POPULATION STATUS, DISTRIBUTION AND HABITAT ASSOCIATION OF WATERBUCK (KOBUS ELLIPSIPRYMNUS ELLIPSIPRYMNUS) IN CHEBERA CHURCHURA NATIONAL PARK, SOUTHWESTERN ETHIOPIA

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ABSTRACT: As part of ecological studies of larger mammals in Chebera Churchura National Park, southwestern Ethiopia, population, distribution and habitat association of the waterbuck, Kobus ellipsiprymnus ellipsiprymnus were studied during wet and dry seasons of 2013-2014. Representative transects across the main habitat types such as wooded grasslands, woodlands, montane forests and riparian habitats were randomly laid and counts were carried out in around 20% of the total area of the park. The estimated population of waterbuck in the park was 577 individuals. Males comprised 29.06%, while females 50.13%. Male to female sex ratio was 1.00: 1.72. Age structure was dominated by adults, which constituted 55.65% of the total population, followed by sub-adults (23.50%) and calves (21.06%). Larger herds of up to 20 individuals were observed during the dry season, while smaller groups of up to 3 individuals were common during the wet season. The mean group size was 13 during the dry season and 5 during the wet season. They were mostly observed in the woodland vegetation type around 1-2 km distance from permanent water source. Presence of water, abundance of food, vegetation cover and topographic features for predator avoidance were major factors governing the distribution of waterbucks in the study area.

Key words/phrases: Chebera Churchura National Park, Distribution, Habitat association, Population structure, Sex ratio, Waterbuck.

INTRODUCTION

The waterbuck, *Kobus ellipsiprymnus ellipsiprymnus* (Ogilby, 1833) is a large antelope adapted to moist savanna ecosystems. Waterbucks, as their name implies, are usually found close to permanent sources of water such as rivers and lakes. They live in the savannah zone of sub-Saharan Africa from South Africa north to Ethiopia and South Sudan, west to Senegal. In Ethiopia, they occur west of the Great Rift Valley in association with most major rivers, lakes and wetlands on both sides. They are not seen in arid areas and in high altitudinal areas (Kingdon, 1997). Waterbucks prefer open habitats with a short to medium sward height for grazing. They are mainly

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grazers although they also feed on leafy vegetation. Their most distinctive feature is the large white circle, which runs around their rump. Males have long rippled horns sweeping gently upwards and forwards in a shallow arc (Kingdon, 1997).

The subfamily Reduncinae of the Family Bovidae has two genus, *Kobus* and *Redunca*. Waterbuck is one of the six species of the Genus *Kobus*. Males of waterbucks are territorial (Estes, 1991). The breeding system of waterbucks is based on territorial defense where only few of the dominant males get chance to mate (Buechner, 1961). Territorial and other disputes between individuals are frequent and follow highly ritualized behavioural repertoires (Leuthold,1977;www.wackywildlifewonders.com/animals/largeantelope/51-waterbuck *Kobus ellipsiprymnus*).

Waterbuck is least studied in Ethiopia. Further, there are only few ecological studies so far held in Chebera Churchura National Park (Aberham Megaze *et al.*, 2012; Demeke Datiko, 2013; Demeke Datiko and Afework Bekele, 2013). Hence, the present investigation was undertaken to study population ecology of waterbucks in this park.

THE STUDY AREA AND METHODS

The study area

Chebera Churchura National Park (CCNP) is located in the southwestern part of Ethiopia between Dawro Administrative Zone and Konta Special Woreda (District) in the Southern Nations Nationalities Administrative Region of Ethiopia, located about 367 km and 580 km southwest of Hawassa, the regional capital, and Addis Ababa, the capital city of Ethiopia, respectively. It covers an area of 1200 km² and lies between the coordinates 36°27'00'-36°57'14"E and 6°56'05"-7°08'02"N (Fig. 1), and is bordered by Konta Special Woreda to the north, Omo River to the south, Dawro Zone to the east and southeast, and Agare high mountains and Omo River to the west. The study area is characterized by a relatively hot climatic condition. Annual rainfall in the area varies from 1000 mm to 3500 mm. Based on the records of the National Meteorological Agency (NMA) station at Ameya, located about 14 km from the study area, the area has uniform and extended rainfall season (between March and September with a peak in July). The dry season of the study area is from November to February, with mean maximum temperature varying between 27°C and 29°C. The hottest months are January and February, while the coldest months are July and August with the mean maximum and minimum temperatures of 28°C and 12°C,

respectively.

