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Consequences of different forms of conservation for large mammals in Tanzania: preliminary analyses

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Summary

We examined the effects of protection from human activities and effects of tourist hunting on densities of 21 large mammal species in Tanzania. Aerial censuses revealed that mammal biomass per km^2 was highest in National Parks. Densities of nine ungulate species were significantly higher in National Parks and Game Reserves than in areas that permitted settlement; these tended to be the larger species favoured by poachers. The presence of tourist hunters had little positive or negative impact on ungulate densities, even for sought-after trophy species; limited ground censuses confirmed these results. Our analyses suggest that prohibition of human activity, backed up by on-site enforcement, maintains ungulate populations at relatively high densities, and challenge the idea that enforcement is only effective when spending is high.

Key words: conservation area, mammal densities, protection, Tanzania, tourist hunting

Résumé

Nous avons examiné les effets de la protection contre toute activité humaine et ceux de la chasse sportive sur la densité de 21 espèces de grands mammiferes en Tanzanie. Les recensements aériens ont montré que la biomasse de mammifères par km^2 était la plus élevée dans les parcs nationaux. La densité de neuf espèces d'ongulés était significativement plus élevée dans les parcs nationaux et dans les réserves de faune que dans les régions où les installations humaines sont autorisées; ces espèces étaient principalement les plus grandes de celles que les braconniers recherchent. La présence de chasseurs sportifs avait peu d'impact, positif ou négatif, sur la densité des ongulés, même pour les espèces dont les trophées sont les plus prisés. Des recensements limités, effectués au sol, ont confirmés ces résultats. Nos analyses suggèrent que l'interdiction de toute activité humaine, renforcée par une surveillance sur le terrain, peut maintenir la densité des populations d'ongulés à un niveau relativement élevé, et remettent en question l'idée que l'application de la loi n'est efficace que si on y consacre beaucoup d'argent.

Introduction

Habitat conservation is widely recognized as the best method for maintaining animal populations in the long term (Western & Pearl, 1989; Bibby *et al.*, 1992). Conservation areas range from nature reserves and national parks, from which most human activities are excluded, to multiple use and managed areas in which economic activities and even human habitation is permitted (IUCN, 1991; World Resources Institute, 1994). Although it is usually assumed that national parks offer the best type of legal protection for wildlife (e.g. Campbell & Hofer, 1995), an influential study of black rhinoceros (*Diceros bicornis* Linnaeus) and elephant (*Loxondata africana* Blumenbach) poaching in Zambia showed that population declines of these species could be stemmed only where conservation spending was high (Leader-Williams & Albon, 1988; Leader-Williams *et al.*, 1990). The implication is that in those developing countries which lack financial resources and infrastructure, animals will be inadequately protected in parks. At present, however, there are too few data to assess the effectiveness of protection in Eastern Africa.

In many African countries, large areas are set aside for tourist hunting to generate revenue for the government and to protect wildlife from human encroachment. Nevertheless, there is a long standing argument as to whether consumptive tourism acts as a deterrent to local exploitation of animal populations, as hunting operators often argue, or whether wildlife fares badly in tourist-hunted areas (e.g. Taylor & Dunstone, 1996). Again, there are virtually no data that specifically address the consequences of tourist hunting on animal densities in developing countries.

Here, we use aerial censuses of 21 species collected in ten census zones across Tanzania that incorporate four types of conservation area, as well as data from ground transects and information on anti-poaching effort, to address both issues. Specifically, we examined how the absence of human settlement, enforced by park rangers or game scouts, and the presence of tourist hunters affect densities of mammal populations in the country.

