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The spatial correlates of wildlife distribution around Garamba National Park, Democratic Republic of Congo

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Abstract. This study explores the relationship between human activity and the distribution of wildlife populations in north-eastern Congo. It is hypothesized that the presence of agricultural communities, proximity to urban markets and conservation practices affect three characteristics of wildlife distribution: the presence (range), abundance and community structure of large mammal populations. The area studied was extensive and required the use of wildlife sampling and remote sensing techniques to generate data on wildlife distribution and the explanatory factors. The results show that wildlife protection is associated with high animal abundance. However, the presence of agricultural populations is not associated with low animal abundance.

1. Introduction

There are two dominant paradigms in African wildlife conservation. One restricts the use of wildlife. This approach is centrally controlled and usually involves the application of wildlife regulations through law enforcement in protected areas. The other approach is driven by economic considerations associated with human subsistence and commercial demands. Much debate has questioned the utility of protected areas, and an array of ecological, ethical and economic criteria have been used to justify these arguments (International Institute for Environment and Development (IIED) 1993, Western *et al.* 1994, Pimbert and Pretty 1995, Gartland 1997). An important and unresolved issue is the level of impact that human activity has on wildlife populations. This research contributes to this debate by examining the influence that differing types of human activity have on wildlife distribution, abundance and community structure.

At Garamba National Park, wildlife managers consider human populations to be a major threat to conservation. The rationale for this assertion is that there are significantly higher mammal densities in the National Park, where human activity is restricted, than in the surrounding reserves where there are resident human communities. This is supported by aerial wildlife census data (table 1). As a

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Table 1. *T*-tests to show the differences between selected large mammal densities in the Park and in the hunting reserves (from Hillman-Smith *et al.* 1995).

Species[a]	Park density	Reserves density	t	P
Elephant	1.92	0.07	3.39	< 0.01
Buffalo	4.57	0.05	87.69	< 0.001
Giraffe	0.03	0.005	1.49	NS (< 0.07)
Kob	0.44	0.09	2.02	< 0.05

[a] Aerial count data in the reserves are subject to an undercount bias because of the high canopy cover. Thus, only data for large mammals with a high detection rate are displayed in this table.

consequence, an active law enforcement programme has been in operation in the National Park for several decades.

However, correlation does not necessarily imply causation, and it is not clear how much of the difference in animal abundance can be attributed to the impact of resident communities. First, numerous studies have shown that rural African communities are complex, as are their interactions with their natural resources (Burnham 1993). For instance, natural resource use studies have shown that non-resident or migrant populations can have a greater negative impact on the sustainability of natural resources than local communities (Abbot 1996). Second, the mammal community within an ecosystem consists of a large number of species with differing physiological and life history traits. Consequently, they respond differently to human and environmental factors. For example, mammal species are not equally susceptible to hunting pressure. In general, only populations of species with low intrinsic rates of growth will diminish when hunted, because they require more time to recover (Freese *et al.* 1982). This is compounded by the hunters' preference for larger species because they provide higher returns for the cost of hunting (Leader-Williams *et al.* 1990). Third, habitat factors may provide a better explanation for low animal abundance than human presence. For example, Hillman-Smith *et al.* (1995) have shown at Garamba that there is a statistically significant negative relationship between elephant abundance and tree cover when aerial count data are analysed for the whole ecosystem. However, habitat differences can partly be explained by high elephant densities in areas that are protected because elephants are known to be important agents of habitat change (Dublin 1995). Thus, the factors that contribute to high animal abundance are complex, but need to be understood so that management strategies for the ecosystem can be improved.

At a broad scale, habitats are relatively homogenous in the hunting reserves, whereas human populations are unevenly distributed, as are the centres of commercial activity where bushmeat is traded. The approach used in this research was therefore to compare the presence, abundance and community structure of wild mammals against measures that represent the level of law enforcement, human presence and commercial activity at 42 different locations within the hunting reserves. The analyses thus explore and test the effect of human-related variables on the distribution of the whole mammal assemblage under relatively homogenous habitat conditions.

A major challenge was to develop sufficiently rigorous demographic data in the absence of precise and timely population census data. Whilst extensive wildlife survey data have been collected by the National Park's research and monitoring programme, socio-economic research in the region has been hampered by logistical difficulties and political conflict in the southern Sudan and Congo (formerly Zaïre). The remote sensing techniques described below provide a viable alternative to traditional demographic surveys that are required to improve our understanding of human–wildlife interactions.

2. Study area: the Garamba ecosystem

Garamba National Park is a UNESCO World Heritage Site of area 4900 km^2 and is surrounded by three hunting reserves. This protected area complex is situated in the north east of the Democratic Republic of Congo, and borders Sudan on the Congo–Nile watershed. Its conservation importance is attributed largely to the last known wild population of the northern white rhinos (*Ceratotherium simum cottoni*). It also contains a unique assemblage of large mammals, including one of the highest densities of elephants (*Loxodonta africana*) in Congo and an endemic subspecies of giraffes (*Giraffa camelopardalis congoensis*). The protected area falls within the Sudano–Guinean savanna zone. Within the National Park the vegetation has been secondarily modified by a combination of fire and high densities of large mammals, notably elephants, to create a long grass savanna. This contrasts with a mosaic of deciduously wooded and bushed savanna, grassland and forest in the surrounding reserves. The legal status of the National Park is of integral protection, maintained by the national wildlife agency, the Institut Congolais pour la Conservation de la Nature (ICCN), and has been supported by an international aid project since 1984.

The hunting reserves were established in 1938 (at the same time as the National Park) to promote the sustainable use of wildlife resources by resident communities. These communities are highly heterogeneous and include Azande Logo and Mondo subsistence agriculturalists together with approximately 90 000 Sudanese refugees. A gold mining community has also settled in the area.

3. Methods

The following section describes the animal distribution data and the variables used to explain the distribution.

3.1. *Animal distribution*

Patterns of wildlife abundance in the hunting reserves were examined by analysing the unpublished raw transect data collected by Nicholas and Ndey (1995) between February and May 1994 (Hillman-Smith *et al.* 1995). Counting animals in the hunting reserves presents a number of difficulties. The geographical extent of the Garamba ecosystem precludes a total wildlife count. Furthermore, counting animal numbers is unreliable in a densely vegetated environment. Thus, sampling techniques were used to reduce the survey effort and counts were made of spoor, which is more easily detected. These are standard techniques and have been used previously by White (1992) and Prins and Reitsma (1989).

Line transect methods were used to estimate mammal presence based on the methods used by Burnham *et al.* (1980). Using a stratified random sampling scheme, 42 transects, each of five kilometres in length, were covered. Data were collected by three observers walking abreast along the transect line. Each observer recorded observations within a 2 m strip width either side of his centre line, to produce an overall sampling width of 12 m. Distances along the transect line were also measured.

Two types of observations were used: wildlife tracks and faecal material. This approach produced abundance data across the transects for 31 mammal species.

3.2. *Explanatory variables*

3.2.1. *The presence of agricultural communities*

A human population census across the reserves is a prohibitively time consuming exercise and census data are unavailable for this region. However, the population density of agriculturalists can be related to the proportion of land that is covered by agricultural fields. The processing of satellite data provides a means of obtaining an estimate of field cover in the areas around the transects.

