

Status of wildlife at trophy hunting sites in the Ugalla Game Reserve of Western Tanzania

Authors: Wilfred, Paulo, and MacColl, Andrew D.C.

Source: Tropical Conservation Science, 9(3)

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/1940082916667336>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Status of wildlife at trophy hunting sites in the Ugalla Game Reserve of Western Tanzania

Tropical Conservation Science
July-September 2016: 1–10
© The Author(s) 2016
Reprints and permissions:
sagepub.com/journalsPermissions.nav
DOI: 10.1177/1940082916667336
trc.sagepub.com



Paulo Wilfred¹ and Andrew D.C. MacColl²

Abstract

In western Tanzania's wildlife ecosystems, both commercial and subsistence uses of wildlife take place. Commercial use is largely through trophy hunting in designated hunting areas while subsistence use is predominantly carried out by local people for food and as a source of cash income. Assessing the status of wildlife populations in hunting areas is of supreme importance if unsustainable use is to be controlled. In this study, we carried out road transect surveys to estimate the density, group size and sex ratio of selected species of exploited wildlife in Ugalla Game Reserve, western Tanzania, to determine whether population characteristics differed between the Ugalla east and Ugalla west hunting sites. Overall, estimates of density and group size were higher at Ugalla east than Ugalla west. Of the individual species, the helmeted guineafowl had the highest population density, followed by impala and topi. Waterbuck had the lowest population density. When comparing our findings with population densities reported in other studies, especially in the more protected Katavi National Park in western Tanzania, our estimates were much lower. Sex ratios varied considerably among species although they were generally skewed towards females. Future studies should integrate data from subsistence and trophy hunting and evaluate the status of wildlife taking into account habitat characteristics.

Keywords

exploited wildlife, density, sex ratio, group size, western Tanzania

Introduction

Wild animals are extensively utilized for various reasons, such as food and commercial, cultural beliefs and medicinal (Davies & Brown, 2007; Festa-Bianchet, 2003; Flesher & Laufer, 2013; Mills, 2007; Smith, 2008). The impacts of wildlife exploitation on declining populations have been widely reported (e.g. Caro, 2008; Fa et al., 2006; Lindsey et al., 2013; Taylor & Dunstone, 1996). However, it is important to note that some species are affected more than others, and some are only affected indirectly (Mills, 2007). For example, biased sex ratios as a result of exploitation can affect species productivity and overall population performance (Milner et al., 2006). In recent years wildlife conservation science has had a strong focus on determining how, why, and to what extent populations of different wildlife species are affected by human exploitation (Caro, Young, Cauldwell, & Brown, 2009; Festa-Bianchet, 2003; Ginsberg & Milner-Gulland, 1994; Swenson et al., 1997).

In developing countries, the main forms of wildlife exploitation are commercial hunting (for example, trophy/tourist hunting) and subsistence hunting (hunting for food and small-scale bushmeat trade). In most instances, subsistence hunting is non-selective and carried out illegally, which has led to concerns about its sustainability as ecological factors such as habitat, species-specific impacts, age, sex and the density of the populations are not taken into consideration (Caro, 2008;

¹Department of Life Sciences, Faculty of Science, Technology and Environmental Studies, Open University of Tanzania, Dar es Salaam, Tanzania

²School of Life Sciences, University of Nottingham, University Park, Nottingham, UK

Received 12 May 2016; Revised 3 July 2016; Accepted 7 July 2016

Corresponding Author:

Paulo Wilfred, Department of Life Sciences, Faculty of Science, Technology and Environmental Studies, Open University of Tanzania, P.O. Box 23409, Dar es Salaam, Tanzania.

Emails: paulo.wilfred@yahoo.co.uk; paulo.wilfred@out.ac.tz



Creative Commons CC BY-NC: This article is distributed under the terms of the Creative Commons Attribution 3.0 License (<http://www.creativecommons.org/licenses/by/3.0/>) which permits any use, reproduction and distribution of the work without further permission provided the original work is attributed as specified on the SAGE and Open Access pages (<https://us.sagepub.com/en-us/nam/open-access-at-sage>).

Ginsberg & Milner-Gulland, 1994). Trophy hunting targets specific individuals of different species through selective hunting in many wildlife areas (Ginsberg & Milner-Gulland, 1994; Solberg, Saether, Strand, & Loison, 1999). Some factors guiding trophy hunting are the sex and age structure of the hunted populations (Milner, Nilsen, & Andreassen, 2007). Selective trophy hunting has also become a source of contention in conservation circles, and its adverse effects have been reported in some wildlife studies (for example, Coltman, O'donoghue, Jorgenson, Hogg, Strobeck, & Festa-Bianchet, 2003; Swenson et al., 1997; Weber, 2000).

In assessing the status of exploited wildlife populations, a number of studies have compared areas where trophy hunting is legal (for example in game reserves, game controlled areas, and open areas) with areas where hunting is not allowed (for example, national parks). Such comparative studies are often carried out in ecosystems where hunting and non-hunting sites are connected and individuals of different wildlife species are able to move between the sites (e.g. Caro, 1999a; Reyna-Hurtado & Tanner, 2007; Setsaas, Holmern, Mwakalebe, Stokke, & Røskoft, 2007; Waltert et al., 2008). In such ecosystems, wildlife populations are said to be stabilized by source-sink metapopulation dynamics in which non-hunting areas are considered as sources and adjacent hunting areas as sinks (Begon, Townsend, & Harper, 2006; Novaro, Redford, & Bodmer, 2000; Pulliam, 1988; Pulliam, & Danielson, 1991). We should, therefore, be careful about extrapolating recommendations from hunting areas that are connected to non-hunting areas to hunting areas that are discrete or isolated.

In this study, we surveyed wildlife in the Ugalla Game Reserve of western Tanzania. The reserve is isolated in that it is not directly connected to any non-hunting area, although it is surrounded by a sea of humanity which exerts pressure on wildlife resources mainly through illegal subsistence hunting (poaching) (Ugalla Game Reserve (UGR), 2006). Poaching in the reserve has led to the demise of a considerable number of both male and female individuals of wildlife species (Ugalla Game Reserve (UGR), 2006). The main legal activity is trophy hunting which, at the time of our study, was performed at two hunting blocks (hereafter, 'hunting sites'), Ugalla east and Ugalla west. Only adult males of selected wildlife species are hunted.