Methods

Legally protected areas in Tanzania

No temporary or permanent settlements are allowed in National Parks (NPs) apart from park headquarters; nor are livestock, beekeeping, hunting, fishing or timber extraction tolerated. These laws are enforced by Tanzania National Park (TANAPA) rangers based at a headquarters and ranger posts throughout the park. Non-consumptive tourism is encouraged in NPs and a substantial portion of revenue is retained for their operating budget, with the rest going to central Government. Game Reserves (GRs) are subject to the same legal restrictions, except that they allow for limited hunting under licence, usually by tourist visitors, for ≈ 6 months of the year. The Department of Wildlife is responsible for GRs, which it divides into blocks that are leased out to hunting companies for all or part of the hunting season, often for several years in succession (although not all blocks are utilized each year). Hunting quotas are set by the Department of Wildlife (PAWM, 1995a) and, in recent years, most hunting blocks have been granted allocations; some have also been subdivided to increase revenue (Sommerlatte, 1995). Game Reserve laws are enforced year-round by game scouts stationed at a headquarters and sometimes at outlying posts. Much of the revenue from hunting allocations goes directly to central Government, and additional sums are sent to the Tanzania Wildlife Protection Fund. Remaining revenue goes to the Wildlife Department for employee salaries, including its game scout field force (PAWM, 1995b). The Wildlife Department has a lower operating budget than TANAPA.

Game Controlled Areas (GCAs) allow for settlement, cattle grazing and timber extraction, but hunting is regulated within them. Regional and District Game Officers are normally responsible for issuing limited hunting permits to Tanzanians or resident expatriates. Since 1990, however, increasing numbers of GCAs have been made available to companies bringing in tourist hunters (PAWM, 1995a). Open Areas (OAs) are similar to GCAs, except that their boundaries are not well delineated. Some OAs have also been made available to hunting companies in recent years. Department of Wildlife game scouts accompany tourist hunters on hunting trips in GRs, GCAs and OAs, but they do not patrol or live in GCAs or OAs. Tanzanians cannot own land in GCAs or OAs, but can gain direct economic benefit by settling, farming and grazing cattle there, whereas resident Tanzanian hunters in nearby towns can eat or sometimes sell animals that they hunt.

We compared wildlife densities in these legally protected areas, but took account of whether the area was open to tourist hunting operations around the time that an aerial census was conducted. Three hunting blocks in censused GRs which had not been granted hunting allocations at the time were, together with NPs, placed in a new classification 'Protection Yes, Hunters No' (P + H–). (Ngorongoro Conservation

Area, a patrolled area in which no hunting is permitted, is occupied by Maasai and their livestock, and could not be included in this classification and was thus excluded). Censused hunting blocks in GRs that had been granted hunting allocations were classified as 'Protection Yes, Hunters Yes' (P + H +). Censused areas of GCAs and OAs that had been leased to hunting companies were classified as 'Protection No, Hunters Yes' (P– H +). Except for hunting blocks in Mkomazi and Burigi–Biharamulo census zones (Fig. 1), aerial censuses over H + areas reflected the impact of tourist hunting because they were conducted after years of sustained hunting activity (Caro *et al.*, 1998). GCAs and OAs with no tourist hunters were classified as Protection No, Hunters No'(P– H–). Note that an unknown amount of resident hunting probably occurred in most GCAs and OAs when tourist hunters were not in the field.

Aerial censuses

Animal populations in wildlife areas of Tanzania have been surveyed regularly from the air over an increasingly large geographical area (reviewed in McNaughton & Campbell, 1991). Most surveys were conducted by the Frankfurt Zoological Society, then by the Serengeti Ecological Monitoring Programme (SEMP) and now by Tanzanian Wildlife Conservation Monitoring (TWCM), using radar-altimeter equipped Cessna light aircraft.

Our methodology followed that described by Norton-Griffiths (1978) for systematic reconnaissance flights (Campbell, 1988a,b; Campbell & Borner, 1995). Surveys were conducted in ten geographically-separated census zones (Fig. 1) in wet (December–June) and dry (July–November) seasons, such that each area was covered at least once every 3 years if possible. The majority were centred on NPs or GRs, but included GCAs and OAs on the periphery (Table 1). After a survey was completed, the point at which the aircraft crossed between areas of different legal status was noted, thus, from SEMP and TWCM reports it was possible to calculate the total area surveyed, the number of animals of each species counted (Table 2), and the extent of human activities in those areas, and hence to derive densities. Densities control for differences in area sampled and were used in preference to species richness or changes in density over time, as the same species were recorded in many different areas and time series data were generally unavailable (but see Caro *et al.*, 1998). To provide a pooled measure of density, information on mammal biomass, calculated from an average of male and female body weights (from Estes, 1991), is also provided. Accurate information on hunting block allocations, necessary to reclassify protected areas into different types of conservation area, were only available from 1988 onwards, thus, we used censuses from October 1987 (the end of the 1987 hunting season) until October 1994.