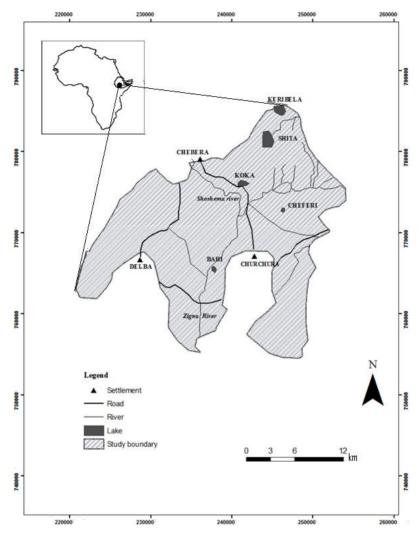


Fig. 1. Location map of the study area.

The vegetation cover of the area is categorized into four major types such as wooded grassland, woodland, montane forest and riparian forest. The wooded grassland is the most abundant of all, which accounts for 62.5% of the study area. It covers most of the undulating landscapes above the floor of the valleys and gorges. Although the grass species show local variation, the dominant grass species includes the elephant grass (*Pennisetum* sp.). The tree species are deciduous that include *Combretum* sp. in association with *Terminalia albiza*. The woodland habitat covers about 8% of the total

area while the riparian forest habitat covers only 3% of the total area of the park. The montane forest habitat covers about 29.5% of the total area of the park. Dominant tree species include Juniperus procera, Podocarpus falcatus and other broad leaved species. Montane forest vegetation occurs in the eastern and northwestern highlands of the study area. It is dominated by tree species and characterized by a crown cover of up to 50%, with multistoried structure. Climbers and saprophytes are important floristic components of the habitat. The dominant trees are Podocarpus sp. and Juniperus sp. (Dereje Woldevohannes, 2006). Riparian forest occurs in about 40 km², along the course of the rivers, Zigna, Shoshima, Wala, Tikurwuha, Mensa, Oma and other small seasonal tributaries. This habitat is characterized by mixed vegetation type composed of large trees and herbaceous species. Dominant plant species in this habitat are Ficus sp., Phoenix sp., Costa sp., Albizia grandibracteata, Chionanthus mildbraedii, Grewia ferruginea, Aspilia mossambicensis, Arundo donax and Ehretia cymosa (Girma Timer, 2005: Meseret Admasu, 2006).

So far, 55 species of mammals (Girma Timer, 2005; Demeke Datiko, 2013) and 137 species of birds (Dereje Woldeyohannes, 2006) have been reported from this National Park. However, except for surveys of larger mammals (Meseret Admasu, 2006; Aberham Megaze *et al.*, 2012) and birds (Dereje Woldeyohannes, 2006), there is inadequate or totally no information about the distribution and habitat association of waterbucks in CCNP as well as in the country as a whole, and hence extended ecological investigation in CCNP is important.

Methods

Before the actual data collection, a reconnaissance survey was made in the study area for two weeks to collect basic information about the location, topography, habitat types, distribution of waterbucks, and to be accustomed to CCNP. Transects for observation were laid based on the four major vegetation categories of the study area as follows:

- 1. Census zone 1 (Wooded grassland): This habitat type covered an estimated area of 744 km^2 in CCNP. A total of 14 transects were laid in this habitat, each around 10 km long and 500 m width.
- 2. Census zone 2 (Woodland): This habitat type covered an estimated extent of 96 km^2 area in CCNP. There were three transects in this habitat, each around 10 km long and 300 m width.
- 3. Census zone 3 (Montane forest): This habitat type covered an area of

336 km^2 , where eleven transects were laid, each around 8 km long and 400 m width.