We used density, group size and sex ratio to assess the status of wildlife in the reserve when comparing Ugalla east and Ugalla west hunting sites. These population characteristics have been used elsewhere in Tanzania as indicators of the performance of conservation and wildlife populations (Caro, 2008; Caro, 1999a, 1999b, 1999c, 1999d; Setsaas et al., 2007; Waltert et al., 2008). Ugalla Game Reserve management controls off-takes at the hunting sites, and this goes hand in hand with

conservation enforcement through anti-poaching patrols. Our contention was that if the aforementioned population parameters differed across species and between the hunting sites, then this could inform conservation efforts for sustainable wildlife resource utilization at Ugalla, and decisions about trophy hunting quota allocations.

Methods

Study area

The study was carried out in Ugalla Game Reserve, western Tanzania (Figure 1) which lies between 5°–6° South and 31°–32° East, and covers approximately 5000 km². It has a tropical climate with a distinct wet season from December – May and a dry season from June – November. The rainfall is between 700–1000 mm per year, and mean maximum and minimum temperatures are between 28–30°C and 15–21°C respectively (Hazelhurst & Milner, 2007; Mbwapbo, 2003). The vegetation is dominated by miombo woodland, containing species such as *Brachystegia speciformis*, *B. microphylla*, *B. bussei*, and *Isobertinia globiflora*. There is a diverse range of wildlife species including impala, hippopotamus, wild dog, Nile crocodile and African elephant. Bird species include helmeted guineafowl, southern ground hornbill, ostrich and shoebill (Ugalla Game Reserve (UGR), 2006; Thomas, 1961).

Road survey

The road survey was designed and executed following the principles of distance sampling theory (Buckland, Anderson, Burnham, & Laake, 1993; Buckland et al., 2001; Pollard, Palka, & Buckland, 2002). Transects were driven from June – September 2009, along the existing roads and tracks in Ugalla Game Reserve, from 0700–1200 am. The surveyed roads were built by the Ugalla management for trophy hunting and patrolling purposes, and covered a substantial part of the reserve. Therefore, off-road driving or the cutting of new tracks was not permitted. We randomized the timing of our surveys between Ugalla east and Ugalla west so that there was no difference in how the hunting sites were surveyed.

In each month, the hunting sites and roads were sampled in a random order. A total of 36 transects were driven, 24 at Ugalla east and 12 at Ugalla west. Transects covered a total distance of 782 km (Ugalla east = 402 km and Ugalla west = 380 km). The survey was undertaken with three personnel in an open vehicle driven at an average speed of 20 km per hour. The observers searched for mammal and large bird species on both sides of each road. Sighting distances and angles were measured using a rangefinder and a compass respectively (Buckland et al., 2001). When groups were spotted, the

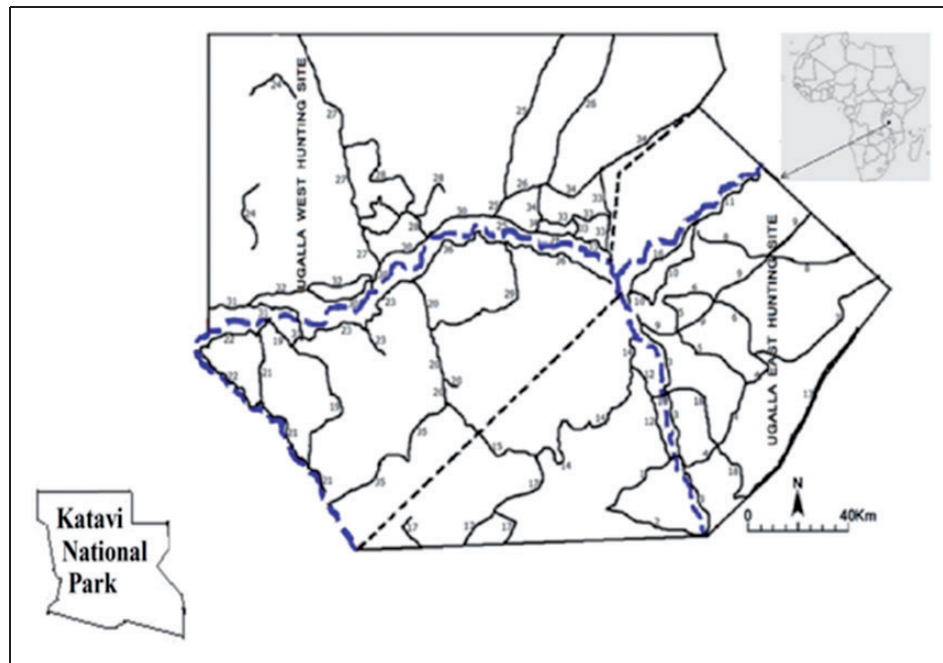


Figure 1. Ugalla Game Reserve (UGR) showing the distribution of roads (numbered lines, repeating numbers show the continuation of the road transect) along which wildlife surveys were conducted. The dotted line demarcates Ugalla east and Ugalla west hunting sites. Meandering broken lines are main rivers. Katavi National Park (mentioned in the text) is also shown. Insert shows the location of UGR in western Tanzania.

sighting distance was measured from the road to the approximate geometric centre of the group. Group size (number of individuals per sighting/observation) and number of males and females (for adult and sub-adult individuals) were recorded.

Statistical analysis

Densities were estimated using Distance software version 5.0. Detection function histograms and goodness-of-fit statistics were used as criteria for the selection of appropriate models and to assess the presence of outliers (Thomas et al., 2006). Data were analyzed using half-normal and hazard rate models for species with at least 15 sightings, in order for there to be enough observations to enable accurate estimates. Sex ratios (the proportion of male/female individuals of a species) were performed for ungulates with the same frequency of sightings, except for hippopotamus as it was not easy to distinguish male and female when they were submerged in water during the day. Species with total observations of <15 were only used to determine group sizes.

Other statistical analyses were performed in GenStat (release 10, VSN International Ltd., Hemel Hempstead, UK) and SPSS 15 for Windows. A non-parametric test, Wilcoxon matched pairs test, was used in the comparisons of sightings, detection probabilities, and group sizes between Ugalla east and west hunting sites.