Rainfall and vegetation type change considerably across Tanzania. Differences in rainfall affect primary productivity and hence herbivore densities, whereas differences in vegetation are associated with different ungulate species. Human pressure also varies geographically as a function of population density and proximity to cities. To take account of all these geographical influences, for each individual census we calculated each species' density and densities of human activities over the total area within each census zone, then calculated the density for each land use area within that census zone, and subtracted that from the census zone overall density to yield a standardized density for that species.

If more than one survey of a census zone had been conducted (Table 1), the average of standardized scores for each land use area was calculated for wet- and dry-season counts separately, and an average of these seasonal averages was taken. Given that wet- and dry-season surveys within a census zone are primarily measuring the same population at different levels of dispersion and location, it was felt that averaging them gave a better picture of mean density, even when those estimates differed significantly across seasons. Statistical tests were conducted on these average standardized scores. Although this method takes regional habitat into account, standardized scores are difficult to interpret visually. Therefore, in figures and text true densities are presented, i.e. densities averaged over same season counts, then between seasons, and finally across the same type of conservation area across the whole country, but it may be misleading to compare true densities directly by eye.

Data were analysed using non-parametric statistics, because densities were not normally distributed and sample sizes for certain species in some land use areas were small. A more sophisticated multivariate approach, such as Generalized Linear Models (GLM), was not presented; because GLM estimates were not robust owing to small sample sizes and high variability in this data set. Also, data were nonnormal for most species, which meant abandoning standard normal GLM in favour of other link functions and distributional assumptions. Given that the species being studied followed no consistent link function or probability distribution, comparability among the parameters would have been difficult. Thus, it was decided to abandon making any distributional assumptions about the data and to use non-parametric tests (Seigel & Castellon, 1988) which prevent statistical examination of the interaction of protection and tourist hunting. Comparisons were made using the more conservative Mann–Whitney *U*-test, rather than the Kruskal–Wallis test; this pairwise test had the added advantage of pinpointing where differences between samples lay.

To determine the influence of protection on species' densities, P+H− were first pooled with P+H+ and these were compared with P−H+ and P−H− taken together. To determine the efficacy of protection without, and then with, tourist hunting, P+H− were next compared with P−H−, and P+H+ with P−H+, respectively.

To investigate the influence of tourist hunting, P+H+ was compared with P+H−, and P−H+ with P−H−, although this latter comparison is confounded by the presence of resident hunting, particularly in P−H− areas. (It was felt inappropriate to pool conservation areas here because it was found previously that differences between P+H− and P−H− were marked.)

Road censuses

To provide an independent comparison of the effects of tourist hunting on mammal densities, a series of road transects were made (by T.M.C.) through three NPs and adjacent GRs in southern Tanzania during the late dry season of 1993. Known distances were driven along established but little used tracks during daylight hours, usually before 11.00 and after 16.00 hours. Records were made of the number of individual animals of all ages seen for 28 species of mammal, most of which are shot by tourist hunters in those GRs in which transects were driven. Transects were classified as open, semi-open and closed habitats and strip widths were conservatively assigned as 100, 75 and 50 m, respectively, either side of the track. For each transect, densities of each species were calculated by summing the total number of individuals seen and dividing by the transect length multiplied by its width. We then compared transects from GRs with those from NPs.