4. Census zone 4 (Riparian forest): This habitat type covered an area of 36 km². There were four transects in this habitat, each around 5 km long and 250 m width.

Special care was taken to keep each consecutive transect at a distance of around 1.0–1.5 km away from each other (Koster and Hart, 1998). Detailed data collection was carried out during August 2013 to September 2013 (wet season) and from January 2014 to March 2014 (dry season). Surveys were conducted on transects at an average speed of 1 km/h in the montane forest, riparian forest and woodland habitats, and 2 km/h in the grassland habitat. The starting and ending GPS co-ordinates of transects were determined prior to starting of the census. Silent detection method was carried out to minimize disturbances in the field (Wilson *et al.*, 1996). During transect walking, the observers recorded the start and end time and start and end GPS locations. Whenever waterbucks were encountered, time, herd size, sighting distance or perpendicular distance, and habitat types were recorded.

Each of the habitat types based on the vegetation, visibility and topography was taken as a census zone. Stratification was made using aerial photograph (scale 1: 30,000), satellite imagery and EMA topography maps (scale 1: 50,000). The survey team was composed of three individuals. Transect counting method (Norton-Griffiths, 1978) was used, following direct observations of waterbucks, and indirect evidences such as droppings, spoors and sound. Transect counts were made to estimate density and to assess waterbuck distribution in each habitat type. The time of counting was between 06:00 h–10:00 h and between 14:00 h–18:00 h. To avoid double counting, the number of individuals and their herd composition, and specific features of any of the individuals in different areas were noted (Wilson *et al.*, 1996). Number, sex, age, time of observation and activities were also recorded.

Population estimate: Transect surveys were conducted during both wet and dry season in order to achieve representative estimates. When waterbucks were spotted, the following information were recorded: N = number of animals seen, L = length of the transect, and W = width of the transect to estimate Density (D) = N/2LW. Population size (P) was estimated as: D x A (total extent of waterbuck habitat in the study area) (Sutherland, 1996).

Herd size: Herd size and composition were recorded during direct observations following Lewis and Wilson (1979). Individuals were considered as members of the same herd if the distance between them was <50 m (Borkowski and Furubayashi, 1998), or if they responded in a related manner to external stimuli and if moving in the same direction with the rest of the members of the herd.

Sex and age structure: Each of the individuals in a herd was identified and categorized into its respective age and sex categories during counting. The categories used were adult male, adult female, sub-adult male and female and calves of both sexes. Identification of sex and age were carried out using the relative size, external genitalia and the presence or absence and the size of horns in males. Sex ratio of the herd was estimated from the data on sex of the animals obtained during direct observations of the animals (Melton, 1983).

Distribution and habitat association: The method of Norton-Griffiths (1978) was used to describe the dry and wet season distribution of waterbucks in the study area by taking each herd or individual sighting as score with respect to the habitat type where they were observed.

Data analyses

Data were analyzed using SPSS version 20 computer software program. Population estimates of waterbucks for wet and dry seasons were compared using one-way ANOVA (P = 0.05). Animals counted during different seasons, density, sex, age category, herd size, distribution and habitat association were compared using t-test for independent samples and Chi-square test (Zar, 1996).

RESULTS

Population estimate

A total of 146 ± 6.8 and 157 ± 6.8 individuals of waterbucks were recorded during wet and dry seasons, respectively, with a mean of 152 individuals. The mean population density estimated was 0.506/km². Population estimates for CCNP during dry and wet seasons were 650 and 564 individuals, respectively, with a mean of 599 individuals (Table 1). There was no significant difference in the population between dry and wet seasons $(\chi^2 = 7.7, df = 1, P > 0.05)$.