Pearson correlation was used to determine the association between detection probability and animal sightings. The Mann-Whitney U test was used to test for differences in densities and group sizes between the hunting sites, for individual species. A generalized linear model (GLM) with normal errors was used to determine the relationship between density and the following fixed effects: species, hunting site, group size and number of observations or sightings. A GLM with a binomial distribution and a logit link function was used to identify the best predictors of sex ratio among the fixed effects group size, species, density and hunting site. The significance level (α) for all statistical tests was set at 0.05.

Results

Detectability

Histograms of distance data for selected species (Figure 2) indicated that animal sightings tended to decline with distance from the centre of the road transect. However, there were some variations in the detectability among species especially within 50 m from the transect. With the exception of giraffe, the detection probability in the first distance category for all species was below 80%. Detection probability had a significant positive correlation with number of animals observed ($n=11$ species with density estimates, $r=0.7082$, $p=0.0147$).

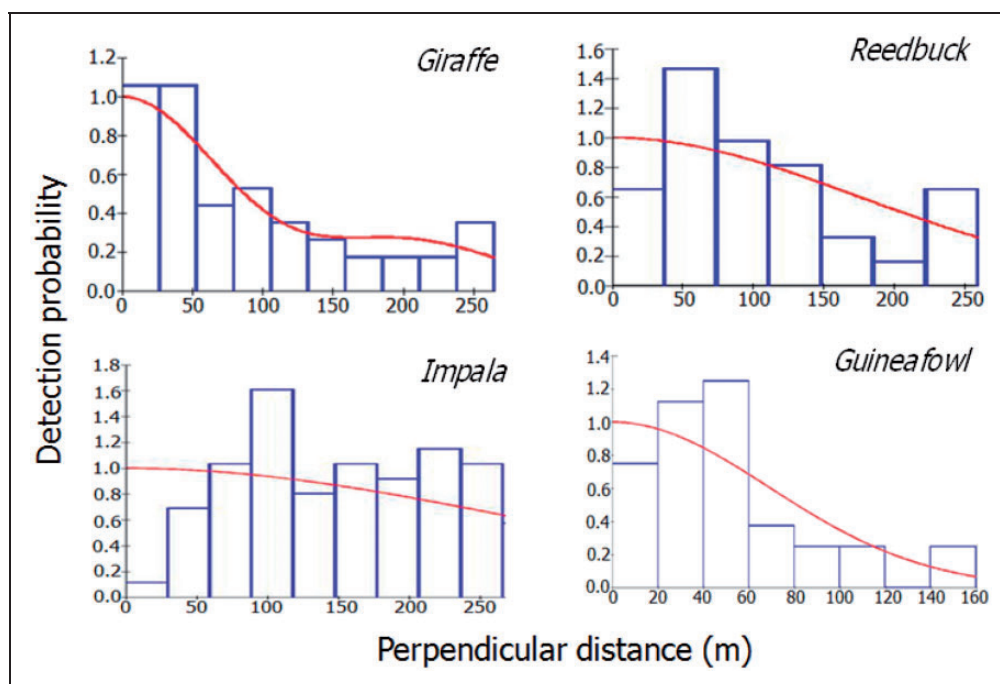


Figure 2. Detection probability curves for selected species in Ugalla Game Reserve.

Overall, detection probability across species at Ugalla east (0.4827 ± 0.0439) was slightly higher than Ugalla west (0.3455 ± 0.0481) ($n = 11$, $p = 0.052$).

Encountered species and their group sizes

Forty-four wildlife species were observed during the survey, and a total of 535 sightings. There were more sightings at Ugalla east (275) than Ugalla west (260) ($n = 44$ species, $z = -2.460$, $p = 0.014$. See Appendix 1). Of the species encountered, 7 had at least 30 sightings and 11 at least 15 sightings. Groups of impala were encountered more frequently at each of the hunting sites than any other mammal species. Among birds, helmeted guinea fowl and southern ground hornbill were observed most frequently. Some species of birds and mammals were only observed at one site; for example, plains zebra was only seen at Ugalla west. Likewise, African wild dog, greater kudu, and African savanna hare were only seen at Ugalla east. Six bird species, namely, African fish eagle, hammerkop, little egret, shoebill, spur-winged goose and glossy ibis were only encountered at Ugalla east.

Mean group sizes within species at Ugalla east exceeded those at Ugalla west ($n = 44$, $z = -2.563$, $p = 0.010$). At the level of the individual species, differences in group sizes between the hunting sites were only tested for those species whose number of observations at each of the hunting sites was ≥ 3 . With the exception of topi and bushbuck, there were no significant differences in group sizes between Ugalla east and Ugalla west, for each of the species (Appendix 1).

Table 1. Results from the GLM of animal density (individuals km^{-2}). The response variable, density, was modeled with a normal distribution.

| Fixed effect | F | df | P | Estimate \pm S.E. |
|--------------|-------|----|--------|---------------------|
| Species | 16.80 | 10 | <0.001 | |
| Giraffe | | | | 0.02 ± 0.25 |
| Guineafowl | | | | 1.14 ± 0.36 |
| Hartebeest | | | | -0.01 ± 0.20 |
| Hippopotamus | | | | 0.33 ± 0.25 |
| Hornbill | | | | -0.11 ± 0.16 |
| Impala | | | | 0.61 ± 0.53 |
| Oribi | | | | 0.06 ± 0.16 |
| Reedbuck | | | | -0.27 ± 0.18 |
| Topi | | | | 0.34 ± 0.26 |
| Warthog | | | | -0.23 ± 0.18 |
| Waterbuck | | | | -0.43 ± 0.18 |
| Hunting site | 11.44 | 1 | 0.007 | |
| Ugalla east | | | | 0.32 ± 0.28 |
| Ugalla west | | | | -0.26 ± 0.25 |
| Group size | 1.48 | 1 | 0.254 | – |
| Observation | 0.32 | 1 | 0.589 | – |

Densities

Species and hunting site were the best predictors of population density (Table 1). This means that density estimates varied among species. For example, guineafowl had the highest density followed by impala, whereas waterbuck