Anti-poaching effort

To determine more precisely the way in which protection affected animal populations, data on anti-poaching effort were collected by E.L.M.S. visiting NP and GR local headquarters, and head offices in Arusha and Dar es Salaam. Records included the annual budget allocated and number of patrols conducted per month between 1981 and 1992, and the number of rangers or game scouts, officers and wardens present and the number of working vehicles and working rifles in 1992. These figures were subsequently divided by the area of each NP or GR to yield densities of people or items per km^2. These densities were then matched to mammal densities as determined by the mean of mean wet- and dry-season densities across seven areas for which both types of data were available: Mikumi NP, Ruaha NP, Tarangire NP, Mkomazi GR, Moyowosi–Kigosi GR, Rungwa GR and Selous GR. These represented a wide geographical spread of protected areas across the country.

All statistical analyses were two-tailed and the null hypothesis was rejected at the 0.05 level. However, for the sake of caution, all significance values below 0.1 are reported.

Results

Overall biomass in different areas

Mammal biomass in sub-Saharan Africa is either reported exclusive of elephants because they contribute disproportionately to biomass and latterly have been subject to heavy poaching (Prins *et al.*, 1994; Dobson & Poole, 1998), or with them. Excluding elephants, biomass per km^2 was significantly higher in the P+H– conservation areas than in other areas (P+H− *vs.* P+H+, Ns=9,9 conservation areas, respectively, Mann–Whitney *U*-test, $z=2.163$ on standardized scores, $P=0.031$; P+H− *vs.* P−H+, Ns=9,23, $z=2.24$, $P=0.025$; P+H− *vs.* P−H−, Ns=9,18, $z=2.73$, $P=0.006$; Fig. 2). Including elephants, P+H– areas still contained a significantly greater biomass than P − H + (Ns = 9,23, z = 2.54, $P = 0.011$) and a marginally greater biomass than P − H − conservation areas (Ns = 9,18, z = 1.955, $P = 0.051$).

The influence of protection

Areas that both prohibited settlement and were protected by guards (i.e. NPs and GRs combined) contained significantly higher densities of nine out of the 21 species than did other areas (GCAs and OAs combined). These species were buffalo (Ns = 17,40 conservation areas, respectively, Xs = 2.93, 1.39 per km^2, z = 3.524 on standardized scores, $P < 0.001$), eland (Ns = 15,37, Xs = 0.19, 0.09 per km^2, z = 2.718, $P = 0.007$), giraffe (Ns = 17,40, Xs = 0.20, 0.22 per km^2, z = 2.059, $P = 0.04$), hartebeest (Ns = 17, 40, Xs = 0.51, 0.15 per km^2, z = 3.506, $P < 0.001$), roan antelope (Ns = 11, 18, Xs = 0.07, 0.02 per km^2, z = 2.880, $P = 0.004$), waterbuck (Ns = 16,37, Xs = 0.11, 0.16 per km^2, z = 3.701, $P < 0.001$) and zebra (Ns = 17, 40, Xs = 1.40, 0.93 per km^2, z = 3.445, $P < 0.001$). This was also true of two species that were difficult to count from the air: bushbuck (Ns = 11,25, Xs = 0.01, 0.02 per km^2, z = 2.617, $P = 0.009$) and hippopotamus (Ns = 10,18, Xs = 0.31, 0.12 per km^2, z = 2.639, $P = 0.008$). Taken together, these nine species were somewhat heavier and therefore carried greater quantities of edible flesh than ungulates whose densities were not significantly affected by protection (Median test using Fisher exact probability test, $P = 0.071$).

When the effects of protection were investigated without the influence of tourist hunting, the same species were found to benefit (Fig. 3). Buffalo, eland, giraffe, hartebeest and zebra were found at significantly higher densities in P + H– than in P– H– conservation areas (buffalo, Ns = 9,17 conservation areas, respectively, z = 2.562 on standardized scores, $P = 0.01$; eland, Ns = 8,15, z = 2.844, $P = 0.005$; giraffe, Ns = 9,17, z = 2.562, $P = 0.01$; hartebeest, Ns = 9,17, z = 2.669, $P = 0.008$; zebra, Ns = 9,17, z = 2.991, $P = 0.003$), and there were trends in the same direction for waterbuck (Ns = 8,20, z = 1.882, $P = 0.06$), hippopotamus (Ns = 4,10, z = 1.847, $P = 0.065$) and warthog (Ns = 9,17, z = 1.806, $P = 0.071$), although the last two were difficult to census accurately.

