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Research Article

Guidelines for wildlife monitoring: savannah herbivores

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Abstract

Wildlife monitoring is an important conservation tool, but in the savannah regions of Africa, cash-strapped and capacity-limited authorities rank it low on their priority list. To try to reduce the time, effort, and financial costs of monitoring large mammals, I examine a 20-year dataset of herbivore records taken from vehicle transects carried out in Katavi National Park, western Tanzania. I find that: (i) population trends obtained from ground transects are similar to those obtained from aerial surveys conducted over a wider area; (ii) the frequency of vehicle surveys driven per year or (iii) across years can be reduced without losing substantial information; (iv) it is inadvisable to stint on numbers of transects driven; and (v) trends in populations of single species do not represent those of others. These findings are encouraging because they indicate that managers can obtain relatively accurate information about herbivore population trends through infrequent and therefore more cost-effective monitoring.

Key words: cost effectiveness, herbivores, monitoring, vehicle transects

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Introduction

Wildlife monitoring is important for conservation because it can provide early warning of impending population declines and local extirpations [1,2]. If population changes can be linked to pressures such as poaching, draining wetlands, agricultural encroachment, development projects, or even zoonoses, ameliorative measures may sometimes be possible. In Africa there is a real need for monitoring programs because land-use pressures on African reserves are growing [3], agricultural expansion and population growth are occurring around reserve borders [e.g. 4], and massive development projects with adverse environmental consequences are imminent [5,6]. Moreover, where long term population records are available, they suggest that mammal populations in west and east African protected areas are declining rapidly [7]. Finally, monitoring is required to measure the effectiveness of upgrading protected areas or following reintroduction programs.

Yet in truth, wildlife managers in poorer African nations often struggle with conflicting demands of anti-poaching activities, including rangers' salaries and vehicle costs, helping local communities to build health clinics and schools on the borders of reserves, and political expenses of visiting and receiving local dignitaries. More often than not, wildlife monitoring is treated as a luxury carried out by foreign researchers, but not important enough to take money and manpower away from other important managerial functions.

For example, in Tanzania, the African country with arguably the greatest biodiversity on the continent, rapid changes are occurring in large mammal populations inside protected areas [8], yet there are very few long term, ground-based wildlife monitoring programs in operation. In only three of the national parks do these occur: Udzungwa National Park (NP) [9], Serengeti NP [10] and Katavi NP [11], each spearheaded by foreign researchers bringing in outside funding that may collapse when researchers leave [12]. Ironically, Tanzania National Parks authorities (TANAPA) have a staff ecologist in each of their national parks charged with accumulating ecological knowledge (mandated monitoring) [see 13]. Although these ecologists have often been trained in counting animals, there are unable to conduct regular ground-based monitoring due to costs, limited capacity to sample and analyze data, and lack of understanding of why monitoring is needed, all of which lead to disinterest. In order to make regular monitoring easier and more effective, I test some simple guidelines for regular ground-based wildlife monitoring in savannah ecosystems in Tanzania and other African nations that will reduce costs, equipment needs, and personnel constraints. I use aerial surveys of large mammal populations as a baseline against which to compare long-running, ground-based surveys in Katavi NP. By examining ways to reduce monitoring effort without losing substantial information, my goal is to make it easier to incorporate monitoring into wildlife management in Africa.

Methods

Study area

The Katavi-Rukwa ecosystem lies in the Great Lakes Region of East Africa north of Lake Rukwa in Katavi Region, Tanzania [14, Fig. 1]. The area is part of the central Zambezi miombo woodlands ecoregion [15], characterized by trees of the *Caesalpininaceae*, *Mimosaceae* and *Papilionaceae* families [16,17]. Great diversity and abundance of large mammals occur in this area [18,19] which is under five different forms of protection. The 4,471km² Katavi NP administered by TANAPA is patrolled regularly by park rangers; no settlements or exploitation are allowed within NP boundaries. Katavi NP was extended to double its original size in 1998. It is surrounded by Rukwa and Lukwati Game Reserves (4,194 and 3,566 km², respectively), Mlele Game Controlled Area (3,544 km²) and Lwafi Game Reserve - Nkamba Forest Reserve (3,369km²) all administered by the Wildlife Division. These areas are patrolled infrequently, and foreign tourists hunt there in the dry season. To the north of the Park is the Msanginia Forest Reserve, administered by the Tanzania Forest Service, where selective tree cutting and a great deal of deforestation have occurred. To the south of Katavi NP and Rukwa Game Reserve lies Usevya Open Area where people live.