Normalized Difference Vegetation Index (NDVI) data were generated from three geo-corrected scenes of Landsat Thematic Mapper (TM) data as a means of detecting agricultural land as an indicator of human presence (Mather 1987). Analysis of NDVI images allows the detection of agricultural land cover when assessed for areas that were well known to the author (see §4 for an assessment).

All three scenes were acquired in December, which coincides with the post-harvest period when there is likely to be a higher proportion of exposed soil on agricultural land (de Schlippé 1953). Thus, low index values were produced for agricultural land relative to the surrounding vegetation. A Geographic Information System (GIS) was used to select areas within five kilometres of the transects. The average NDVI value within these areas was used as an index of field cover.

Figure 1 shows one of the NDVI scenes representing a land surface of 200 km × 180 km containing most of the Garamba ecosystem. The histogram below this scene shows that the data are bimodal. The darker areas on the image, corresponding to low NDVI values, appear to represent three types of land features: open water (major rivers); burned savanna vegetation cover; and areas clustered around settlements. Low NDVI values around settlements are hypothesized to correspond to exposed agricultural soil following the early dry season harvest.

3.2.2. *The effects of urban markets*

Distances between each of the transects and the main markets in and around the reserves (figure 2 (*b*)) were used as an indicator of the influence of markets on the local wildlife population. Markets are defined as large commercial centres estimated to have resident populations of more than 4000.

3.2.3. *The effects of conservation practices*

Wildlife protection in the Garamba ecosystem is concentrated within areas adjacent to the National Park. Therefore, the analysis tests whether distance from the National Park, where intensive law enforcement has taken place for over twelve years, affects variability in wildlife distribution in the reserves (figure 2 (*c*)).

3.2.4. *Habitats*

Tree cover estimates in 1993 were used to distinguish between the main habitat categories (grassland savanna, bush savanna and forest). Percentage tree cover was estimated during the aerial count for 5 km × 5 km subunits surrounding the flight lines (figure 2 (*d*)) (Norton-Griffiths 1978, Hillman-Smith *et al.* 1995).

4. **Appraisal of the methods used**

The validity of the data used in these analyses can be evaluated according to the following three criteria.

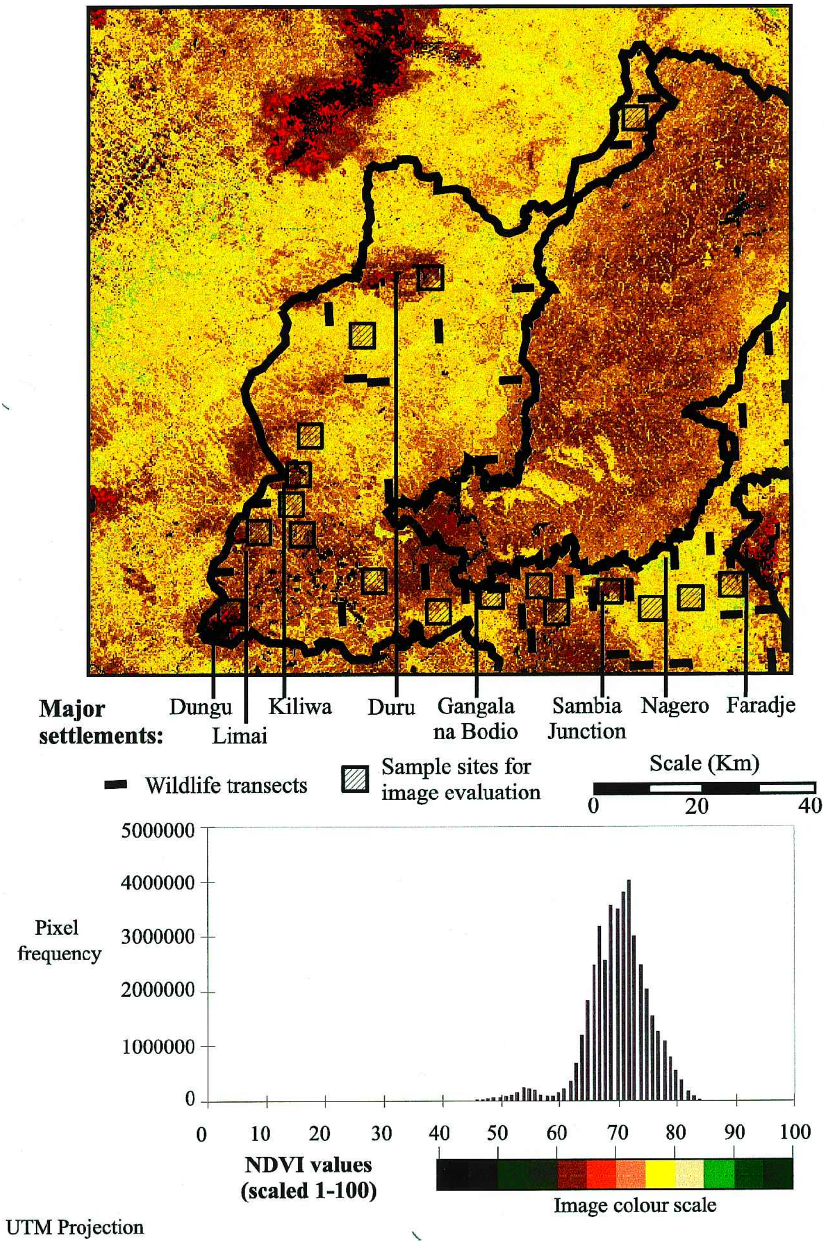

Figure 1. Upper figure: NDVI image covering a proportion of the Garamba ecosystem showing the sample sites used to test the relationship between low index values and human presence. Lower figure: frequency histogram for NDVI pixel values for the entire image.

1. Are the variables meaningful in biological and/or socio-economic terms?
2. Are the factors being accurately represented by the measures used?
3. Are any of the variables confounded by other variables?