Comparing P + H + with P– H + areas, the following were found at higher densities in protected areas: bushbuck (Ns = 5,14 conservation areas, respectively, z = 2.317 on standardized scores, $P = 0.021$), although this result should be treated with caution, hartebeest (Ns = 8,23, z = 2.302, $P = 0.021$), roan antelope (Ns = 7,11, z = 2.951, $P = 0.003$) and waterbuck (Ns = 8,17, z = 3.207, $P = 0.001$). Buffalo (Ns = 8,23, z = 1.941, $P = 0.052$), sable antelope (Ns = 7.11, z = 1,768, $P = 0.077$) and zebra (Ns = 8,23, z = 1.851, $P = 0.064$) showed similar trends.

Examining the relationship between antipoaching effort per km^2 and species' densities across a sub-sample of protected areas, densities of buffalo and zebra were significantly positively correlated with density of working vehicles ($N = 6$ legally-protected areas, $r_s = 0.829$, $P = 0.042$; $N = 7$, $r_s = 0.821$, $P = 0.023$, respectively). Zebra densities were also significantly associated with the number of patrols per month ($N = 6$, $r_s = 0.829$, $P = 0.042$), and marginally associated with densities of rangers and their rifles ($N = 7$, $r_s = 0.679$, $P = 0.094$; $N = 7$, $r_s = 0.714$, $P = 0.071$, respectively).

The influence of tourist hunters

Aerial censuses

Comparing P + H + with P + H– conservation areas, the presence of tourist hunters was associated with significantly higher densities of sable antelope and perhaps small antelope (Ns = 7,6 conservation areas, respectively, z = 2.286, P = 0.022; N = 5,2, z = 1.937, P = 0.053, respectively; Fig. 3), although counts are unreliable for small antelope species. Conversely, tourist hunting was marginally associated with lowered densities of eland and giraffe (Ns = 7,8, z = –1.852, P = 0.064; Ns = 8,9, z = − 1.828, P = 0.068, respectively).

In the absence of protection, warthog densities were significantly higher in P − H + than in P − H − areas (Ns = 23,17 conservation areas, respectively, z = 2.722, $P = 0.007$), whereas roan antelope densities were marginally lower (Ns = 7,11, z = − 1.953, $P = 0.051$). Tourist hunters thus had little additional impact on mammal densities in the absence of protection.

Ground transects

Buffalo, elephant, giraffe and zebra densities were significantly lower in southern

GRs than in southern NPs. There were significantly higher densities of oribi and squirrel, and marginally greater densities of hyrax and sable antelope in GRs than in NPs (Table 3).

Human activity

There were significantly greater densities of villages and thorn stockades in areas without protection (GCAs and OAs) compared to those under protection (NPs and GRs) (Ns = 15,7 conservation areas, Xs = 0.06, 0.01/km^2, z = 2.435 on standardized scores, $P = 0.015$). Average densities of individual houses, and subsistence activities (fields and fallow pastures) and livestock were higher in areas without protection than in areas with protection, but not significantly so (houses, Ns = 17,8 conservation areas, Xs = 0.51, 0.08 per km^2; fields and pastures, Ns = 11,5, Xs = 1.22, 0.43 per km^2; livestock, Ns = 18,12, Xs = 4.25, 1.25 per km^2).

Figure 4 shows that there were higher densities of houses, subsistence activities, and tree felling activities in P−H− than in P−H+ areas, although differences were not significant. This probably reflects the fact that tourist hunting is allowed in some settled GCAs and OAs. In contrast, there was a greater density of poachers and poaching camps containing snares and meat in P−H+ than in P−H− areas (z = 1.976, $P = 0.048$) and a greater density in P−H+ than in P+H− areas (z = 2.041, $P = 0.041$; Fig. 4).

Poaching activity was negatively correlated with eight out of 21 species of mammal censused from the air, but achieved significance only in the case of elephants (N = 22 conservation areas, $r_s = -0.427$, $P = 0.048$). These eight species, buffalo, bushpig, eland, elephant, giraffe, kudu, topi, and zebra, tended to be heavier than the other 13 species (Median test using a Fisher exact probability test, $P = 0.1$).