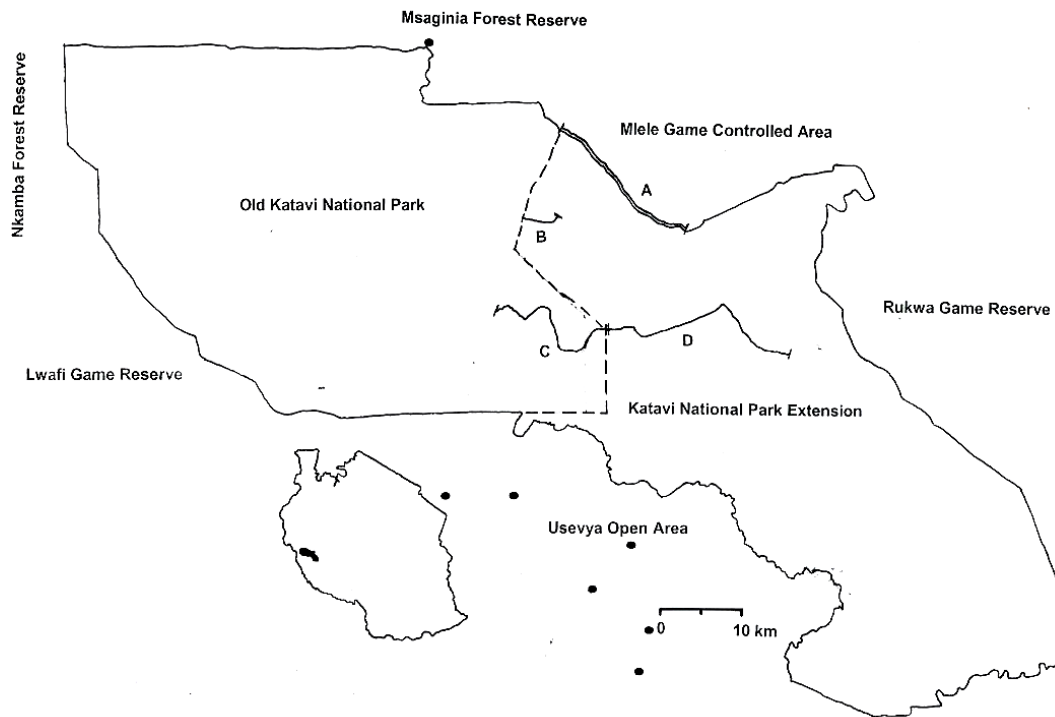


Fig. 1. Map of Katavi National Park showing the location of the 4 ground transects and legally protected areas mentioned in the text. Lukwati Game Reserve is to the southeast of Rukwa Game Reserve. The four transects (A-D, see text) used in time series in this study are shown. Dashed line shows boundary of the old NP and NP Extension; filled ovals show locations of important villages. Inset (below) shows location of Katavi NP (filled in) in Tanzania.

Population trends

Mammal ground surveys were conducted by regularly driving four vehicle transects along minor tracks in Katavi NP (Figure 1) at <10 km/hour. Transect A was along the Park Extension - Mlele Game Controlled Area border ("Kapapa" 23.6km in length); transect B was through the western edge of the NP Extension ("X" 6.0km); transect C went through the eastern portion of the original NP ("North Chada" 22.1km); and transect D went through the centre of the NP Extension ("Paradise" 28.7km) [see 11, 20 for details]. Transects were driven in 1995, 1996, 1998, 2000, 2002-2005, 2007-2011, 2013 and 2014 (N = 15 years), in almost every case by the author and usually with one assistant who helped spot animals and recorded the data (usually Oska Ulaya). Transects were always driven early in the morning, always in the dry season, and usually twice per year except in one year some were driven once, and in one other year some three times. In total, transects were driven 112 times amounting to 2,165 km.

For each species, numbers of individuals seen up to 500m on either side of the transects were recorded as number of individuals/km. This is an index and not true abundance and was used to circumvent estimating the area needed to calculate densities. Area can be determined using a rangefinder to record distance of each sighting from the transect or can simply be estimated by eye. The first requires equipment, including batteries, whereas the second requires different observers to be consistent, which introduces an additional source of

error. The individuals/km index only requires different observers to agree on a single 500m distance and to be comparable in spotting mammals. Because sighting distances were not scored, DISTANCE sampling was impossible, but this did not matter because there were insufficient numbers of many of the rarer species, such as eland (*Taurotragus oryx*) or bushpig (*Potamochoerus porcus*), to derive a suitable detection function [21], and less common species are particularly interesting for management. Population indices (individuals/km) are valid for the general purpose of detecting broad trends in savannah habitats, as detection probabilities between dry seasons are unlikely to change along the same transects, except in the case of fire clearing areas of high grass.