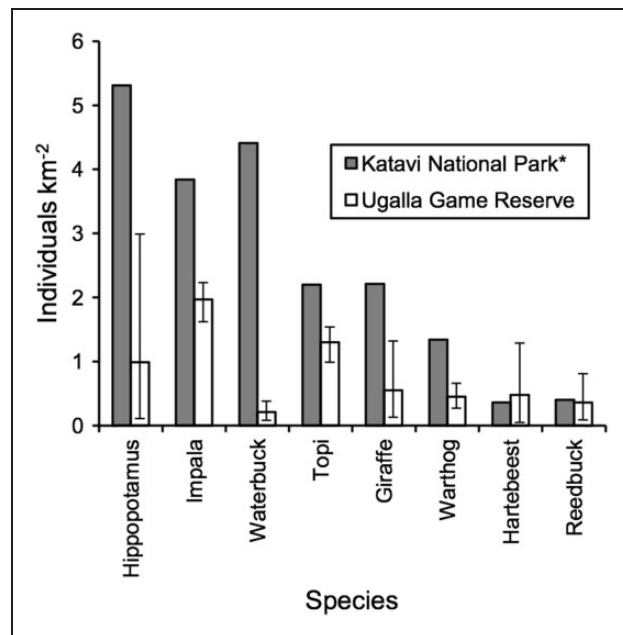


Figure 3. A comparison of species densities between Katavi National Park and Ugalla Game Reserve (*adapted from 27) (Caro, 1999b). The error bars are 95% confidence intervals.

had the lowest density (Appendix 1). Similarly, densities differed between the hunting sites with Ugalla east having greater wildlife density than Ugalla west (Table 1 and Appendix 1). Densities of warthog, topi, guineafowl and hippopotamus were significantly higher at Ugalla east than Ugalla west, but there were no significant differences in other species between the hunting sites (Appendix 1). To determine the differences between Ugalla and a non-hunting protected area we plotted our estimates (for selected species) against Katavi National Park situated in the Katavi-Rukwa ecosystem in western Tanzania (Figure 3). The oribi was not plotted due to lack of data for Katavi.

Sex ratios

Sex ratios were determined for 8 of 11 species with density estimates (Figure 4). Only group size ($\chi^2 = 6.39$, $df = 1$, $p = 0.011$) and species ($\chi^2 = 2.94$, $df = 7$, $p = 0.024$) were significant predictors of sex ratio. Sex ratios varied significantly among species. For example, impala had many more females than other species whereas giraffe had only marginally more females than males. Sex ratios were more skewed towards females for species with relatively big group sizes.

Discussion

Densities

In general, densities of wildlife across individual species in Ugalla Game Reserve varied remarkably between

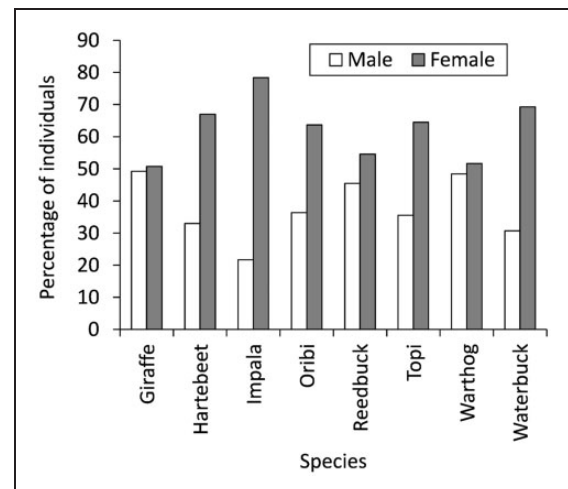


Figure 4. Percentages of males and females of selected species in Ugalla Game Reserve.

Ugalla east and Ugalla west hunting sites with higher estimates at Ugalla east. Combined estimates from Ugalla were compared to a previous road-based survey in Katavi National Park (Caro, 1999b). The terrestrial habitats in the national park were similar to Ugalla, but consumptive utilization was not permitted there. Densities of all species in our study area were noticeably lower than Katavi except for hartebeest and reedbuck which had low densities in both protected areas. While these differences could be attributed to factors other than extractive utilization, such as food and habitat availability, climate and species behaviors (Caro, 2001; Waltert, Meyer, & Kiffner, 2009), subsistence hunting could also play a central role in Ugalla (Wilfred & MacColl, 2014a, 2014b). Our study did not estimate levels of trophy hunting in the reserve, but Wilfred (2012) argues that it has had a significant impact on the number of individuals of different species in the area. Studies in other areas have used density estimates as evidence of the difference in exploitation intensity between hunting and non-hunting areas (e.g. Reyna-Hurtado & Tanner, 2007.). Other studies have focused on differences between hunting areas with varying hunting intensities (Topp-Jørgensen, Nielsen, Marshall, & Pedersen, 2009), while still others on differences between different sites within the same protected area (Njoroge et al., 2009). The majority of these studies indicate that densities of species are lower at exploited sites than less exploited ones.

We also attempted to draw attention to the status of the large bird species in Ugalla Game Reserve. We obtained a sufficient number of observations for helmeted guineafowl and southern ground hornbill. Large savanna birds are not only targeted for trophy/commercial hunting (Lamprey, Buhanga, & Omoding, 2003), but are harvested by local communities for bushmeat (Bassett, 2005; Magige et al., 2009; Thiollay, 2006).

Guineafowl had the highest population density among all the surveyed species. Although the density estimate for guineafowl might still be lower than in non-hunting areas, it nevertheless indicates that ungulate species are more affected than birds (see Ginsberg & Milner-Gulland, 1994; Milner, Nilsen, & Andreassen, 2007; Solberg, Saether, Strand, & Loison, 1999). We sighted southern ground hornbills in the open grasslands at Ugalla east and Ugalla west. There was no significant difference in their density between the hunting sites. Notwithstanding the fact that it has been categorized as a 'vulnerable' species (Birdlife International (BI), 2010) due to harvesting by people (Thiollay, 2006; Trail, 2007) and, perhaps even more importantly, due to habitat loss as a result of unsustainable human activities (Morrison et al., 2005; Trail, 2007), the observed total density of the southern ground hornbill in the reserve seemed fairly healthy, probably because protected areas are strongholds for them (Thiollay, 2006; van Essen, 2006), and Ugalla is no different (Ugalla Game Reserve (UGR), 2006). Because of the international appeal for its conservation (CARNIVORA, 2008), particularly in southern Africa, empirical studies for estimating the abundance and distribution of southern ground hornbills in Ugalla, and indeed across the country, are of chief importance.