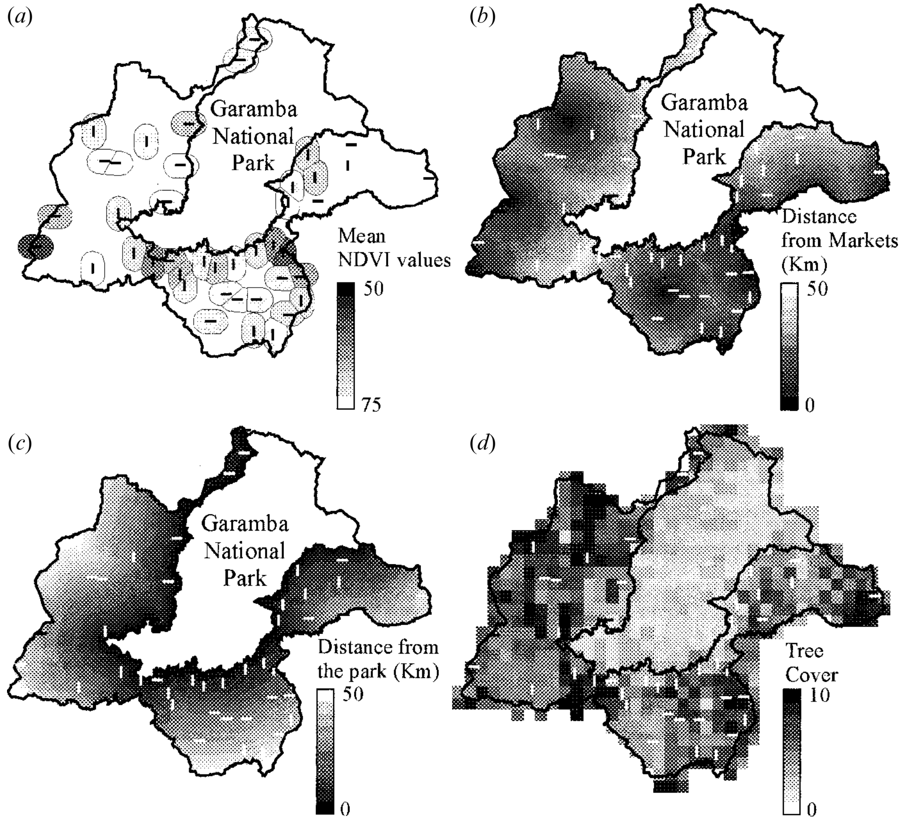

Figure 2. Explanatory variables used to explain mammal distribution, abundance and community structure on 42 5 km wildlife transects (shown on the map as black or white rectangles).

4.1. *Dependent variables*

Inferring animal density measures from faecal counts can produce spurious results. The problems involved in calculating population densities from faecal material and spoor have been extensively documented (e.g. Barnes *et al.* 1995, Plumptre and Harris 1995). Underestimation is caused by the low detection rates due to the dense understorey vegetation cover. Barnes *et al.* also stress the extent to which detection is affected by species-specific parameters such as faecal size and decomposition rates, together with site-specific variables such as rainfall and canopy cover. Furthermore, obtaining an acceptable density estimate for a particular species requires a minimum of 40 faecal observations on a transect (Morrison *et al.* 1992). This is relatively rare for any of the species in the dataset. These difficulties explain why there appear to be only two examples in the literature where precise population densities for a large assemblage of African tropical moist forest mammals have been calculated using indirect observations (Prins and Reitsma 1989, White 1992).

4.2. *Explanatory variables*

4.2.1. *The presence of agricultural communities*

A number of questions are raised in an assessment of the presence of agricultural communities. First, does variation in agricultural land cover correlate with agricultural population density? In this research the variance of total field size per household was found to be small for a sample of 121 households surveyed. The mean landholding per household was determined to be 0.83 ha ± 0.12 ha (95% confidence intervals, $n = 121$). Therefore, the percentage field cover is likely to be closely correlated to agricultural population density.

A second question relates to the validity of using NDVI as a measure of field cover. To test this, eighteen sample sites of 5 km × 5 km were selected. Nine of these corresponded to areas known to contain relatively high human population densities. The other nine were of unsettled areas. All of these sites had been visited by the author at least once between 1993 and 1996. Mean pixel values were calculated for these sites. The results are shown in table 2. Settled areas have significantly lower NDVI values, which validates the use of NDVI as a measure of field cover.

4.2.2. *Distance as an indicator of market and conservation influences*

Local species abundance is compared with the intensity of conservation and market activity using distance from the Park and from markets as indices of the intensity of those factors. Clearly these parameters do not constitute a perfect quantitative representation of these factors, however, they do provide the best available measure of the effect of these factors at the transect location.

4.2.3. *Tree cover*

Tree cover values were based on an observer's estimate of the percentage tree canopy cover for an area corresponding to approximately 5 km × 5 km. Observations were made from a light aircraft at an altitude of approximately 300 feet. The problems associated with aerial measurements are well documented (Inamdar 1996), however, the data obtained here were sufficiently precise to allow a distinction to be made between the primary habitat categories, namely forest, grassland savanna and woodland savanna.

4.2.4. *Confounding explanatory variables*

Table 3 cross tabulates correlations between all of the explanatory variables. The only variables found to be significantly correlated are tree cover and estimated number of fields. None of the human-related explanatory variables are correlated and thus their effects are unlikely to be confounded.

Table 2. The difference in mean NDVI pixel values for settled and unsettled sites.

Mean NDVI value	Standard error	Mean difference	*DF*	*t*	*P*
62.03 (Settled)	1.32	8.43	16	4.35	< 0.001
70.47 (Unsettled)	1.42				

Table 3. Spearman rank correlations to test for confounding explanatory variables amongst those used to explain species distributions.

	Distance from the Park	Field cover	Distance from markets
Field cover	0.156 $p = 0.351$		
Distance from markets	0.261 $p = 0.113$	− 0.056 $p = 0.74$	
Estimated tree cover	− 0.156 $p = 0.351$	0.372 $p = 0.02$	0.161 $p = 0.334$

5. Analysis and results

The relationship between species presence and the explanatory variables was examined using measures of association. Mammal community structure was analysed in relation to the explanatory variables using richness indices and according to the physiological, behavioural, habitat and life history traits of the species assemblage.

5.1. *Species presence*

Jaccard's Index (JI) of association is used to examine the relationship between the presence of two species, or one species and one binary explanatory variable (Ludwig and Reynolds 1988):

$$JI = \frac{a}{a+b+c} \tag{1}$$

where a is the number of transects where both species A and B occur; b is the number of transects where species A occurs but not species B; c is the number where species B occurs but not species A. The technique requires a more or less equal number of transects for each of the two outcomes, that is, where the animal is present or absent. As a result, only a sub-sample of species surveyed could be used in this analysis. The rarer species, such as chimpanzees and bongos, which are absent in most transects, and the very common species, such as duikers, which are present in most transects, were removed from the analysis. The explanatory variables were converted to binary format by classifying variables into high or low values. Table 4 shows the classification used. Analytical requirements determined the partitioning of data (each category, high or low, had to be represented by a more or less equal number of transects). In this technique species are plotted on two axes using polar ordination (Kent and Coker 1992), and the resulting biplot displays the species and explanatory variables in terms of association distance. The significance of the relationships described on the biplot is assessed using Pearson's chi-squared independence tests.

Figure 3 shows the polar ordination biplot using Jaccard's Index of association. The biplot shows that buffalo, kob and elephants are typically close to the Park, whereas baboons, porcupines and warthogs occupy areas further from the Park.

The results of the chi-squared analysis are shown in table 5. There is a danger of obtaining spuriously significant results when tests are repeated several times (in this case four times for each species). However, the statistical significance of the association between the Park and elephants and kob is unlikely to be the result of a type one error because the significance is extremely high ($p < 0.001$).

5.2. *Species richness*

Richness indices provide a single measure to represent the importance of the transects in terms of the number of species present (Ludwig and Reynolds 1988).

Table 4. Conversion of explanatory variables to binary format.