Season	Individual observed	Density/km ²	Estimate
Dry	157.2 ± 6.8	0.542 ± 0.036	650.2 ± 43.2
Wet	146.0 ± 6.8	0.470 ± 0.036	564 ± 43.2
Mean	151.6 ± 6.8	0.506 ± 0.036	598.6 ± 43.2

Table 1. Population estimate of waterbuck in Chebera Churchura National Park (Mean ± SE).

Herd size

Waterbuck herds were composed of all age groups. Herd size, composition and structure were different during wet and dry seasons. There was difference in young and adults between herds. Adults were consistently more than young in all herds. An average herd size of 5 and 13 individuals were recorded during the wet and dry seasons, respectively ($\chi^2 = 12.49$, df = 1, p<0.05).

Population structure

Out of the total individuals observed, 21% was adult males, 34% adult females, 8% sub-adult males, 16% sub-adult females and 22% was calves of both sexes (Table 2). The ratios of male to female for the wet and dry seasons were 1:1.70 and 1:1.75, respectively. In general, 56% of the total population was adults, whereas 23% was young of both sexes and 21% was sub-adults. There was no significant difference in the age distribution and sex ratio of waterbucks during wet and dry seasons ($\chi^2 = 2.4$, df = 4, P>0.05).

Table 2. The proportion of age and sex categories of waterbuck population observed during wet and dry seasons.	

Catagorias	Number of individuals (Mean ± SE)			
Categories	Wet season	Dry season	Mean	Percentage
Adult male	32.5 ± 1.764	31.8 ± 1.764	32.15 ± 1.764	(21.2%)
Adult female	51.2 ± 3.101	52.9 ± 3.101	52.05 ± 3.101	(34.3%)
Sub-adult female	24.3 ± 1.369	23.2 ± 1.369	23.75 ± 1.369	(16.1%)
Sub-adult male	11.8 ± 1.749	11.8 ± 1.749	11.8 ± 1.749	(7.9%)
Calf of both sexes	23.2 ± 1.369	40.5 ± 1.369	31.85 ± 1.369	(21.5%)
Ratio				
Male: female	1:1.70	1:1.75	1:1.72	
Adult: others	1:1.41	1:1.8.5	1:1.79	
Calves: others	1:5.16	1:3.88	1:4.75	
Sub-adult: others	1:4.1	1:4.49	1:4.26	

Distribution and habitat association

The relative use of different habitat types by waterbucks is given in Table 3 as revealed from the number of individuals observed in each vegetation community. Waterbucks showed high preference to woodland vegetation during both dry and wet seasons. Out of the 146 individuals observed during the wet season, 61% utilized woodland habitat and 63% used this habitat during the dry season. Distribution of waterbucks in different habitat types during wet and dry seasons showed no significant variation ($\chi^2 = 2.01$, df = 1, P>0.05).

	Number of individuals in each habitat type				
Season	Wooded grassland	Woodland	Montane forest	Riparian forest	
Wet	17.6 (12.4%)	89.0 (61.0%)	18.6 (12.7%)	20.8 (13.8%)	
Dry	17.8 (11.3%)	98.2 (62.5%)	17.9 (11.4%)	23.3 (14.8%)	
Mean	17.7 (11.8%)	93.6 (61.9%)	18.3 (12.1%)	22.2 (14.6%)	

Table 3. Number of individuals observed in each habitat type and their percentage.

DISCUSSION

It is difficult to assess long term population trend of waterbuck in CCNP as periodic censuses of this species had not been conducted in the study area. However, factors such as habitat destruction and poaching are considered leading factors for population decline of species (Sinclair, 1977; Sutmoller *et al.*, 2000). This might not have similar effects on the waterbuck population today in CCNP. According to the National Park managers, waterbucks were heavily hunted before the establishment of the park for meat and horns. Their horns were used to make utensils such as spoons and cups. However, after the establishment of the park, illegal hunting of waterbucks is under control. This may be due to the attitudinal change of the local people towards illegal hunting. In addition to these, protection of the National Park by the management and scouts, and awareness creation by the park staff also helped to bring better protection of waterbucks in the study area.