Discussion

The majority of our findings are based on aerial censuses. These suffer from several shortcomings, the chief of which are difficulties in observing species in wooded habitats, and problems with seeing small or cryptic species (Norton-Griffiths, 1978; Krebs, 1989; Campbell & Hofer, 1995). Because different census zones are made up of different habitat types, we endeavoured to control for habitat differences by comparing mammal densities in different conservation areas within each census zone using standardized scores; conservation areas within each census zone differ little in habitat characteristics. Additionally, this method partially controls for any differences between flight crews taking part in different censuses. Differential species visibility cannot be controlled for in this way; instead we have exercised extreme caution in interpreting results for more cryptic species.

Despite these precautions, our results should be treated only as suggestive, as they involve censuses carried out over a vast geographical area, involve techniques that carry considerable measurement error, were conducted by different personnel, and the analyses necessitated condensation of many data sets. Nevertheless, they do provide a good first approximation of the factors affecting mammal populations in East Africa at the present time.

Human activity

Densities of human habitation, agricultural subsistence and tree felling operations were low in NPs and GRs. Prohibition of settlement enforced by teams of disciplined rangers or game scouts is therefore effective in protected areas of Tanzania. However, the fact that differences between protected and unprotected were, in most cases, non-significant suggests that human population pressure in rural areas is not particularly strong, although there are notable exceptions (e.g. Mara and Morogoro Regions). An alternative explanation, and one that we cannot assess, is that survey pilots refrained from flying over areas with high densities of human habitation. This would spuriously reduce densities of human activity in GCAs and OAs. The most important aspect of human activity may be cattle grazing, with average densities reaching 6.5 cows per km^2 in unprotected areas with no tourist hunting (principally OAs).

In unprotected areas there was a higher density of poachers and their activities in conservation areas allocated to tourist hunters than in those where no tourist hunting occurred. This may have been because somewhat higher densities of small antelope, bushbuck, eland, giraffe, hippopotamus, topi, warthog, wildebeest and zebra in these areas attracted poachers' attention (see Fig. 3). Arcese *et al.* (1995) showed that in the Serengeti National Park, buffalo, eland, giraffe, impala, topi, warthog and waterbuck are species favoured by poachers, whereas poachers favour buffalo, hippopotamus, and giraffe around Katavi National Park (H. Batiho, A. Kikote and R. Kusamba, personal communication). If poachers aggregate in areas containing abundant large species, their presence in tourist hunting blocks is not surprising. It is well known that poachers move into areas during the rains when tourist hunters are absent.

Overall biomass in different areas

Across the four types of conservation area, large herbivore density, including elephants, was 11.2 per km^2 (SD = 20.6, N = 59 conservation areas) and biomass was 4522.0 kg per km^2 (SD = 7128.8, N = 59). Herbivore biomass was higher in conservation areas where settlement was prohibited and enforced and where hunters were absent (mostly NPs) than in any other area, whether elephants were included or not. At first glance these results are not surprising, as NPs in Tanzania were often gazetted in areas where large mammals were abundant especially in the dry season. Nevertheless, the results show that effective protection of most species has not eroded 20–30 years after these NPs were gazetted (although NPs have lost rhinoceroses and many elephants). Our results do not support the idea that multiple-use areas are equivalent to or are better conservation strategies than complete protection. This is true despite the fact that mammals are still able to move seasonally in and out of most NPs into areas under different legal protection, places that might be expected to show similarly high mammal densities during certain seasons.

The influence of protection

Nearly half of the ungulate species counted showed higher population densities in areas that prohibited settlement and that contained a guard force (Fig. 3), but this effect was more marked for species of larger body weight. Arcese *et al.* (1995) showed that illegal hunters in Serengeti preferred larger species to smaller ones. Similarly, Dublin *et al.* 1990) showed that poachers removed ≈85% of buffalo from the northern Serengeti. Our analyses show that, across the country, densities of heavier species benefited from protection, which suggests that the presence of guards in an area, be it NP or GR, does deter poachers. Buffalo and zebra densities were positively correlated with the density of anti-poaching vehicles in protected areas and corroborate the findings by Arcese *et al.* (1995) that vehicles had a positive effect on rangers' ability to observe and arrest illegal hunters while on patrol.