Variable	High	Low
Proximity to the Park	0 to 10 km	more than 10 km
Estimated agricultural land cover	NDVI < 66.25	NDVI > 66.25
Proximity to markets	0 to 8 km	more than 8 km
Estimated tree cover	0 to 60%	more than 60%

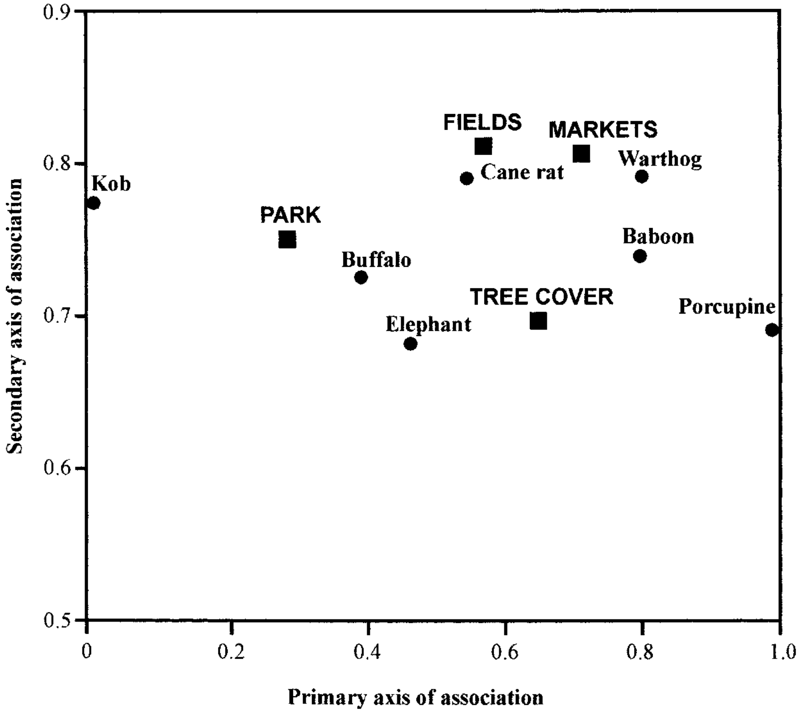

Figure 3. Polar ordination biplot using Jaccard's Index of association on five species and four explanatory variables.

Table 5. Pearson's chi-squared test for the independence between selected species and explanatory variables ($n = 38$, df $= 2$).

	Park distance		Agricultural land*		Market distance		Tree cover	
Species	x^2	p	x^2	p	x^2	p	x^2	p
Black and white colobus	0.93	NS	0.03	NS	0.93	NS	3.02	NS
Serval cat	1.22	NS	1.99	NS	3.77	NS	0.07	NS
Porcupine	0.84	NS	1.38	NS	0.23	NS	0.05	NS
Kob	13.07	< 0.001	5.14	< 0.05	2.54	NS	0.18	NS
African elephant	15.2	< 0.001	0.42	NS	0.42	NS	0.42	NS
Olive baboon	3.14	NS	0.18	NS	1.2	NS	0.06	NS
Warthog	5.98	< 0.05	1.2	NS	0.06	NS	0.18	NS
Buffalo	3.52	NS	0.84	NS	0.84	NS	6.63	< 0.01
Cane rat	0.91	NS	2.59	NS	2.59	NS	0.1	NS

Emmons' study (1984) of the geographical variation of mammal densities in Amazonia showed that, 'the observed pattern of variation in numbers of individuals is mirrored by species richness differences'. Thus, species richness provides a simple but effective measure to analyse the effect of the explanatory variables on species distribution.

The results of the regression models are shown in table 6. The effect of the

Table 6. Linear regression coefficients and significance for the relationship between species richness and the explanatory variables.

Explanatory variable	Slope, B	R^2	p
Field cover	− 0.03	0.04	0.19
Distance from markets	0.03	0.019	0.41
Distance from the Park	− 0.11	0.38	< 0.0001

distance from the Park significantly explains variation in species richness. This confirms the importance of the Park as a major determinant of wildlife distribution.

5.3. *Species abundance and community structure*

Species presence alone does not provide the detail required to understand animal distribution. Typically, a species will respond to an explanatory variable that influences its distribution in the following way (ter Braak and Looman 1995). Species densities will peak at an optimal level of a particular explanatory variable. Above and below, on the scale of the explanatory variable, the species performance is inferior and therefore densities are lower. At a certain point either side of the optimum, a threshold is reached beyond which the species cannot survive. This pattern produces a Gaussian curve referred to as a unimodal response curve. Analysis of animal distribution and abundance must take account of the extent to which human-related environmental factors provoke this unimodal response curve in the distribution of large mammal species. Faecal counts are used as a relative index of animal abundance as part of an exploratory analysis to examine patterns of spatial variation in the abundance of mammal populations.

Testing the effects of various explanatory variables on the abundance of a large species assemblage is complex because of the number of dependent variables (species) that make up the dataset. Ordination provides a useful means of exploring the patterns of variance in the distribution of the 31 species (Kent and Coker 1992, ter Braak 1995). A benefit of ordination is that the data retain a high level of detail because all the species, as well as the frequency of observations at each of the transects, are analysed. Furthermore, species can be grouped and analysed according to physiological, behavioural, habitat and life history characteristics.

Principal Components Analysis (PCA) is an ordination procedure used when the underlying species abundance patterns are linear. PCA arranges the species along a series of axes according to variation in the abundance of those species between the transects. Furthermore, it will arrange the transects along axes according to how they vary in their species composition. Thus, PCA provides an effective method for analysing mammal community structure. The first axis, or component, uses a least-squares algorithm to minimize the residual sum of squares of the distribution of all species. 'Eigenvalues' represent the relative contribution of the axis to the overall distribution of species. The advantage of using PCA is that the first few components are expected to reflect non-random variation in the overall distribution of the species assemblage. As such, they represent a 'latent structure' in the data. Thus, explanatory variables that are strongly correlated with these 'principal components' of variation in the data have a strong influence on species distribution.

The first two components of the PCA yielded eigenvalues of 0.657 and 0.145 respectively. This means that the first two components explain more than 80% of the variance in the species abundance. The relationship between the transect values on the first two axes and the explanatory variables is shown in table 7.

Transect values for the first component are significantly correlated with distance from Park. This suggests that most of the variance (65.7%) in species abundance across the transects is largely explained by the distance from the National Park (table 7). None of the other explanatory variables correlate with the first principal component. There are no statistically significant relationships between the second principal component and any of the explanatory variables, although distance from the main markets approaches significance (table 7).

These results assess the effects of the explanatory variables on the whole species assemblage. All species do not, however, conform to the same patterns of distribution. In order to examine the effects of a species' biological and behavioural attributes, a number of characteristics, including body size, home range size, type of social organization, diet, preferred habitat and activity time, were obtained for each species from a review of the literature (see table 8). Species were also characterized according to the way that they are exploited locally. The dominant hunting techniques in the reserves include the use of firearms (automatic weapons and locally constructed shotguns, known as fabrications) and traditional techniques using nets (including the use of dogs and spears) and various traps and snares. The hunting techniques associated with each species (see table 8) were derived from tracking 59 hunts. Both successful and unsuccessful stalks were used to associate a hunting technique with a particular species. In addition, semi-structured interviews with hunters were used to identify the principal hunting technique for that species. If this failed to produce an association, the species was considered unexploited.