Most of the species in our study showed road avoidance behavior at least in the presence of our survey vehicle. This could be a good indication of exploitation intensity (e.g. Setsaas et al., 2007). With the exception of the giraffe, most individuals of all species with density estimates were observed at a truncation distance of at least 50 m. Giraffes were frequently seen browsing near the survey roads (<50 m from the centre of the road). The giraffe is a national symbol of Tanzania (Kaltenborn, Nyahongo, & Mayengo, 2003), and thus not included in hunting quotas. Since trophy hunting clients visiting Ugalla shoot animals from cars, and off-road driving in search of the quarry is not encouraged (Wilfred, 2012), giraffe do not seem to be afraid of vehicles and roads. However, the total density of giraffe was less than in Katavi National Park where hunting is not permitted (Caro, 1999b). This may be attributed to illegal hunting, which normally takes place on foot in the interior areas of the reserve far from roads to avoid game rangers (Wilfred & MacColl, 2014). Baran et al. (2008) report that the giraffe is a priority species in illegal subsistence hunting, targeted by poachers because it provides a substantial amount of meat (J. Lymo, pers. comm.). During the survey, we frequently encountered remnants of giraffe killed by poachers (pers. obs.).

Group sizes and sex ratios

Animals at Ugalla east were observed in larger groups than Ugalla west. In other wildlife areas in western

Tanzania exploited species tend to congregate in either larger or smaller groups in response to pressure from hunting (Caro, 1999c). The impact of human disturbance on reducing group sizes of ungulate species has also been reported elsewhere, such as in Israel (Manor & Saltz, 2003). Similarly, a study of the status of the white-lipped peccary in the Calakmul Biosphere Reserve in Mexico found that the species in non-hunting areas congregate in larger groups than in hunting areas (Reyna-Hurtado, 2009).

Sex ratios did not statistically differ between the hunting sites, but most of the species had sex ratios significantly skewed towards female. While this is common in nature (FitzGibbon & Lazarus, 1995), studies suggest that the pattern is more pronounced in exploited populations (FitzGibbon & Lazarus, 1995; Marealle, Fossøy, Holmern, Stokke, & Røskoft, 2010; Milner et al., 2007; Milner-Gulland, Bennett, & the SCB 2002 Annual Meeting Wild Meat Group, 2003; Setsaas et al., 2007). Further research is required to evaluate the relevance of group size and sex ratio differences in monitoring exploited species with respect to hunting sites in Ugalla.

Implications for conservation

The intention of this study was to define some parameters that might positively influence the conservation of the exploited wildlife in Ugalla Game Reserve. The analyses of density, group size and sex ratio suggest that the status of wildlife varies spatially across the reserve. This indicates the need for an in depth assessment of Ugalla wildlife in the context of the effectiveness of conservation and of consumptive use.

The observed variation among species suggests that different species in the reserve respond differently to the intensity of wildlife utilization, which is also the case in previous studies elsewhere (Caro, 2008; Caro, 1999a, 1999c; Naranjo & Bodmer, 2007; Reyna-Hurtado & Tanner, 2007). Therefore, reliable and up-to-date species-specific population density and other population parameters should be carefully considered when deciding hunting quotas and other conservation measures, as is also argued by Caro et al. (1998).

Our species estimates may be influenced by environmental factors such as the distribution of water points within the reserve. For instance, hippopotami are susceptible to prolonged dry seasons when the main rivers in the reserve shrink and form chains of pools which become more crowded (J. Lymo, pers. comm.). In most cases this results in hippopotamus 'die-offs' (Caro, 2008). This is another reason why future studies should include habitat characteristics in wildlife status evaluations.

Appendix I.

Species sighted, total number of observations (N), mean group size (MGS, number of observations in brackets), density estimates (D [individuals km^{-2}] \pm standard error [S.E.]). Z-values and probabilities-p based on Mann-Whitney U-tests are also presented to test for significant differences in group sizes and densities between Ugalla east (East) and Ugalla west (West) hunting sites. Species are listed in decreasing total number of observations. Where species have the same total number of observations, alphabetical order is followed.