The population indices for the four transects were added together within each session, and then averaged among sessions within any given year. Average annual figures were then averaged, using a running mean of the two years either side of each (the next year in the cases of 1995 and 2014). Running means were used to reduce high variability in the counts of some species due to local annual differences in rainfall or burning that could cause herds to move off or onto the transect lines. Running mean population indices were then matched against years that transects were driven and examined using Spearman rank order correlation coefficients.

In one analysis, however, I used a different data set derived from seven transects driven in Katavi NP during 1995 and 1996 nearly always by myself [18]. These transects were each driven 14 times over the course of an 18-month period using the same protocol as described above. In this earlier study, numbers of individual animals sighted were expressed as densities by dividing numbers by the total area visible along each transect [see 19 for details of comparing different methods of calculating densities].

Aerial census data for the whole of the Katavi-Rukwa ecosystem were obtained from Serengeti Ecological Monitoring Programme (SEMP), Tanzania Wildlife Conservation Monitoring Programme (TWCM), and Conservation Information Monitoring Unit (CIMU) reports of repeated systematic reconnaissance flights of an area of approximately 12,000km² or more [see 22 for map and further details]. Densities of 17 species of ungulates were calculated by dividing the total population estimate by total area surveyed. Densities were plotted against the year that the survey was conducted between 1977 and 2014, and Spearman rank order correlation coefficients were used to examine the data. Significance levels were all set at $\alpha = 0.1$ to be sensitive to possible declines of populations in advance.

Results

Population trends

Figure 2 shows population densities of large mammalian herbivores in the whole Katavi-Rukwa ecosystem over a period of 26 - 37 years, depending on the species, based on aerial census data. Of 17 species, 11 are in significant ($P < 0.1$) decline, five are in decline (that is declining but non-significantly), and two show an increase (*i.e.*, a non-significant increase) (see legend Figure 2). Switching to numbers of individuals/km seen on vehicle transects driven over a 20-year period in Katavi NP (1995-2014), four species showed a significant decline ($P < 0.1$), seven showed a decline, one showed an increase, four a significant increase, and there were too few sightings of sable antelope (*Hippotragus niger*) to discern a trend. Spearman correlation coefficients were ($N = 15$ years in all cases): buffalo (*Syncerus caffer*), $r_s = +0.586$, $p = 0.022$; bushbuck (*Tragelaphus scriptus*) $r_s = +0.688$, $p = 0.007$; bushpig, $r_s = -0.185$, NS; duiker (*Sylvicapra grimmia*), $r_s = -0.750$, $p = 0.001$; eland, $r_s = -0.500$, $p = 0.058$; elephant (*Loxodonta africana*), $r_s = -0.584$, $p = 0.022$; giraffe (*Giraffa camelopardalis*), $r_s = -0.271$, NS; hartebeest (*Alcelaphus buselaphus*), $r_s = -0.383$, NS; hippopotamus (*Hippopotamus amphibious*), $r_s = +0.871$, $p < 0.0001$; impala (*Aepyceros melampus*), $r_s = +0.879$, $p < 0.0001$; reedbuck (*Redunca redunca*) $r_s = +0.807$, $p < 0.0001$; roan antelope (*Hippotragus equinus*), $r_s = +0.396$, NS; topi (*Damaliscus lunatus*), $r_s = -0.863$; $p < 0.0001$; warthog (*Phacochoerus africanus*), $r_s = -0.857$; $p < 0.0001$; waterbuck (*Kobus ellipsiprymnus*), $r_s = -0.563$, $p = 0.029$; and zebra (*Equus burchelli*), $r_s = -0.364$, NS.