The influence of tourist hunters

There were few significant differences in mammal densities between protected areas that were and were not hunted by tourists. As these correspond closely to GRs and NPs, respectively, this shows that GRs are an effective form of protection in Tanzania. One confounding factor is that tourist hunting pressure may exert an effect only after several years. Tourist hunting, however, was reopened in 1978, 10 years earlier than the data used in these analyses and most of the areas that we classified as hunted had been hunted since that time (see Table 1 in Caro *et al.*, 1998). Nevertheless, the relative effects of sustained and intermittent hunting pressure on mammal populations requires investigation.

Eland, roan antelope and giraffe populations were somewhat depressed in hunted as opposed to non-hunted areas. Certainly, eland and roan are favoured trophy species but it is unclear why giraffe fare poorly, as they are not shot by tourists. Warthog, a species that is difficult to census, may live at higher densities in P– H– areas than in P – H + areas because they are heavily targeted by tourists or more likely because they are attracted to crops grown in some OAs where hunters do not operate. It is unclear why small antelope and sable antelope fare better in P + H + than in P + H – areas. Ground transects corroborated some of the results obtained from the air, showing lower densities of giraffe in GRs than in NPs but higher densities of oribi (one of the small antelope species) and sable.

Elephant densities did not differ significantly across different conservation areas. In the past, elephant poachers had little respect for either guards or hunting operators and reduced elephant populations indiscriminately across the country. Alternatively or additionally, elephants may move over such large areas within census zones that concentrations within a particular conservation area are rare. High densities of elephants in areas with no protection and no hunters bear further examination.

Conclusions

Our analyses suggest that guards are important for enforcing the prohibition of settlement and in deterring poachers. This is surprising, because protected areas are allocated only small sums of money for fuel and vehicle maintenance by the Government, reducing the ability of rangers and especially game scouts to conduct patrols over large areas. Nevertheless, rangers in NPs and game scouts in GRs are equipped with uniforms, boots and some working rifles, they have radio contact with other posts and, in general, morale is reasonably high. When possible, they conduct vehicle, foot and mixed vehicle–foot patrols. These poorly supported enforcement teams still appear to deter poachers. Our results concerning the protection of meat species therefore differ from studies of protection of economically valuable species, which show that effective protection only occurs where manpower, patrols and financial resources are concentrated in very small areas (Leader-Williams & Albon, 1988; Leader-Williams *et al*., 1990). Taking these contrasting findings together, the idea that protection can only be effective in areas where it is heavily funded is relevant to just a small minority of African mammals and is not applicable generally.

Tourist hunting had few direct benefits for wildlife protection in the country. Poaching activity was high in areas used by hunters but not patrolled by guards. Specifically, poachers move into these areas soon after the end of the hunting season and occupy them intermittently for as much as half the year. Species' densities in areas used by hunters were either similar to equivalent non-hunted areas, or were lower. Some species sought after by tourist hunters were present at higher densities in GRs, such as sable, whereas others, such as eland and roan, were present at lower densities. Tourist hunting benefits wildlife indirectly, however, by providing revenue with which the Government can support and equip game scouts that protect GRs. Thus, the increasing allocation of GCAs and OAs to hunting consortia should be complimented by reclassifying these areas as GRs and supplying them with a ranger force.

In summary, our results, preliminary at present, indicate that legal protection, backed up by on ground protection, still has an important role to play in maintaining densities of large mammal species in Tanzania. This is because guards arrest and deter poachers as well as prevent people from settling and conducting subsistence activities. Tourist hunters have little positive or negative effect on species' densities. Over the course of a year, the intermittent presence of hunters prevents them from acting as 'bush policemen' in lieu of official guards, as some hunters claim.

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