| Species | N | East | West | For group size | | East | West | Total | For density | |
|--|----|-----------|-----------|----------------|-------|---------------------|---------------------|---------------------|-------------|-------|
| | | MGS | MGS | Z-value | P | $D \pm \text{S.E.}$ | $D \pm \text{S.E.}$ | $D \pm \text{S.E.}$ | Z-value | P |
| Impala (<i>Aepyceros melampus</i>) | 86 | 10.21(39) | 10.91(47) | -0.203 | 0.839 | 2.19 ± 0.44 | 1.75 ± 0.55 | 1.97 ± 0.23 | -0.642 | 0.521 |
| Common warthog (<i>Phacochoerus africanus</i>) | 51 | 2.20(25) | 2.46(26) | -0.355 | 0.722 | 0.66 ± 0.20 | 0.24 ± 0.17 | 0.45 ± 0.11 | -2.934 | 0.003 |
| Topi (<i>Damaliscus korrigum</i>) | 50 | 4.73(37) | 6.92(13) | -1.928 | 0.054 | 1.72 ± 0.20 | 0.91 ± 0.62 | 1.30 ± 0.16 | -2.605 | 0.009 |
| Oribi (<i>Ourebia ourebi</i>) | 38 | 2.14(21) | 2.17(17) | -0.140 | 0.888 | 0.90 ± 0.45 | 0.58 ± 0.37 | 0.76 ± 0.48 | -1.734 | 0.083 |
| Helmeted guinea fowl (<i>Numida meleagris</i>) | 34 | 11.54(16) | 8.62(18) | -0.611 | 0.541 | 6.75 ± 2.06 | 3.39 ± 1.88 | 5.07 ± 1.77 | -2.605 | 0.009 |
| Bohor reedbuck (<i>Redunca redunca</i>) | 33 | 2.32(19) | 2.50(14) | -0.444 | 0.657 | 0.33 ± 0.38 | 0.39 ± 0.49 | 0.33 ± 0.46 | -0.863 | 0.388 |
| Waterbuck (<i>Kobus defassa</i>) | 33 | 3.90(10) | 4.00(23) | -0.040 | 0.968 | 0.20 ± 0.15 | 0.19 ± 0.05 | 0.21 ± 0.06 | -0.928 | 0.353 |
| Southern ground hornbill (<i>Bucorvus cafer</i>) | 26 | 3.73(15) | 3.72(11) | -0.370 | 0.711 | 0.51 ± 0.24 | 0.32 ± 0.18 | 0.42 ± 0.22 | -1.359 | 0.174 |
| Hippopotamus (<i>Hippopotamus amphibius</i>) | 21 | 6.13(16) | 9.40(5) | -0.247 | 0.805 | 1.56 ± 2.82 | 0.43 ± 1.32 | 0.99 ± 1.42 | -2.464 | 0.006 |
| Giraffe (<i>Giraffa camelopardalis</i>) | 19 | 4.40(10) | 2.22(9) | -1.629 | 0.103 | 0.60 ± 0.79 | 0.49 ± 0.61 | 0.55 ± 0.73 | -0.825 | 0.409 |
| Hartebeest (<i>Alcelaphus buselaphus</i>) | 17 | 6.09(11) | 6.17(6) | -0.051 | 0.960 | 0.49 ± 0.75 | 0.46 ± 0.88 | 0.48 ± 0.84 | -1.622 | 0.095 |
| African elephant (<i>Loxodonta africana</i>) | 13 | 4.00(10) | 1.67(3) | -1.159 | 0.246 | | | | | |
| Olive baboon (<i>Papio anubis</i>) | 9 | 7.83(6) | 4.33(3) | -0.651 | 0.515 | | | | | |
| Sable antelope (<i>Hippotragus niger</i>) | 9 | 5.33(4) | 4.33(5) | -0.664 | 0.507 | | | | | |
| Bushbuck (<i>Tragelaphus scriptus</i>) | 7 | 1.01(4) | 2.10(3) | -1.936 | 0.053 | | | | | |
| Roan antelope (<i>Hippotragus equinus</i>) | 7 | 4.00(4) | 4.33(3) | 0.000 | 1.000 | | | | | |
| African buffalo (<i>Syncerus caffer</i>) | 6 | 9.50(3) | 17.00(3) | -0.775 | 0.439 | | | | | |
| Egyptian goose (<i>Alopochen aegyptiaca</i>) | 6 | 9.75(4) | 2.33(2) | | | | | | | |
| Greater kudu (<i>Tragelaphus strepsiceros</i>) | 6 | 2.48(6) | 0.00(0) | | | | | | | |
| Nile crocodile (<i>Crocodylus niloticus</i>) | 5 | 7.20(3) | 4.60(2) | | | | | | | |
| Vervet monkey (<i>Chlorocebus pygerythrus</i>) | 5 | 3.62(3) | 2.30(2) | | | | | | | |
| Common Duiker (<i>Sylvicapra grimmia</i>) | 4 | 1.00(1) | 1.00(3) | | | | | | | |
| Marabou Stork (<i>Leptoptilos crumeniferus</i>) | 4 | 1.85(3) | 1.00(1) | | | | | | | |
| Eland (<i>Taurotragus oryx</i>) | 3 | 3.50(2) | 1.00(1) | | | | | | | |
| Kirk's dik-dik (<i>Madoqua kirkii</i>) | 3 | 2.00(1) | 2.00(2) | | | | | | | |
| Open bill stork (<i>Anastomus lamelligerus</i>) | 3 | 2.00(2) | 1.00(1) | | | | | | | |
| Plains zebra (<i>Equus burchelli</i>) | 3 | 0.00(0) | 6.59(3) | | | | | | | |
| Spotted hyena (<i>Crocuta crocuta</i>) | 3 | 3.50(2) | 2.00(1) | | | | | | | |
| White-backed vulture (<i>Gyps africanus</i>) | 3 | 18.00(1) | 15.00(2) | | | | | | | |
| African fish-eagle (<i>Haliaeetus vocifer</i>) | 2 | 1.50(2) | 0.00(0) | | | | | | | |
| African wild dog (<i>Lycaon pictus</i>) | 2 | 6.50(2) | 0.00(0) | | | | | | | |
| Bushpig (<i>Potamochoerus larvatus</i>) | 2 | 3.00(1) | 2.00(1) | | | | | | | |
| Great egret (<i>Ardea alba</i>) | 2 | 1.00(1) | 3.00(1) | | | | | | | |
| Grey heron (<i>Ardea cinerea</i>) | 2 | 2.00(2) | 1.00(1) | | | | | | | |
| Hadada ibis (<i>Bostrychia hagedash</i>) | 2 | 1.00(1) | 1.00(1) | | | | | | | |
| Hamerkop (<i>Scopus umbretta</i>) | 2 | 1.00(2) | 0.00(0) | | | | | | | |
| Little egret (<i>Egretta garzetta</i>) | 2 | 5.00(2) | 0.00(0) | | | | | | | |
| Ostrich (<i>Struthio camelus</i>) | 2 | 1.00(1) | 1.00(1) | | | | | | | |
| Saddle-billed stork (<i>Ephippiorhynchus senegalensis</i>) | 2 | 3.00(1) | 2.00(1) | | | | | | | |
| Shoebill (<i>Balaeniceps rex</i>) | 2 | 1.00(1) | 0.00(0) | | | | | | | |
| Spur-winged goose (<i>Plectropterus gambensis</i>) | 2 | 12.38(2) | 0.00(0) | | | | | | | |

(continued)

Appendix I. Continued.

| Species | N | East | West | For group size | | East | West | Total | For density | |
|--|---|---------|---------|----------------|---|----------|----------|----------|-------------|---|
| | | MGS | MGS | Z-value | P | D ± S.E. | D ± S.E. | D ± S.E. | Z-value | P |
| Yellow-billed stork (<i>Mycteria ibis</i>) | 2 | 9.00(1) | 7.00(1) | | | | | | | |
| African savanna hare (<i>Lepus microtis</i>) | 1 | 1.00(1) | 0.00(0) | | | | | | | |
| glossy ibis (<i>Plegadis falcinellus</i>) | 1 | 1.00(1) | 0.00(0) | | | | | | | |

Acknowledgements

We thank the Commonwealth Scholarship Commission for financial support. The Wildlife Division of Tanzania granted permission to conduct fieldwork in Ugalla Game Reserve (UGR). We also thank the project manager of UGR at the time of the study, Mr. Edward Lutabingwa, and his assistant Mr. Japhary Lymo, for their huge support and encouragement during the fieldwork. Abbas Mgweni, Denis Mwangwa, Charles Gagi, Abdallah Mdee, George Mwanakusha, Anyabwire Mwamaso, and Aristedi Msaki provided invaluable assistance during the transect surveys. Last but not least, we cordially thank Tim Caro for the wildlife survey manuscripts.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: The work was carried out with the assistance of a Commonwealth Scholarship awarded to Paulo Wilfred.