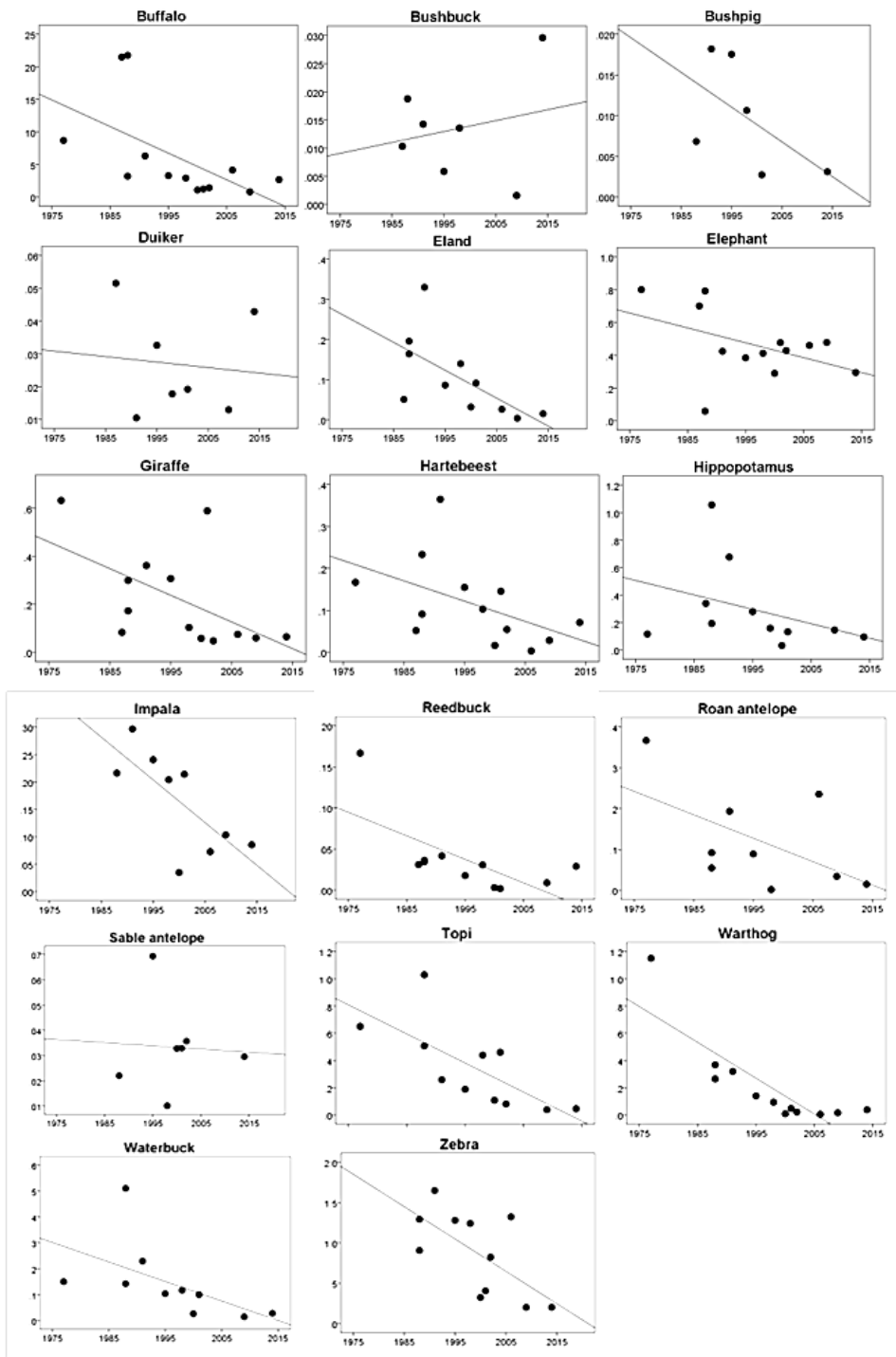


Fig. 2. Long term trends of large herbivore populations in the Katavi-Rukwa ecosystem. Density (individuals/km²) of 17 herbivore species determined from aerial surveys plotted against date of survey to the nearest month of each year. Buffalo, N = 13, $r_s = -0.732$, $p = 0.004$; bushbuck, N = 7, $r_s = +0.036$, NS; bushpig, N = 6, $r_s = -0.600$, NS; duiker, N = 7, $r_s = -0.071$, NS; eland, N = 11, $r_s = -0.715$, $p = 0.013$; elephant, N = 13, $r_s = -0.294$, NS; giraffe, N = 13, $r_s = -0.613$, $p = 0.026$; hartebeest, N = 13, $r_s = -0.542$, $p = 0.056$; hippopotamus, N = 11, $r_s = -0.510$, NS; impala, N = 9, $r_s = -0.700$, $p = 0.036$; reedbuck, N = 11, $r_s = -0.779$, $p = 0.005$; roan antelope, N = 9, $r_s = -0.569$, NS; sable antelope, N = 7, $r_s = +0.179$, NS; topi, N = 11, $r_s = -0.856$, $p = 0.001$; warthog, N = 12, $r_s = -0.855$, $p < 0.0001$; waterbuck, N = 10, $r_s = -0.851$, $p = 0.002$; zebra, N = 11, $r_s = -0.597$, $p = 0.053$. Trend lines are added to appreciate patterns (not as regression functions).

Table 1 shows the congruence between population trends based on aerial censuses over a very large area of the ecosystem and longer time span, and indices derived from vehicle transects conducted over a much smaller area and over a shorter time period. Trends regarding two species, topi and warthog, were in strong agreement; eight were in agreement in that both showed a decline, one of which was usually a significant decline. For two species, impala and reedbuck, there were strong disagreements in that one showed a significant increase but the other showed a significant decline; finally four were in disagreement either because one showed an increase but the other a decline, or because trends using one method were clear but were not in another. Overall, then, 10 out of 16 comparisons were in agreement.