Figure 4 shows how species are distributed on the first two component axes when they are grouped according to various characteristics. The first principal component was highly correlated with distance from the Park (table 7). Species groups with values that deviate significantly from zero indicate groups that contribute substantially to the variation contained in the principal component. 95% confidence intervals for the mean values for species scores are also shown to distinguish those groups that have significantly different scores to the rest of the species. Thus, the species that are more strongly influenced by the first component include species that are hunted using firearms, have large home ranges, use savanna habitats, are large bodied, diurnal, cover dependent and are browsers or folivores. Species that are strongly influenced by the second component include traditionally hunted species, species that have small home ranges, are non-cover dependent and are browsers or folivores.

Table 7. Matrix for Spearman's rank correlation coefficients between the transect scores on the first two principal components and explanatory variables.

	PCA first axis	PCA second axis
Distance from the Park	− 0.477 ($n=42$, $p=0.001$)	− 0.11 ($n=42$, $p=$ NS)
Estimated per cent field cover	0.262 ($n=38$, $p=$ NS)	− 0.253 ($n=38$, $p=$ NS)
Distance from main markets	− 0.032 ($n=42$, $p=$ NS)	0.278 ($n=42$, $p=$ NS, 0.075)
Estimated tree cover	− 0.108 ($n=42$, $p=$ NS)	0.029 ($n=42$, $p=$ NS)

Table 8. The ecology, hunting and social and reproductive organization of large mammal species encountered in the reserves.

Name	English name	H	S	R	O	Di	Ha	C	A	References
Artiodactyla										
Redunca redunca	Bohor reedbuck	n	45	2	M	G	fl	Y	n	Estes 1992
Tragelaphus euryceros	Bongo	Sh	270	3	a1	B	gf	N	n	Kingdon 1982, Hillman 1986
Alcelaphus buselaphus	Hartebeest	r	134	3	a2	G	g	N	d	Gosling 1974, Estes 1992
*Syncerus caffer**	Buffalo	r	631	4	a2	G	g	N	d	Sinclair 1977, Mlosweski 1983
Tragelaphus scriptus	Bushbuck	s	72	2	s	B	fe	Y	b	Allsop 1971, Waser 1974, 1975
Cephalophus spp.*	Duiker	n	22	2	m	F	gf	Y	b	Dubost 1983, Estes 1992, Kingdon 1982
Hylochoerus meinertzhageni	Giant forest hog	Sh	205	—	f	B	gf	N	n	Kingdon 1982
Giraffa camelopardalis	Giraffe	r	900	4	a1	B	ws	N	b	Pellew 1984a, b, Leuthold and Leuthold 1972, 1978
Hippopotamus amphibius	Hippopotamus	r	1900	3	a2	G	sp	N	n	Laws 1984, Olivier and Laurie 1974
Potamochoerus porcus	Bushpig	Sh	70	2	f	O	of	Y	n	Skinner *et al.* 1976, Estes 1992
*Kobus kob**	Kob	Sh	78	2	a2	G	g	N	b	Kingdon 1982, Leuthold 1966
*Phacochoerus aethiopicus**	Warthog	Sh	74	3	f	Mf	s	N	d	Cumming 1973
Kobus ellipsiprymnus	Waterbuck	r	205	2	a1	G	sp	N	b	Spinage 1982, Hanks *et al.* 1969
Proboscidea										
*Loxodonta africana**	Elephant	r	4000	5	a2	Mf	m	N	b	Laws 1970, Hillman-Smith *et al.* (1995), Moss and Poole (1983)
Tubulidentala										
Orycteropus afer	Aardvark	s	—	2	s	I	m	Y	n	Kingdon 1980
Rodentia										
Poelagus marjorita	Rabbit	s	2	1	a2	H	s	Y	n	Kingdon 1980
Thryonomys spp.*	Cane Rat	s	1	1	s	O	m	Y	n	Kingdon 1980
Hystrix spp.	Porcupine	s	3	1	m	Mf	s	Y	n	Kingdon 1980
Primates										
*Papio cynocephalus**	Baboon	Sh	17	4	a2	O	s	N	d	Altmann 1980, Altmann and Altmann 1970
Pan troglodytes	Chimpanzee	Sh	35	3	a2	O	gf	Y	d	Goodall 1983, Suzuki 1969
*Colobus abyssinicus**	Colobus	Sh	10	2	p	Fo	gf	Y	d	Mckey 1978, Dunbar and Dunbar 1976, Rose 1978
Cercopithecus mona	Mona	Sh	6	3	p	Fo	gf	Y	d	Estes 1992
Erythrocebus patas	Patas	Sh	8	3	p	Fo	ws	N	d	Hall *et al.* 1965

Table 8. (*Continued*).

Name	English name	H	S	R	O	Di	Ha	C	A	References
Cercopithecus aethiops	Vervet	Sh	5	m	a2	O	ws	N	d	Hall and Gartlan 1965, Cheney and Seyfarth 1986
Carnivora										
*Civettictis civetta**	Civet	s	14	3	s	O	gf	N	n	Ewer and Wemmer 1974
Genetta felina	Genet	Sh	2	3	s	C	ws	N	n	Wemmer 1977
Panthera pardus	Leopard	x	47	4	s	C	ws		b	Bertram 1976
Panthera leo	Lion	x	157	5	a1	C	s	n	b	Schaller 1972, Packer and Pusey 1982
Atilax paludinosus	Mongoose	n	3	2	s	C	sp	y	n	Kingdon 1977, Estes 1992
Felis serval	Serval	Sh	12	3	S	C	s	n	d	Geertsema 1976, Estes 1992
Crocuta crocuta	Hyena	x	65	4	a2	C	s	n	b	Frank 1986, Kruuk 1972

Key: H Associated hunting techniques: sh = shotgun; r = automatic rifle; n = nets; s = snares and traps; x = not hunted.

S Species size (in kg).

R Home range: 1 = < 0.01 km^2; 2 = 0.01–1 km^2; 3 = 1–25 km^2; 4 = 25–100 km^2; 5 = > 100 km^2; m = migratory/not territorial.

O Organization: s = solitary; m = monogamous pairs; f = family unit; p = polygamous groups; a = aggregated (1 = 3–10, 2 = 10).

Di Diet: g = grazers; b = browsers; mf = mixed feeders; f = frugivores; o = omnivorous; fo = folivores.

Ha Preferred habitat: m = mixed habitats; fl = floodplains; s = wooded and grassland savanna; g = open grassland; ws = woody savanna; sp = specialized (in/near water); gf = gallery forest; fe = forest edge.

C Cover dependent: y = yes; n = no.

A Time of activity: d = diurnal; n = nocturnal; b = both.

6. Discussion

A high level of consistency was noted between the analyses of presence and abundance. Of the three variables representing human activity, distance from the National Park appears to have the strongest influence on the distribution of wildlife. The chi-squared analysis showed that the presence of both elephants and kob was significantly associated with proximity to the National Park. Mammal species richness is also highly correlated with distance from the Park. Finally, the first principal component, which accounted for 65.7% of the variation of the abundance of all species across the transects, was highly correlated with distance from the Park.