During the present investigation, more waterbucks were encountered during the dry season than the wet season. This might be due to the fact that there was annual fire in most of the woodland and grassland habitats and the habitats were open and there was better condition for counting during the dry season. The prolonged rainy season, which lasts about nine months permits new growth of grass early in November after the fire. Grass becomes very tall, less edible and dry during the main rainy season, and this might have effect on visibility of the animal leading to biased observation and counting. However, fresh and better quality grass is available for the grazers during the dry season in CCNP.

Breeding is not strictly seasonal in waterbuck, and they may give birth at any time of the year. But, the peak was observed during the dry season in CCNP. This might be due to the availability of food and a better quality grass during the dry season. In the present study more calves were counted during the dry season. On average, 41 and 23 calves were counted during the dry and wet seasons, respectively. This may be due to availability of resources and better conditions for counting. As mentioned earlier, the habitat is open because of forest fire during the dry season. However, in contrast to the present findings, Pienaar (1963) recorded birth peaks of waterbucks in the Kruger National Park (South Africa) in October and February to March. In Kruger National Park area, September–May is the rainy season. September and October may be dry, but rains culminate in late October.

There was no significant difference in the counts within each habitat type during different seasons. However, count of waterbucks in the hilly woodland habitat closer to the permanent water source was the relatively preferred habitat of waterbucks in this study area. Abundance of animals is naturally associated with preferred habitats. This depends on what the habitat provides in terms of food, breeding site and protection from predators. Habitat selection may be influenced by vegetation type and water sources (Smith et al., 2007), topographical features (Redfern et al., 2003) and predator avoidance (Cowlishaw, 1997). Such habitat preference might be due to the tendency of waterbucks to seek for a habitat with good supply of nourishment and predator avoidance. In the study area, most of the waterbucks were counted in the woodland habitat in places where there were good supply of food, vegetation cover and permanent water source. The highest number of waterbucks and the highest herd size were recorded during both seasons in the woodland habitat. There were no waterbucks sighted in areas where there was no permanent water source nearby.

It was also common to observe pug marks of lions and leopards after hoofmarks of waterbucks in the open grassland habitat. This might show the suitability of grassland habitat for predators, where they can easily detect, chase and entangle their prey in open areas. In the woodland habitat, waterbucks showed high preference for rocky and hilly areas, where they can easily detect predators and escape. It is also not easy for predators to locate, chase and entangle their prey in this habitat type due to the vegetation cover and topographic features. It is also common to observe two or more adult waterbucks, which might be herd leaders, simply standing on the top of the rocky hills to detect the presence of predators while members of the herd were grazing. Treydte *et al.* (2010) stated that the African savannah grazing ungulates preferentially select beneath-canopy grasslands rather than open grasslands despite its wider availability. ASG (1998) also supports this finding by stating that waterbucks occupy a wide range of habitats close to permanent water sources and high quality grassy areas. The occupation of hills helps to avoid overgrazed areas but occupy prime habitats because of competition with other species as already stated by Melton (1978).

Information on sex ratio and age distribution is vital for evaluating the viability of a species because these variables reflect the structure and the dynamics of populations. Sex and age structures of a population at any given time are also indicators of the status of the population (Wilson *et al.*, 1996). The high proportion of females indicates a healthy, increasing waterbuck population in the study area. However, relatively low proportion of calves to other age groups was observed during the wet season in the present investigation. In addition to difficulties in observing and counting calves due to the dense vegetation cover during the wet season, as the young ones are more vulnerable to predators, they are usually hidden under dense grasses and vegetation during this season. There was also scarcity of food during this period and as a result, the breeding peak was high during the dry season. This supports the findings of Spinage (1982), who confirmed that at this stage of their lives, calves are highly vulnerable to predation, and peak breeding was during the dry season.