Table 1. Can vehicle transects uncover ecosystem population trends? Summary of population changes over time measured using aerial censuses of the Katavi-Rukwa ecosystem and vehicle transects (using 3-year running means) in Katavi NP. Significant ($p < 0.1$) Spearman correlation coefficients are indicated in bold; not clear refers to $+0.1 > r_s > -0.1$. Also shown is an indication of agreement.

Species	Aerial 26-37 years	Vehicle 20 years	Agreement
Buffalo	Decline	Decline	Yes
Eland	Decline	Decline	Yes
Giraffe	Decline	Decline	Yes
Impala	Decline	Increase	Strongly no
Hartebeest	Decline	Decline	Yes
Reedbuck	Decline	Increase	Strongly no
Topi	Decline	Decline	Strongly yes
Warthog	Decline	Decline	Strongly yes
Waterbuck	Decline	Decline	Yes
Zebra	Decline	Decline	Yes
Bushpig	Decline	Decline	Yes
Elephant	Decline	Decline	Yes
Hippopotamus	Decline	Increase	No
Roan antelope	Decline	Increase	No
Sable antelope	Increase	No sightings	Not applicable
Duiker	Not clear	Decline	No
Bushbuck	Not clear	Increase	No

Reducing the frequency of vehicle transects

To determine whether driving effort could be reduced in any given year, I compared trends derived from the first time that transects were driven each year, and those from the second time they were driven each year, with those averaged over both sessions each year (Table 2). There was general concordance between trends derived from transects driven once per year with those averaged over two drives. Of 17 species monitored, halving the effort would yield 12 concordant changes (Table 2) of which 10 were in strong agreement. Of the remaining five species, two trends showed strong disagreement. Arguably, this indicates that transects could be driven just once per annum with little loss of information.

Table 2. Can effort be reduced in any given year? Summary of population changes over time measured using vehicle transects in Katavi NP comparing trends derived from the whole dataset with those derived from the first transect driven in a year, or the second transect driven; 3-year running means were used in all cases. Significant ($p < 0.1$) Spearman correlation coefficients are indicated in bold; no change denotes $+0.1 > r_s > -0.1$. Also shown is whether transects could simply be driven once each per year.

Species	Whole dataset using mean of transects driven twice	First transect only	Second transect only	Will driving transects once suffice?
Buffalo	Increase	Increase	Increase	Yes definitely
Bushbuck	Increase	Increase	Decline	No
Hippopotamus	Increase	Increase	Increase	Yes definitely
Impala	Increase	Increase	Increase	Yes definitely
Reedbuck	Increase	Increase	Increase	Yes definitely
Roan antelope	Increase	Increase	No change	Yes
Duiker	Decline	Decline	Increase	No
Eland	Decline	Decline	Decline	Yes definitely
Elephant	Decline	Decline	Increase	No
Topi	Decline	Decline	Decline	Yes definitely
Warthog	Decline	Decline	Decline	Yes definitely
Waterbuck	Decline	Decline	Decline	Yes definitely
Bushpig	Decline	Decline	Decline	Yes definitely
Giraffe	Decline	Decline	Increase	No definitely
Hartebeest	Decline	Decline	Decline	Yes definitely
Zebra	Decline	No change	Decline	Yes

Spearman correlation coefficients for first and second transect each year respectively using 3-year running means ($N_s = 15$): buffalo, $r_s = +0.421$, NS, $r_s = +0.854$, $p < 0.0001$; bushbuck, $r_s = +0.521$, $p = 0.046$, $r_s = -0.329$, NS; hippopotamus, $r_s = +0.786$, $p = 0.001$, $r_s = +0.889$, $p < 0.0001$; impala, $r_s = +0.811$, $p < 0.0001$, $r_s = +0.896$, $p < 0.0001$; reedbuck, $r_s = +0.875$, $p < 0.0001$, $r_s = +0.665$, $p < 0.007$; roan antelope, $r_s = +0.483$, $p = 0.068$, $+0.053$, NS; duiker, $r_s = -0.928$, $p < 0.0001$, $r_s = +0.191$, NS; eland, $r_s = -0.537$, $p = 0.039$; $r_s = -0.324$, NS; elephant, $r_s = -0.704$, $p = 0.003$, $r_s = +0.201$, NS; topi, $r_s = -0.811$, $p < 0.0001$, $r_s = -0.879$, $p < 0.0001$; warthog, $r_s = -0.874$, $p < 0.0001$, $r_s = -0.615$, $p = 0.015$; waterbuck, $r_s = -0.543$, $p = 0.037$, $r_s = -0.279$, NS; bushpig, $r_s = -0.231$, NS, $r_s = -0.185$, NS; giraffe, $r_s = -0.288$, NS, $r_s = +0.519$, $p = 0.048$; hartebeest, $r_s = -0.379$, NS, $r_s = -0.227$, NS; zebra, $r_s = -0.093$, NS; $r_s = -0.136$, NS; greater kudu, cant test, $r_s = -0.107$, NS. For whole dataset, see text.