The relationship between distance from markets and mammal distribution was non-significant. However the correlation between the second principal component, which accounts for 14.5% for the variation in the density of faecal counts, and the distance from markets approached statistical significance ($p = 0.075$). This suggests that markets may influence the distribution of hunting intensity. Furthermore, both the distribution of species on the second principal component axis (figure 4) and the polar ordination (figure 3) suggest that some of the smaller species, such as baboons, warthogs and porcupines, are negatively associated with proximity to markets. This has ecological repercussions for wildlife populations. A number of authors have

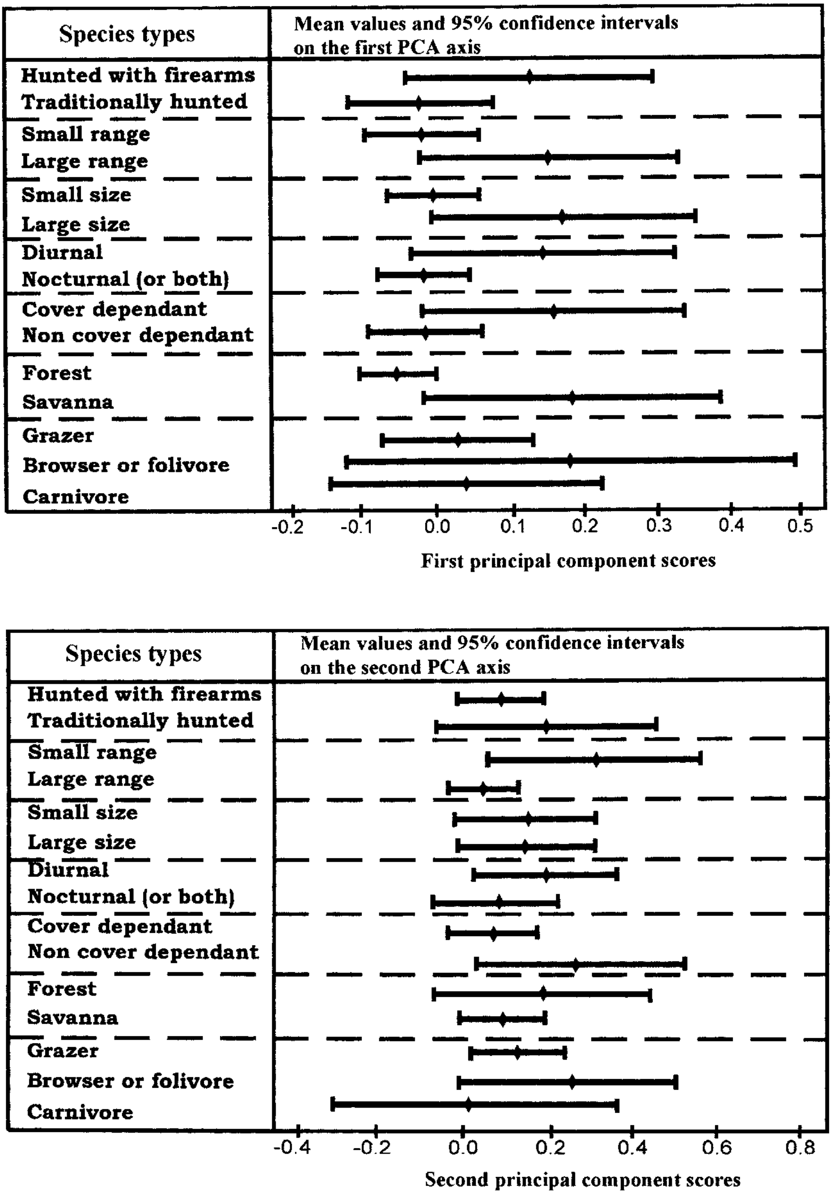

Figure 4. Means and their 95% confidence intervals for species categories on the first and second principal components.

shown that the monetary value of bushmeat varies spatially as a function of transport costs (Godoy *et al.* 1993). The urban profit margin makes it more beneficial to exploit non-timber forest products at closer proximity to markets (Abbot 1996). This suggests that wildlife population densities vary as a function of distance from urban markets and from principal transport networks leading to those markets.

Analysis of Landsat TM data showed that the presence of agricultural communities is not associated with a statistically significant decrease in the presence and abundance of mammals. Indeed, the presence of agricultural communities is associated with a non-significant increase in mammal species richness. Wilkie and Finn (1990) studied the relationship between human presence and the diversity and abundance of terrestrial mammals of the Ituri Forest in the Democratic Republic of Congo. They found that forest clearing associated with agricultural activity did not significantly affect 16 of the 19 mammal species examined. The other three species—okapi, yellow backed duikers and leopards—are less abundant in secondary forest. The larger ungulates appeared to be less abundant near villages, but Wilkie and Finn suggest that this could equally be due to increased hunting pressure near the markets. They conclude that secondary forest is probably able to support populations at similar or greater densities to climax forest, and refer to the findings of Eisenberg and Seidensticker (1976) to support their claims. Johns and Skorupa's (1987) review of the effects of habitat modification on primates shows that moderate habitat disturbance from agriculture is unlikely to provoke a decline in primate populations.

Distance from the National Park consistently explained animal distribution and abundance. However, it is difficult to disassociate the effects of habitat from those of wildlife protection because the two are spatially correlated. One plausible explanation is that high species richness around the National Park can be attributed to the unique habitat of the area, whilst the high abundance of large mammals can be attributed to the protection regime in the National Park. Indeed, the 31 large mammal species recorded in the reserves is an unusually high number for an African ecosystem, if compared to both forested habitats (Prins and Reitsma 1989, Wilkie and Finn 1990, White 1994) and savanna habitats (Leuthold and Leuthold 1976). An explanation for this may lie in the habitat structure of the ecosystem. The area closest to the National Park represents a forest savanna boundary, where both savanna and forest mammals coexist. This may explain the significantly higher species richness associated with proximity to the National Park: past inventories have recorded a total of 46 mammals in the reserves compared to 35 in the Park (Verschuren 1958, Hillman-Smith 1989).

The abundance of large savanna mammals at close proximity to the National Park is perhaps best explained by the protection regime within the Park. This corroborates an assessment (based on aerial counts) of animal distributions as a whole, which shows the greatest abundance of large mammals to be concentrated in the National Park (Hillman-Smith *et al.* 1995). A number of studies have shown that investment in anti-poaching measures contributes to the higher abundance of large targeted mammals (Leader-Williams and Albon 1988, Jachman and Billiouw 1997). The comparison between animal densities inside the Park, where investment in conservation is high, and in the reserves, where investment is low (table 1), supports this. Even giraffes, whose more suitable habitat is in the reserves, are more abundant in the Park. Similar patterns were revealed in this work when mammal community structures were examined in relation to the explanatory factors. PCA showed that mammals whose abundance varied the most with distance from the Park were typically large savanna species. This was also shown by the polar ordination (figure 3). Such species are also targeted by hunters, and their abundance is likely to be greatest in the National Park where off-take through poaching is restricted.

Whilst the exact causes of variation in mammal distribution and abundance are difficult to establish from these data, what has become clear from this research is that the low-density presence of subsistence agricultural populations does not have a significant impact on wildlife distribution within the reserves. This is an important finding if human communities are to be perceived as an integral part of a sustainable ecosystem.