The differences in the sex ratio may be largely due to increased mortality of male waterbucks due to predation. Male waterbucks leave the natal herd, distribute in less favourable habitats and suffer an increased predation pressure compared to females of the same age class, which stay in the natal herd (Spinage, 1982). While nursery herds are free to seek the best grazing areas in their home range, bachelor herds remain at peripheral areas. Young males, however, may soon be displaced due to antagonistic behaviour of territorial males. Tomlinson (1980) also revealed that bachelor groups are forced to occupy marginal areas in order to avoid conflicts with territorial males.

Even though, waterbucks showed no significant difference in their habitat preferences during both seasons, large herd sizes were recorded during the dry season. It is likely that changes in herd size are closely associated with the availability of edible grasses and sometimes due to reproductive activities. This is supported by the findings of Jarman and Jarman (1973) that waterbucks made a large group of mixed male, female and young during the breeding period, and herd size varied due to reproductive behaviour and environmental disturbances.

During the dry season, forest fires were common in CCNP, and there were new growth of a better quality grass due to the unique rainfall pattern in the area. Open and free spaces were also available in this season and large herd size of waterbucks was recorded. In contrast to this, waterbucks were dispersed and formed smaller herds for intensive foraging of the available edible food resources during the wet season. This is against the findings of Melton (1978), who stated that in Kwazulu Natal there was an increase in herd size during the winter and fragmentation of the herd during the summer, due to the scarcity of the preferable food, which was also scattered in distribution. By living in small herds, they may get access to extra resources that are too sparse for large herds. There were tall and dry grasses during the main rainy season, which were not edible for waterbucks. The annual elephant grass grown early in November and, on which waterbucks depended upon, will be very tall, dry, less edible and low in nutritive value during the main rainy season due to the growth factor.

In this study area, the diet of waterbucks comprised grass species, mainly the elephant grass during both dry and wet seasons. Smaller herds of 3–5 adults, mostly of bachelor herds, were recorded during the main rainy season foraging in the patches of grass that were too small to support large herds. This is also against the findings of Melton (1978), who confirmed that there was an increase in group size of waterbucks during the summer and fragmentation of the group during the winter in Kwazulu Natal.

Current conservation efforts in CCNP are promising, and hence populations of most of the larger animals are expected to grow. For sustainable conservation and management of wildlife, baseline data on all large mammals in the area are essential. Even though there was chance for underestimation of the population of waterbucks during the present investigation due to the large area of the park and the tall grassy habitats, the present data will serve as baseline information for future studies on the population trend of waterbucks in CCNP.