To assess whether a reduced fieldwork effort would yield similar results to that obtained using 15 years' data collection over a 20-year time span, I dropped every other year's data, recalculated running means with this reduced data set, and then correlated these against year. I performed this procedure first starting in 1995 ($N = 8$ years over a 20-year span) and then second beginning in 1996 ($N = 7$ years over a 20-year span). On average, both procedures represented a 2.8 year gap between years that transects were driven. Table 3 shows that there was a great deal of concordance in population trends between numbers of individuals/km counted using the full dataset and those in which alternate sampling years were omitted. Of 17 species monitored, reduced effort would yield 14 concordant changes in indices of which 10 were in strong agreement. This indicates that transects could be driven approximately every 3 years with little loss of information.

Table 3. Can effort be reduced through less frequent transects? Summary of population changes over time measured using vehicle transects in Katavi NP comparing trends derived from the whole dataset with those derived from dropping every other year's transect effort; 3-year running means were used in all cases. Significant ($p < 0.1$) Spearman correlation coefficients are indicated in bold. Also shown is whether frequency can be reduced to every 3 years.

Species	Whole dataset (N = 15)	2.8 year gap start 1995 (N = 8)	2.8 year gap start 1996 (N = 7)	Can frequency be reduced?
Buffalo	Increase	Decline	Increase	No
Bushbuck	Increase	Increase	Increase	Yes definitely
Hippopotamus	Increase	Increase	Increase	Yes definitely
Impala	Increase	Increase	Increase	Yes definitely
Reedbuck	Increase	Increase	Increase	Yes definitely
Roan antelope	Increase	Increase	No change	Yes
Duiker	Decline	Decline	Decline	Yes definitely
Eland	Decline	Decline	Decline	Yes
Elephant	Decline	Decline	Decline	Yes definitely
Topi	Decline	Decline	Decline	Yes definitely
Warthog	Decline	Decline	Decline	Yes definitely
Waterbuck	Decline	Decline	Decline	Yes definitely
Bushpig	Decline	Cant test	Decline	Yes
Giraffe	Decline	Decline	Decline	Yes definitely
Hartebeest	Decline	No change	No change	No
Zebra	Decline	Decline	No change	Yes
Greater kudu	No change	Decline	No change	No definitely

Spearman correlation coefficients for 2.8 year gaps starting either 1995 or 1996 (Ns = 8 and 7 respectively): buffalo, $r_s = -0.571$, NS, $r_s = +0.964$, $p < 0.0001$; bushbuck, $r_s = +0.921$, $p = 0.001$, $r_s = +0.906$, $p = 0.005$; hippopotamus, $r_s = +0.786$, $p = 0.021$, $r_s = +0.607$, NS; impala, $r_s = +0.786$, $p = 0.021$, $r_s = +0.964$, $p < 0.0001$; reedbuck, $r_s = +0.922$, $p = 0.001$, $r_s = +1.000$, $p < 0.0001$; roan antelope, $r_s = +0.527$, NS, $r_s = +0.056$, NS; duiker, $r_s = -0.874$, $p = 0.005$, $r_s = -0.730$, $p = 0.063$; eland, $r_s = -0.506$, NS, $r_s = -0.414$, NS; elephant, $r_s = -0.810$, $p = 0.015$, $r_s = -0.929$, $p = 0.003$; topi, $r_s = -0.738$, $p = 0.037$, $r_s = -0.964$, $p < 0.0001$; warthog, $r_s = -0.667$, $p = 0.071$, $r_s = -0.991$, $p < 0.0001$; waterbuck, $r_s = -0.619$, NS, $r_s = -0.750$, $p = 0.052$; bushpig, cant test; $r_s = -0.318$, NS; giraffe, $r_s = -0.619$, NS, $r_s = -0.607$, NS; hartebeest, $r_s = -0.119$, NS, $r_s = -0.126$, NS; zebra, $r_s = -0.571$, NS; $r_s = -0.143$, NS; greater kudu, $r_s = -0.726$, $p = 0.041$, $r_s = +0.122$, NS. For whole dataset, see text.

To determine whether vehicle transects could be reduced in frequency even further and so save additional time and money, I used a separate procedure to examine the data using a "sliding window" in which I recorded simply whether numbers/km increased or declined or remained the same between two years spaced either 5.4 years apart on average, or 9.3 years apart on average. I then recorded how many of these "sliding window" comparisons were in the same direction as the 3-year running means using the whole dataset, and expressed these as a percentage of the 11 or 8 "windows" respectively (Table 4). For each species except three (*i.e.*, 14 species), the majority ($\geq 50\%$) of one or other "sliding window" comparisons was in the same direction as that seen in the whole data set. In 10 of the 17 comparisons there was greater congruence using the longer 9.3 year time interval than the 5.4 year interval, in that more of the "sliding window" comparisons went in the same direction as the population trend determined from using all the data. This indicates that long, almost decadal

long time intervals will give a reasonable approximation of local population changes determined from ground counts.