7. Conclusion

Understanding the relationship between human and animal populations is fundamental to the development of effective conservation management strategies. The results of this study show that human presence, as indicated by agricultural field cover, does not appear to affect mammal distribution and abundance. The results contribute to an increasing body of evidence of substantial ecological data that suggest that, contrary to perceived wisdom, human presence alone does not provoke wildlife depletion.

Proximity to the National Park was taken as an indicator of the effects of conservation activities on wildlife distribution and abundance. This variable is highly correlated with animal presence and abundance, emphasizing the importance of the National Park for protecting large mammals. The exploratory analysis of mammal community structure suggests that the National Park boundary represents a niche overlap for forest and savanna type species. This would explain the greater species richness near the Park. The significantly greater large mammal abundance close to the Park would appear to result from the Park's quality as a 'sanctuary' for these species. Thus, wildlife protection appears to be critical to the conservation of wildlife at Garamba. However, there is no evidence to suggest that the presence of human populations is associated with a reduction in the abundance of large mammals.

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References

Abbot, J., 1996, Rural Subsistence and Protected Areas: Community Use of the Miombo Woodlands of Lake Malawi National Park. Ph.D. Thesis, University College London, UK.

Allsop, R., 1971, Seasonal breeding in bushbuck, *Tragelaphus scriptus. East African Wildlife Journal*, **9**, 146–49.

Altmann, J., 1980, *Baboon Mothers and Infants* (Cambridge, MA: Harvard University Press).

Altmann, S. A., and Altmann, J., 1970, *Baboon Ecology* (Chicago: University of Chicago Press).

Barnes, R. F. W., Blom, A., and Alers, M. P. T., 1995, A review of the status of forest elephants *Loxodonta africana* in central Africa. *Biological Conservation*, **71**, 125–132.

Bertram, B. C., 1979, Serengeti predators and their social systems. In *Serengeti, Dynamics of an Ecosystem*, edited by A. R. E. Sinclair and M. Norton Griffiths (Chicago: University of Chicago Press).

Burnham, P., 1993, The cultural context of rainforest conservation in Cameroon. *Proceedings of the Thirty-Sixth Annual Meeting of the African Studies Association, Boston.*

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

Cheney, D. L., and Seyfarth, R. M., 1986, The recognition of social alliances by vervet monkeys. *Animal Behaviour*, **34**, 1722–31.

Cumming, D. H. M., 1975, A field study of the ecology and behaviour of warthog. *Museum Memoir*, **7**, Salisbury, Rhodesia.

de Schlippè, P., 1953, *Ecocultures d'Afrique* Editions Terre et Vie, l'Harmattan, Nivelles, Belgique.

Dublin, H., 1995, Vegetation dynamics in the Serengeti-Mara Ecosystem: the role of elephants, fire, and other factors. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*, edited by A. R. E. Sinclair and P. Arcese (Chicago: University of Chicago Press).

Dubost, G., 1983, Le comportement du *Cephalophus monticola* Thunberg et *C. dorsalis* Gray, et la place des céphalophes au sein des ruminants, Part I. *Mammalia*, **47**, 281–310.

Dunbar, R. I. M., and Dunbar, E., 1976, Contrasts in social structure among black-and-white colobus monkey groups. *Animal Behaviour*, **24**, 84–92.

Eisenberg, J., and Seidensticker, 1976, Habitat, economy and society: some correlations and hypotheses for the neotropical primates. In *Primate Ecology and Human Origins*, edited by I. S. Bernstein and E. O. Smith (New York: Gartland STPM), pp. 215–262.

Emmons, L. H., 1984, Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica*, **16**, 210–222

Estes, R. D., 1992, *The Behaviour Guide to African Mammals* (University of California Press).

Ewer, R. F., and Wemmer, C., 1974, The behaviour in captivity of the African civet, *Civettictis civetta* (Schreber). *Z. Tierpsychol.*, **34**, 359–94.

Fienburg, S. E., 1979, *The Analysis of Cross-classified Categorical Data* (Cambridge, MA: Massachusetts Institute of Technology Press).

Frank, L. G., 1986, Social organisation of the spotted hyena (*Crocuta crocuta*), I: Demography. *Animal Behaviour*, **34**, 1510–27.

Freese, C. H., Heltne, P. G., Castro, N. R., and Whitesides, G., 1982, Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *International Journal of Primatology*, **3**, 53–90.

Gartland, S., 1997, Every man for himself and God against all: history, social science and the conservation of Nature. *Proceedings of the WWF Annual Conference 1997*.

Geertsema, A., 1976, Impressions and observations on serval behaviour in Tanzania, East Africa. *Mammalia*, **40**, 13–19.

Godoy, R., Lubowski, R., and Markandya, A., 1993, A method for the economic valuation of non-timber tropical forest products. *Economic Botany*, **47**, 220–233.

Goodall, J., 1983, Population dynamics in one population of free living chimpanzees in the Gombe National Park, Tanzania. *Primates*, **21**, 545–49.

Gosling, L. M., 1974, The social behaviour of Coke's hartebeest (*Alcelaphus buselaphus cokei*). In *The Behaviour of Ungulates and its Relation to Management,* IUCN Publication New Series No. 24, edited by V. Geist and F. R. Walthur (Morges, Switzerland: IUCN).

Hall, K. R. L., Boelkins, R. C., and Goswell, M. J., 1965, Behaviour of Patas, *Erythrocebus patas*, in captivity, with notes on the natural habitat. *Folia Primatol.*, **3**, 22–49.

Hall, K. R. L., and Gartlan, J. S., 1965, Ecology and behaviour of the vervet monkey, *Cercopithecus aethiops*, Lolui Island, Lake Victoria. *Proceedings of the Zoological Society of London*, **17**, 37–56.

Hanks, J., Stanley-Price, R. W., and Wrangham W., 1969, Some aspects of the ecology and behaviour of the defassa waterbuck (*Kobus defassa*) in Zambia. *Mammalia*, **33**, 473–97.

Hillman, J. C., 1986, Aspects of the biology of the bongo antelope, *Tragelaphus eurycerus* Ogilby 1837, in southwest Sudan. *Biological Conservation*, **38**, 255–72.

Hillman-Smith, A. K. K., 1989, *Ecosystem Resource Inventory*. Unpublished manuscript of the Garamba National Park Project.

Hillman-Smith, A. K. K., De Merode, E., Nicholas, A., Buls, B., and Ndey, A., 1995, Factors affecting elephant distribution at Garamba National Park and surrounding reserves, Zaïre, with a focus on elephant–human conflict. *Pachyderm*, **19**, 39–48.

Inamdar, A., 1996, The Ecological Consequences of Elephant Depletion. Ph.D. Thesis, University of Cambridge, UK.

International Institute for Environment and Development (IIED), 1993, *Whose Eden?* (London: IIED).

Jachman, H., and Billiouw, M., 1997, Elephant poaching and law enforcement in the central Luangwa Valley, Zambia. *Journal of Applied Ecology*, **34**, 233–244.

Johns, A. D., and Skorupa, J. P., 1987, Responses of rain-forest primates to habitat disturbance: a review. *International Journal of Primatology*, **8**, 157–191.