References

- Baran, P., Mmbaga, A., Godwin, E., Lobora, A., Durrant, S. M., Foley, C., & Ramadhani, J. (2008). *Survey of Ugalla Game Reserve, Urambo, Mpanda and Sikonge Districts, Western Tanzania*. Survey Report. Tanzania Wildlife Research Institute, Arusha, Tanzania.
- Bassett, T. J. (2005). Card-carrying hunters, rural poverty, and wildlife decline in northern Côte d'Ivoire. *The Geographical Journal*, 170, 71–82.
- Begon, M., Townsend, C. R., & Harper, J. L. (2006). *Ecology: From individuals to ecosystems*. Oxford, England: Blackwell Publishing Ltd.
- Birdlife International [BI] (2010). *Species factsheet: Bucorvus cafer*. Retrieved from <http://www.birdlife.org/>
- Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J. L. (1993). *Distance sampling: Estimating abundance of biological populations*. London, England: Chapman and Hall.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. Oxford, England: Oxford University Press.
- CARNIVORA. (2008). *Southern Ground-Hornbill – Bucorvus cafer*. Retrieved from <http://carnivoraforum.com/>
- Caro, T. (2008). Decline of large mammals in the Katavi-Rukwa ecosystem of western Tanzania. *African Zoology*, 43, 99–116.
- Caro, T. (1999a). Densities of mammals in partially protected areas: The Katavi ecosystem of western Tanzania. *Journal of Applied Ecology*, 36, 205–217.
- Caro, T. (1999b). Abundance and distribution of mammals in Katavi National Park, Tanzania. *African Journal of Ecology*, 37, 305–313.
- Caro, T. (1999c). Demography and behaviour of African mammals subject to exploitation. *Biological Conservation*, 91, 91–97.
- Caro, T. (1999d). Conservation monitoring: Estimating mammal densities in woodland habitats. *Animal Conservation*, 2, 305–315.
- Caro, T. M. (2001). Species richness and abundance of small mammals inside and outside an African national park. *Biological Conservation*, 98, 251–257.
- Caro, T., Pelkey, N., Borner, M., Severre, E. L. M., Campbell, K. L. I., Huish, S. A., ... Woodworth, B. L. (1998). The impact of tourist hunting on large mammals in Tanzania: An initial assessment. *African Journal of Ecology*, 36, 321–346.
- Caro, T., Young, C. R., Cauldwell, A. E., & Brown, D. D. E. (2009). Animal breeding systems and big game hunting: Models and application. *Biological Conservation*, 142, 909–929.
- Coltman, D. W., O'donoghue, P., Jorgenson, J. T., Hogg, J. T., Strobeck, C., & Festa-Bianchet, M. (2003). Undesirable evolutionary consequences of trophy hunting. *Nature*, 426, 655–658.
- Davies, G., & Brown, D. (Eds.) (2007). *Bushmeat and livelihoods: Wildlife management and poverty reduction*. London, England: Blackwell Publishing Ltd and Zoological Society of London.
- Fa, J. E., Seymour, S., Dupain, J., Amin, R., Albrechtsen, L., & Macdonald, D. (2006). Getting to grips with the magnitude of exploitation: Bushmeat in the Cross-Sanaga rivers region, Nigeria and Cameroon. *Biological Conservation*, 129, 497–510.
- Festa-Bianchet, M. (2003). Exploitative wildlife management as a selective pressure for the life-history evolution of large mammals. In: M. Festa-Bianchet, & M. Apollonio (Eds.). *Animal behaviour and wildlife conservation* (pp. 191–207). Washington, DC: Island Press.
- FitzGibbon, C. D., & Lazarus, J. (1995). Anti-predator behaviour of Serengeti ungulates: Individual differences and population consequences. In: A. R. E. Sinclair, & P. Arcese (Eds.). *Serengeti II – Dynamics, management, and conservation of an ecosystem* (pp. 274–296). Chicago, IL: The University of Chicago Press.
- Flesher, K. M., & Laufer, J. (2013). Protecting wildlife in a heavily hunted biodiversity hotspot: A case study from the Atlantic Forest of Bahia Brazil. *Tropical Conservation Science*, 6, 181–200.
- Ginsberg, J. R., & Milner-Gulland, E. J. (1994). Sex-biased harvesting and population dynamics in ungulates: Implications for