Table 4. Can effort be reduced through very infrequent transects? Summary of population changes over time measured using vehicle transects in Katavi NP comparing trends derived from 3-year running means of the whole dataset with those derived from "sliding window" comparisons. Percentage of comparisons in which individuals/km changed in the same direction as the whole data set is shown in the body of the table. Significant ($p < 0.1$) Spearman correlation coefficients are indicated in bold. Whether an average gap of 5.4 or 9.3 years gives a result more congruent with the whole dataset is also shown.

Species	Whole dataset (N = 15)	5.4 year gap (N = 11)	9.3 year gap (N = 8)	Which interval is better?
Buffalo	Increase	63.6	50.0	Shorter
Bushbuck	Increase	63.6	50.0	Shorter
Hippopotamus	Increase	54.5	62.5	Longer
Impala	Increase	63.6	100.0	Longer
Reedbuck	Increase	72.7	87.5	Longer
Roan antelope	Increase	36.4	50.0	Longer*
Duiker	Decline	45.5	50.0	Longer*
Eland	Decline	54.5	62.5	Longer
Elephant	Decline	63.6	50.0	Shorter
Topi	Decline	63.6	87.5	Longer
Warthog	Decline	81.8	87.5	Same
Waterbuck	Decline	63.6	87.5	Longer
Bushpig	Decline	63.6	62.5	Same
Giraffe	Decline	63.6	62.5	Same
Hartebeest	Decline	36.4	37.5	Same*
Zebra	Decline	63.6	87.5	Longer
Greater kudu	No change	54.5	62.5	Longer

* poor congruence even in the most promising year-gap

Reducing the numbers of species counted

It is common practice in conservation biology to use certain species' presence or population size or population trends as approximations for those of others since this can save considerable time and effort [23]. Counting large herds of ungulates from the ground is time consuming and subject to error, especially for species aggregating in very large herds such as buffalo. Therefore I wanted to see whether some species could represent other species by showing similar population trends over time. If so, one might be able to reduce the number of species being counted in the course of driving vehicle transects. I therefore ran Spearman correlation coefficients for the 16 herbivore species for which I had sufficient data, using 3-year running means of the whole 20-year data set. Very few species showed more than three significant positive correlations ($P < 0.1$) with others. Those that did were elephant, giraffe and reedbuck (four significant correlations out of a possible 15), duiker (5) and warthog (6). No species showed more than six significant positive correlations with other species, suggesting that no single species could characterize others. Nonetheless, hippopotamus and reedbuck indices were both significantly correlated with megaherbivore indices (elephant, hippopotamus and giraffe combined),

ungulate indices (all herbivore species combined other than the three just mentioned) and with primate indices (yellow baboons *Papio cynocephalus* and vervet monkeys *Cercopithecus pygerythrus* combined). Further, bushbuck trends were significantly positively correlated with megaherbivores, and buffalo with ungulates. Therefore hippopotamus and reedbuck may be promising candidates for obtaining a broad approximation of changing mammalian biomass.

Inter-transect variation

The 20-year data set consisted of only four transects, but at the beginning of the study, I drove seven transects each month within Katavi NP over an 18-month period [18]. These were along tourist tracks kept open by TANAPA authorities that traversed areas of miombo woodland, ran along the side of floodplains, and followed rivers, the relative proportions of which differed between transects. At that time, I recorded population sizes as densities based on visible area [19] and here I revisit these data (see Table 1 of [18]) in order to explore whether transects could be reduced in number. As reported in that paper, densities of species differed significantly between transects, as determined from Kruskal-Wallis tests for 13 out of 16 species (all except bushbuck, bushpig and greater kudu), indicating great variation in species' densities depending on transect location. On some transects, especially the short one, no individuals of a particular species were ever sighted (Table 5).

Table 5. Can effort be reduced through driving fewer transects in an area? Percent differences between means of seven transects (numbered 1-7) driven 14 times over 18-months and species' overall mean densities (left hand column) in Katavi NP 1995-1996. – denotes no individuals recorded. Averages of percentages are shown at the foot of the table. Right hand column shows the percent range of variation in transect means from the overall mean assuming a species was seen on a transect (from [18]).