Kent, M., and Coker, P., 1992, *Vegetation Description and Analysis: A Practical Approach* (Chichester: Wiley).

Kingdon, J. S., 1977, *East African Mammals*, Volume 3a (carnivores) (New York: Academic).

Kingdon, J. S., 1980, *East African Mammals*, Volume 3b (large herbivores) (New York: Academic).

Kingdon, J. S., 1982, *East African Mammals*, Volumes 3c and 3d (bovids) (New York: Academic).

Kruuk, H., 1972, *The Spotted Hyena* (Chicago: University of Chicago Press).

Laws, R. M., 1970, Biology of African elephants. *Science Progress*, **58**, 251–62.

Laws, R. M., 1984, Hippopotamuses. In *The Encyclopedia of Mammals*, edited by D. W. Macdonald (New York: Facts on File), pp. 506–511.

Leader-Williams, N., and Albon, S. D., 1988, Allocation of resources for conservation. *Nature*, **336**, 533–535.

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

Leuthold, B. M., and Leuthold, W., 1972, Food habits of giraffe in Tsavo National Park, Kenya. *East African Wildlife Journal*, **10**, 129–41.

Leuthold, B. M., and Leuthold, W., 1978, The ecology of the giraffe in Tsavo East National Park, Kenya. *East African Wildlife Journal*, **16**, 1–20.

Leuthold, W., 1966, Variations in territorial behaviour of Uganda kob, *Adenota kob thomasi* (Neumann 1896). *Behaviour*, **27**, 214–57.

Ludwig, J. A., and Reynolds, J. F., 1988, *Statistical Ecology: A Primer of Methods and Computing* (Chichester: Wiley).

Mather, P., 1987, *Computer Processing of Remotely-sensed Images* (New York: Wiley).

Mckey, D., 1978, Soils, vegetation and seed eating by black colobus monkeys. In *The Ecology of Arboreal Folivores*, edited by G. G. Montgomery (Washington, DC: Smithsonian Institute Press), pp. 423–439.

Mloszewski, M. J., 1983, *The Behaviour and Ecology of the African Buffalo* (Cambridge: Cambridge University Press).

Morrison, M. L., Marcot, B. G., and Mannon, R. W., 1992, *Wildlife–habitat Relationships: Concepts and Applications* (University of Wisconsin Press).

Moss, C. J., and Poole, J., 1983, Relationships and social structure of African elephants. In *Primate Social Relationships: An Integrated Approach*, edited by R. Hinde (Oxford: Blackwell).

Nicholas, A., and Ndey, A., 1995, The results of a transect exercise in the Domaines de Chasses surrounding Garamba National Park, Zaïre. Technical Report, Garamba National Park Project, IZCN, WWF.

Norton-Griffiths, M., 1978, *Counting Animals* (African Wildlife Foundation).

Olivier, R. C. D., and Laurie, W. A., 1974, Habitat utilisation by hippopotamuses in the Mara River. *East African Journal of Ecology*, **12**, 32–48.

Packer, C., and Pusey, A. E., 1982, Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature*, **296**, 740–42.

Pellew, R. A., 1984 a, Giraffe and okapi. In *The Encyclopedia of Mammals*, edited by D. W. Macdonald (New York: Facts on File), pp. 534–541.

Pellew, R. A., 1984 b, The feeding ecology of a selective browser, the giraffe (*Giraffa Camelopardalis*). *Journal of the Zoological Society of London*, **202**, 57–81.

Pimbert, M. P., and Pretty, J. N., 1995, Parks, people and professionals: putting 'participation' into protected area management. Discussion Paper 57, UNRISD, IIED, WWF.

Plumptre, A. J., and Harris, S., 1995, Estimating the biomass of large mammalian herbivores in a tropical montane forest: a method of faecal counting that avoids using a 'steady state' system. *Journal of Applied Ecology*, **32**, 111–120.

Prins, H. H. T., and Reitsma J. M., 1989, Mammalian biomass in an African equatorial rain forest. *Journal of Animal Ecology*, **58**, 851–861.

Rose, M. D., 1978, Feeding and associated positional behaviour in black and white colobus monkeys (*Colobus guereza*). In *The Ecology of Arboreal Folivores*, edited by G. G. Montgomery (Washington, DC: Smithsonian Institute Press), pp. 423–439.

Schaller, G., 1972, Predators of the Serengeti. *Natural History*, **81**, 60–69.

Sinclair, A. R. E., 1977, *The African Buffalo* (Chicago: University of Chicago Press).

Sinclair, A. R. E., and Arcese, P., 1995, *Serengeti 2: Dynamics, Management and Conservation of an Ecosystem* (Chicago: University of Chicago Press).

Skinner, J. D., Braytenback, G. J., and Maberly, C. T. A., 1976, Observations on the ecology and biology of bushpig (*Potamochoerus porcus*) in the northern Transvaal. *S. Afr. J. Wildl. Res.*, **6**, 123–28.

Spinage, C. A., 1982, *A Territorial Antelope: The Uganda Waterbuck* (New York: Academic).

Suzuki, A., 1969, An ecological study of chimpanzees living in savanna woodland. *Primates*, **10**, 103–148.

Ter Braak, C. J. F., 1995, Ordination. In *Data Analysis in Community and Landscape Ecology*, edited by R. H. G. Jongman, C. J. F. ter Braak and O. F. R. van Tongeren (Cambridge: Cambridge University Press).

Ter Braak, C. J. F., and Looman, C. W. N., 1995, Regression. In *Data Analysis in Community and Landscape Ecology*, edited by R. H. G. Jongman, C. J. F. ter Braak and O. F. R. van Tongeren (Cambridge: Cambridge University Press).

Verschuren, J., 1958, Ecologie et biologie des grands mammifères. In: *Exploration du Parc National de la Garamba*, edited by H. de Seager (Brussels: Institut des Parcs Nationaux du Congo Belge).

Waser, P. M., 1974, Spatial association and social interactions in a 'solitary' ungulate: the bushbuck *Tragelaphus scriptus* (Pallas). *Z. Tierspychol.*, **37**, 24–36.

Waser, P. M., 1975, Diurnal and nocturnal strategies of the bushbuck *Tragelaphus scriptus*. *East African Wildlife Journal*, **13**, 49–63.

Wemmer, C. M., 1977, Comparative ethology of the large spotted genet (*Genetta tigrina*) and some related viverrids. *Smiths. Contrib. Zool.*, **239**, 1–93.

Western, D., Wright, R. W., and Strum, S. C., 1994, *Natural Connections* (Chicago: University of Chicago Press).

White, L. J. T., 1992, Vegetation History and Logging Disturbance: Effects on Rain Forest Mammals in the Lopé Reserve, Gabon. Ph.D. Thesis, University of Edinburgh, Scotland.

White, L. J. T., 1994, Biomass of rain forest mammals in the Lopé Reserve, Gabon. *Journal of Animal Ecology*, **63**, 499–512.

Wilkie, D. S., and Finn, J. T., 1990, Slash-burn cultivation and mammal abundance in the Ituri Forest, Zaïre. *Biotropica*, **22**, 90–99.