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REFERENCES

- Aberham Megaze, Gurja Belay and Balakrishnan, M. (2012). Population ecology of the African buffalo (*Syncerus caffer* Sparrman, 1779) in Chebera Churchura National Park, Ethiopia. *Afr. J. Ecol.* **51**: 393–401.
- ASG (1998). African Antelope Database. IUCN/SSC Antelope Specialist Group, International Union for Conservation of Nature and Natural Resources, Gland.
- Borkowski, J. and Furubayashi, K. (1998). Seasonal and diet variation in group size among Japanese Sika deer in different habitats. J. Zool. Lond. **245**: 29–34.
- Buechner, H.K. (1961). Territorial behaviour in Uganda kob. Science 133: 698-699.
- Cowlishaw, G. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim. Behav.* **53**: 667–686.
- Demeke Datiko (2013). Species Composition, Distribution, Habitat association, Feeding Ecology of Small Mammals, and Conservation Challenges in Chebera Churchura, National Park, Ethiopia. Ph.D. Dissertation, Addis Ababa University, Addis Ababa.
- Demeke Datiko and Afework Bekele (2013). Conservation challenge: Human–carnivore conflict in Chebera-Churchura National Park, Ethiopia. *Greener J.* **3**: 108–115.
- Dereje Woldeyohannes (2006). **Diversity, Distribution and Relative abundance of Avian Species of Chebera Churchura National Park, Ethiopia**. M.Sc. Thesis, Addis Ababa University, Addis Ababa.
- Estes, R. (1991). The Behavior Guide to African Mammals: Including Hoofed Mammals, Carnivores, Primates. University of California Press, California.
- Girma Timer (2005). Diversity, Abundance, Distribution and Habitat Association of Large Mammals in the Chebera Churchura National Park, Ethiopia. M.Sc. Thesis, Addis Ababa University, Addis Ababa.
- Jarman, M.V. and Jarman, P.J. (1973). Daily activity of impala. E. Afr. Wildl. J. 11: 75-92.
- Kingdon, J. (1997). The Kingdon Field Guide to African Mammals. Academic Press, London.
- Koster, S.H. and Hart, J.A. (1998). Methods to estimate ungulate population in tropical forest. *Afr. J. Ecol.* **26**: 117–126.
- Leuthold, W. (1977). African Ungulates: A Comparative Review of their Ethology and Behavioural Ecology. Springer Verlag, Berlin.
- Lewis, J.G. and Wilson, R.T. (1979). The ecology of Swayne's hartebeest. *Biol. Conserv.* **15**: 1–12.
- Melton, D.A. (1978). Ecology of Waterbuck Kobus ellipsiprymnus (Ogilby, 1833) in the Umfolosi Game Reserve. D.Sc. Dissertation, University of Pretoria, Pretoria.
- Melton, D.A. (1983). Population dynamics of waterbuck in the Umfolozi Game Reserve.

Afr.J. Ecol. 21: 77–91.

- Meseret Admasu (2006). History and Status of the Population of African Elephant (*Loxodonta africana* Blumenbach, 1797) and Human–Elephant Conflict in Chebera Churchura National Park, Ethiopia. M.Sc. Thesis, Addis Ababa University, Addis Ababa.
- Norton-Griffiths, R. (1978). Counting Animals. Handbook No.1. 2nd edn. African Wildlife Foundation, Nairobi.
- Pienaar, U.V. (1963). The large animals of the Kruger Park their distribution and presentday status. *Koedoe* 6: 1–37.
- Redfern, J.V., Grant, R., Biggs, H. and Getz, W.M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84: 2092– 2107.
- Sinclair, A.R.E. (1977). The African Buffalo: A Study Resource on Limitation of Population. Chicago University Press, Chicago.
- Smith, I.P., Grant, C.C. and Devereux, B.J. (2007). Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biol. Conserv.* 136: 85–99.
- Spinage, C.A. (1982). A Territorial Antelope: The Uganda Waterbuck. Academic Press, London.
- Sutherland, J.W. (1996). Ecological Census Technique, Handbook. Cambridge University Press, Cambridge.
- Sutmoller, P., Thomson, G.R., Hargreaves, S.K., Foggin, C.M. and Anderson, E.C. (2000). The foot and mouth disease risk posed by African buffalo within wildlife conservancies to the cattle industry of Zimbabwe. *Prev. Vet. Med.* 44: 43–60.
- Tomlinson, D.N.S. (1980). The Daily Activity and Behaviour Patterns of Waterbuck in Relation to its Seasonal Utilization of Feeding Habitats in the Lake McIlwaine Game Enclosure. M.Sc. Thesis, University of Rhodesia, Rhodesia.
- Treydte, A.C., Riginos, C. and Jeltsch, F. (2010). Enhanced use of beneath-canopy vegetation by grazing ungulates in African savannahs. *J. Arid. Environ.* **74**: 1597–1603.
- Wilson, D.E., Cole, F.R., Nichols, J.D., Rudran, R. and Foster, M. (1996). Measuring and Monitoring Biological Diversity. Standard Methods for Mammals. Smithsonian Institution Press, Washington, DC.
- Zar, J.H. (1996). Biostatistical Analysis. 3rd edn. Prentice Hall, New Jersey.