 1994). These categories of conservation area exclude local people, aside from photographic or hunting tourism, respectively, and provide on ground protection from rangers or game scouts. Although such patrols are poorly funded and equipped and are therefore irregular, activities of local people are greatly reduced and wildlife populations are higher in fully than in partially protected areas in Tanzania, as determined from aerial censuses (Caro *et al.* 1998a). Nonetheless, we do not yet have evidence to show that upgrading a given area's legally protected status unequivocally results in an increase in wildlife populations. Although community-based conservation and upgrading protection are likely to be better or equivalent conservation options for wildlife than state-owned partially protected areas, long-term monitoring of wildlife populations under both schemes is essential to assess their comparative merits.

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References

Alpert, P. (1996) Integrated conservation and development projects. *Bioscience*, **46**, 845–855.

Arcese, P., Hando, J. & Campbell. K. (1995) Historical and present-day anti-poaching efforts in Serengeti. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 506–533. University of Chicago Press, Chicago.

Barrett, C.B. & Arcese, P. (1995) Are integrated conservation- development projects (ICDPs) sustainable? On the conservation of large mammals in sub-saharan Africa. *World Development*, **23**, 1073–1084.

Bergin, P. (1996) Tanzania National Parks Community Conservation Service. *Community-Based Conservation in Tanzania*. (eds N. Leader-Williams, J.A. Kayera & G.L. Overton), pp. 67–70. IUCN, Gland, Switzerland.

Burnham, K.P., Anderson, D.R. & Laake, J.L. (1980) Estimation of density from line transect sampling of biological populations. *Wildlife Monographs*, **72**, 1–202.

Campbell, K. & Borner, M. (1995) Population trends and distribution of Serengeti herbivores: implications for management. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 117–145. University of Chicago Press, Chicago.

Caro, T.M. (in press, a) Abundance and distribution of mammals in Katavi National Park. *African Journal of Ecology*, in press.

Caro, T.M. (in press, b) Conservation monitoring: estimating mammal densities in woodland habitats. *Animal Conservation*.

Caro, T.M., Pelkey, N., Borner, M., Campbell, K.L.I., Woodworth, B.L., Farm, B.P., ole Kuwai, J., Huish, S.A. & Severre, E.L.M. (1998a) Consequences of different forms of conservation for large mammals in Tanzania: preliminary analyses. *African Journal of Ecology*, **36,** 303–320.

Caro, T.M., Pelkey, N., Borner, M., Severre, E.L.M., Campbell, K.L.I., Huish, S.A., ole Kuwai, J., Farm, B.P. & Woodworth, B.L. (1998b) The impact of tourist hunting on large mammals in Tanzania: an initial assessment. *African Journal of Ecology*, in press.

Crowe, T.M., Smith, B.S., Little, R.M. & High, S.H. (1997) Sustainable utilization of game at Rooipoort estate, northern Cape Province, South Africa. *Harvesting Wild Species: Implications for Biodiversity and Conservation* (ed. C.H. Freese), pp. 359–392. John Hopkins University Press, Baltimore.

Estes, R.D. (1991) *The Behavior Guide to African Mammals*. University of California, Berkeley.

FitzGibbon, C.D., Mogaka, H. & Fanshawe, J.H. (1995) Subsistence hunting in Arabuko-Sokoke Forest, Kenya and its effects on mammal populations. *Conservation Biology*, **9**, 1116–1126.

Greene, C., Umbanhowar, J., Mangel, M. & Caro, T. (1998) Animal breeding systems, hunter selectivity, and consumptive use in wildlife conservation. *Behavioral Ecology and Conservation Biology* (ed. T. Caro), pp. 271–305. Oxford University Press, New York.

Hanna, S., Folke, C. & Maler, K.-G. (1996) Property rights and the natural environment. *Rights to Nature: Ecological, Economic, Cultural, and Political Principles of Institutions for the Environment*. (eds S.S. Hanna, C. Folke & K.-G. Maler), pp. 1–10. Island Press, Washington, DC.

Hofer, H., Campbell, K.L.I., East, M.L. & Huish, S.A. (1996) The impact of game meat hunting on target and non-target species in the Serengeti. *The Exploitation of Mammal Populations* (eds V.J. Taylor & N. Dunstone), pp. 117–146. Chapman & Hall, London.

International Institute for Environment and Development. (1994) *Whose Eden? An Overview of Community Approaches to Wildlife Management*. Overseas Development Administration, UK.

Jachmann, H. & Billouw, M. (1997) Elephant poaching and law enforcement in the central Luangwa Valley, Zambia. *Journal of Applied Ecology*, **34**, 233–244.

Jolly, G.M. (1969) Sampling methods for aerial census of wildlife populations. *East African Agriculture and Forestry Journal*, **34**, 46–49.

Kikula, I.S. (1980) Landsat satellite data for vegetation mapping in Tanzania: the case of the Rukwa region. Bureau of Resource Assessment and Land Use Planning, *Research Report No*. 41, University of Dar es Salaam.

Kiss, *A*. (1990) *Living with Wildlife: Wildlife Resource Management with Local Participation in Africa*. World Bank, Washington DC.

Kock, M.D. (1996) Zimbabwe: a model for the sustainable use of wildlife and the development of innovative wildlife management practices. *The Exploitation of Mammal Populations* (eds V.J. Taylor & N. Dunstone), pp. 229–249. Chapman & Hall, London.