- conservation and sustainable use. *Conservation Biology*, 8, 157–166.
- Hazellhurst, S., & Milner, D. (2007). *Watershed assessment of the Ugalla landscape*. USDA, Forest Service Technical Assistance Trip Report. Retrieved from www.rmportal.net/library/content/usda-forest-service/USFS_Watershed_Assessment_of_the_Ugalla_Landscape.pdf/view
- Kaltenborn, B. P., Nyahongo, J. W., & Mayengo, M. (2003). *People and wildlife interactions around Serengeti National Park, Tanzania*. NINA Project Report 22. Trondheim, Norway: Norwegian Institute for Nature Research.
- Lamprey, R. H., Buhanga, E., & Omoding, J. (2003). *A study of wildlife distributions, wildlife management systems, and options for wildlife-based livelihoods in Uganda*. Kampala, Uganda: International Food Policy Research Institute & USAID.
- Lindsey, P. A., Balmea, G., Beckerc, M., Beggd, C., Bentoe, C., Bocchinof, C., . . . Zisadza-Gandiwa, P. (2013). The bushmeat trade in African savannas: Impacts, drivers and possible solutions. *Biological Conservation*, 160, 80–96.
- Magie, F. J., Holmern, T., Stokke, S., Mlingwa, C., & Røskft, E. (2009). Does illegal hunting affect density and behaviour of African grassland birds? A case study on ostrich (*Struthio camelus*). *Biodiversity & Conservation*, 18, 1361–1373.
- Manor, R., & Saltz, D. (2003). Impact of human nuisance disturbance on vigilance and group size of a social ungulate. *Ecological Applications*, 13, 1830–1834.
- Marealle, W. N., Fossey, F., Holmern, T., Stokke, B. G., & Røskft, E. (2010). Does illegal hunting skew Serengeti wildlife sex ratios? *Wildlife Biology*, 16, 419–429.
- Mbwambo, L. (2003). Off-forest tree resources conservation and tree planting in selected villages in Tabora Region, Tanzania. *TAFORI Newsletter*, 3, 26–31.
- Mills, L. S. (2007). *Conservation of wildlife populations: Demography, genetics and management*. Oxford, England: Blackwell Publishing Ltd.
- Milner, J. M., Bonenfant, C., Mysterud, A., Gaillard, J. M., Csányi, S., & Stenseth, N. C. (2006). Temporal and spatial development of red deer harvesting in Europe: Biological and cultural factors. *Journal of Applied Ecology*, 43, 721–773.
- Milner, J. M., Nilsen, E. B., & Andreassen, H. P. (2007). Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology*, 21, 36–47.
- Milner-Gulland, E. J., Bennett, E. L., & the SCB 2002 Annual Meeting Wild Meat Group. (2003). Wild meat: The bigger picture. *Trends in Ecology & Evolution*, 7, 351–357.
- Morrison, K., Daly, B., Burden, D., Engelbrecht, D., Jordan, M., Kemp, A., . . . Friedmann, Y. (Eds.). (2005). *Southern ground hornbill, PHVA workshop report*. Johannesburg, South Africa: Conservation Breeding Specialist Group, Southern Africa & Endangered Wildlife Trust.
- Naranjo, E. J., & Bodmer, R. E. (2007). Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. *Biological Conservation*, 138, 412–420.
- Njoroge, P., Yego, R., Muchane, M., Githiru, M., Njeri, T., & Giani, A. (2009). A survey of the large and medium sized mammals of Arawale National Reserve, Kenya. *Journal of East African Natural History*, 98, 119–128.
- Novaro, A. J., Redford, K. G., & Bodmer, R. E. (2000). Effect of hunting in source-sink systems in the neotropics. *Conservation Biology*, 14, 713–721.
- Pollard, J. H., Palka, K., & Buckland, S. T. (2002). Adaptive line transect sampling. *Biometrics*, 58, 862–870.
- Pulliam, H. R. (1988). Sources, sinks and population regulation. *American Naturalist*, 132, 652–661.
- Pulliam, H. R., & Danielson, B. J. (1991). Sources, sinks and habitat selection: A landscape perspective on population dynamics. *American Naturalist*, 137, 50–66.
- Reyna-Hurtado, R. (2009). Conservation status of the white-lipped peccary (*Tayassu pecari*) outside the Calakmul Biosphere Reserve in Campeche, Mexico: A synthesis. *Tropical Conservation Science*, 22, 159–172.
- Reyna-Hurtado, R., & Tanner, G. W. (2007). Ungulate relative abundance in hunted and non-hunted sites in Calakmul Forest (southern Mexico). *Biodiversity and Conservation*, 16, 743–756.
- Setsaas, T., Holmern, T., Mwakalebe, G., Stokke, S., & Røskft, E. (2007). How does human exploitation affect impala populations in protected and partially protected areas? A case study from the Serengeti Ecosystem, Tanzania. *Biological Conservation*, 136, 563–570.
- Smith, D. A. (2008). The spatial patterns of indigenous wildlife use in western Panama: Implications for conservation management. *Biological Conservation*, 141, 925–937.
- Solberg, E. J., Saether, B. E., Strand, O., & Loison, A. (1999). Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology*, 68, 186–204.
- Swenson, J. E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R., & Wabakken, P. (1997). Infanticide caused by hunting of male bears. *Nature*, 386, 450–451.
- Taylor, V. J., & Dunstone, N. (Eds.). (1996). *The exploitation of mammal populations*. London, England: Chapman & Hall.
- Thiollay, J. M. (2006). Large bird declines with increasing human pressure in savanna woodlands (Burkina Faso). *Biodiversity & Conservation*, 15, 2085–2108.
- Thomas, D. K. (1961). The Ugalla River Controlled Area. *The Journal of the Tanganyika Society*, 57, 126–130.
- Thomas, L., Laake, J. L., Strindberg, S., Marques, F. F. C., Buckland, S. T., Borchers, D. L., . . . Marques, T. A. (2006). *Distance 5.0. release 1*. Research Unit for Wildlife Population Assessment, University of St. Andrews, England. Retrieved from <http://www.ruwpa.st-and.ac.uk/distance/>
- Topp-Jørgensen, E., Nielsen, M. R., Marshall, A. R., & Pedersen, U. (2009). Relative densities of mammals in response to different levels of bushmeat hunting in the Udzungwa Mountains, Tanzania. *Tropical Conservation Science*, 2, 70–87.
- Trail, P. W. (2007). African hornbills: Keystone species threatened by habitat loss, hunting and international trade. *Ostrich*, 78, 609–613.
- Ugalla Game Reserve (UGR). (2006). *A checklist of plants, animals and birds in Ugalla Game Reserve*. Unpublished Report, Ugalla Game Reserve Project, Tabora, Tanzania.
- van Essen, L. P. (2006). Southern ground hornbill. *African Indaba e-Newsletter*, 4, 4[^].
- Waltert, M., Meyer, B., & Kiffner, C. (2009). Habitat availability, hunting or poaching: What affects distribution and density of large mammals in western Tanzania woodlands? *African Journal of Ecology*, 47, 737–746.
- Waltert, M., Meyer, B., Shanyangi, M. W., Balozi, J. J., Kitwara, O., Qolli, S., . . . Mühlenberg, M. (2008). Foot surveys of large mammals in woodlands of western Tanzania. *Journal of Wildlife Management*, 72, 603–610.

- Weber, M. (2000). *Effects of hunting on tropical deer populations in South-Eastern Mexico* (MSc Thesis), Royal Veterinary College, University of London, London, England.
- Wilfred, P. (2012). Trophy hunting and trophy size in Ugalla Game Reserve, western Tanzania. *Tanzania Journal of Science*, 38, 111–122.
- Wilfred, P., & MacColl, A. D. C. (2014a). Legal subsistence hunting trends in the Ugalla ecosystem of western Tanzania. *European Journal of Wildlife Research*, 60, 371–376.
- Wilfred, P., & MacColl, A. D. C. (2014b). The pattern of poaching signs in Ugalla Game Reserve, western Tanzania. *African Journal of Ecology*, 52, 543–551.