Kremen, C., Merelender, A.M. & Murphy, D.D. (1994) Ecological monitoring: a vital need for integrated conservation and development programs in the tropics. *Conservation Biology*, **8**, 388–397.

Krishke, H., Lyamuya, V. & Ndunguru, I.F. (1996) The development of community-based conservation around Selous Game Reserve. *Community-Based Conservation in Tanzania* (eds N. Leader-Williams, J.A. Kayera & G.L. Overton), pp. 75–83. IUCN, Gland, Switzerland.

Leader-Williams, N., Albon, S.D. & Berry, P.S.M. (1990) Illegal exploitation of black rhinoceros and elephant populations: patterns of decline, law enforcement and patrol effort in Luangwa Valley. Zambia. *Journal of Applied Ecology*, **27**, 1055–1087.

Leader-Williams, N., Kayera, J.A. & Overton, G.L. (eds) (1996) *Community-Based Conservation in Tanzania*. IUCN, Gland, Switzerland.

Lewis, D.M. (1993) The Zambian way to Africanize conservation. *Voices from Africa: Local Perspectives on Con-*

servation (eds D. Lewis & N. Carter), pp. 79–98. World Wildlife Fund, Washington DC.

Lewis, D.M., Kaweche, G.B. & Mwenya, A.N. (1990) Conservation outside protected areas: lessons from an experiment in Zambia. *Conservation Biology*, **4**, 171–180.

Lindsay, W.K. (1987) Integrating parks and pastoralists: some lessons from Amboseli. *Conservation in Africa: People, Policies and Practice* (eds D. Anderson & R. Grove), pp. 149–167. Cambridge University Press, Cambridge.

Little, P.D. (1994) The link between local participation and improved conservation: a review of issues and experiences. *Natural Connections: Perspectives in Community-Based Conservation* (eds D. Western & R.M. Wright), pp. 347–372. Island Press, Washington DC.

Marks, S.A. (1996) Local hunters and wildlife surveys: an assessment and comparison of counts for 1989, 1990 and 1993. *African Journal of Ecology*, **34**, 237–257.

Mduma, S. (1995) Distribution and abundance of oribi, a small antelope. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (eds A.R.E. Sinclair & P. Arcese), pp. 220–230. University of Chicago Press, Chicago.

Metcalfe, S. (1994) The Zimbabwe communal areas management programme for indigenous resources (CAMPFIRE). *Natural Connections: Perspectives in Community-Based Conservation*. (eds D. Western & R.M. Wright), pp. 161–192. Island Press, Washington DC.

Moffett, J.P. (1958) *Handbook of Tanganyika*, 2nd edn. Government of Tanganyika, Dar es Salaam.

Norton-Griffiths, M. (1978) *Counting Animals*. Handbook No 1, Techniques in African Wildlife Ecology. African Wildlife Foundation, Nairobi.

Noss, A.J. (1998) The impacts of cable snare hunting on wildlife populations in the forests of the Central African Republic. *Conservation Biology*, **12**, 390–398.

Pratt, D.J., Greenway, P.J. & Gwynne, M.D. (1966) A classification of the East African rangeland. *Journal of Applied Ecology*, **3**, 369–382.

Redford, K.H. (1992) The empty forest. *Bioscience*, **42**, 412–422.

Robin Hurt Safaris (1996) *The Cullmann Wildlife Project. Community-Based Conservation in Tanzania* (eds N. Leader-Williams, J.A. Kayera & G.L. Overton), pp. 97–100. IUCN, Gland, Switzerland.

Rodgers, W.A. (1996) The miombo woodlands. *East African Ecosystems and Their Conservation* (eds T.R. McClanahan & T.P. Young), pp. 299–325. Oxford University Press, New York.

Schaller, G.B. (1972) *The Serengeti Lion: A Study in Predator–Prey Relations*. University of Chicago Press, Chicago.

Serengeti Ecological Monitoring Programme (1989) Katavi-Rukwa reconnaissance survey, December 1988.

Sinclair, A.R.E. & Arcese. P. (1995) *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*. University of Chicago Press, Chicago.

Stuart, S.N. & Adams, R.J. (1990) *Biodiversity in sub-saharan Africa and its islands: conservation, management, and sustainable use*. IUCN Species Survival Commission. No 6.

Tanzania Wildlife Conservation Monitoring (1992) Wildlife census Katavi-Rukwa, November 1991.

Tanzania Wildlife Conservation Monitoring (1994) Aerial survey Marang Forest Reserve, February 1994.

Verlinden, A. (1997) Human settlements and wildlife distribution in the southern Kalahari of Botswana. *Biological Conservation*, **82**, 129–136.

Western, D. (1994) Ecosystem conservation and rural development: the case of Amboseli. *Natural Connections: Perspectives in Community-Based Conservation* (eds D. Western & R.M. Wright), pp. 15–52. Island Press, Washington DC.

Wilkie, D.S., Curran, B., Tshombe, R. & Morelli, G.A. (1998) Modelling the sustainability of subsistence farming and hunting in the Ituri Forest of Zaire. *Conservation Biology*, **12,** 137–147.

World Resources Institute/United Nations Environment Programme/United Nations Development Programme/The World Bank (1996) *World Resources 1996–97*. Oxford University Press, New York.

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