Species	Number per km ²	1	2	3	4	5	6	7	Difference from mean*
<i>Length in kms</i>		18.3	22.9	26.9	26.2	26.7	11.9	1.8	
Buffalo	21.64	115	100	22	144	95	180	27	22-180%
Zebra	5.82	192	158	37	122	68	97	-	37-192%
Hippopotamus	5.31	192	249	-	-	235	-	-	192-249%
Waterbuck	4.41	109	222	45	6	146	151	-	6-222%
Impala	3.84	244	239	1	20	51	124	-	1-244%
Giraffe	2.21	53	283	81	87	77	62	62	53-283%
Topi	2.2	287	132	42	110	17	88	-	17-287%
Elephant	2.02	149	87	49	204	26	167	-	26-204%
Eland	1.49	13	249	10	77	305	26	-	10-305%
Warthog	1.34	96	54	103	44	99	190	114	44-190%
Reedbuck	0.4	33	3	-	-	648	-	-	3-648%
Hartebeest	0.36	-	161	94	128	28	261	-	28-261%
Bushpig	0.08	-	100	138	-	50	350	-	50-350%
Duiker	0.06	-	150	117	233	33	167	-	33-233%
Bushbuck	0.04	100	200	-	25	25	400	-	25-400%
Roan antelope	0.02	-	100	50	500	50	30	-	30-500%
Greater kudu	0.01	-	-	-	400	-	-	-	-
Average %		93.1	132.2	46.4	123.5	114.9	134.9	11.9	

* assuming an individual was seen

Taking the overall mean density of each species in seven transects over an 18-month period to be an accurate description of species' population densities based on vehicle transects, I calculated for each herbivore species, the percent to which average densities recorded on a given transect were more or less than the overall mean figure (Table 5). On average among all species, transects 1 and 5 matched overall mean species values reasonably well (93.1% and 114.9%), but transects 2, 4, and 6 overestimated mean densities by nearly 25% or more (132.2%, 123.5% and 134.9% respectively). In contrast, transect 3 underestimated densities by an average of 46.4%. Transect 7 differed enormously from the overall mean (only 11.9%) but was only 1.8km in length. Examining variation from the overall mean, but now on a species by species basis, and assuming an individual was sighted, there was considerable deviation for all species except zebra, warthog, and arguably buffalo. For other mammals, some transects generated densities of more than 200% greater than the overall mean. In short, great variation in mammal densities among transects strongly suggests that it is important to maximize the number of transect lines that are driven.

Discussion

The goal of this study was to develop guidelines for monitoring large herbivores in African savannah ecosystems using vehicle transects, since ground-based surveys are within the limited budget of authorities charged with protecting wildlife in most African reserves. Unusually, however, in Tanzania there is a program of surveying large mammal populations by airplane throughout the major national parks and game reserves, which has been in place for nearly 40 years [24]. It provides a platform for making policy decisions and a baseline against which other sorts of population surveys can be judged. In this study, I compared changes in the populations of large herbivores obtained from a regular but limited number of vehicle transects over a 20-year period to aerial surveys conducted over a far larger geographic area over a 35-year period. I found that a preponderance of population changes derived from vehicle surveys (10 out of 16) matched those conducted from the air. Only measures for two out of 16 comparisons showed a strong disagreement. This suggests that vehicle surveys are indeed an important alternative for monitoring savannah herbivore population trends (although not necessarily for assessing densities), if aerial censuses are impossible or intermittent due to funding limitations. While vehicle surveys necessarily have lower spatial coverage and can be impeded by road conditions, they have great financial advantages. Comparing costs of the 2014 aerial census to the six vehicle transects (see below) highlights the enormous cost discrepancy between the two methods of wildlife monitoring: aerial surveys cost 29-34 times more than vehicle surveys (Table 6).

To examine whether costs for budget-constrained and capacity-limited government organizations could be saved through less intensive ground monitoring, I first examined how findings would change if the number of transects driven per annum was reduced by half to being conducted just once per year. I found that almost two thirds of population trends over time derived from one drive were broadly similar to those derived from the mean of two, although there were some discrepancies. Possibly then, transects could be driven once only during the dry season in any given year, reducing the cost by half.

I also compared results of ground surveys conducted with approximately 3-10 year time lags with those carried out almost annually. I found that surveys could be reduced greatly in frequency but still uncover increasing, decreasing and stable population trends similar to those derived from near-annual surveys, and that vehicle transects conducted even once a decade could yield valuable information. This is an important cost-cutting measure, since transects in this particular study, for example, would cost an estimated \$1,369 – 1,487 per annum to drive and to reach, so that decadal transects would constitute total savings of between \$12,321 and \$13,383 compared to annual counts.

Table 6. Comparison of estimated costs in US \$) of an aerial census conducted over four days in 2014, and six vehicle transects driven twice each in 2014. (1 US \$ = 2160 Tanzania shillings).

<i>Aerial census 2014</i>	
Flying (40.2 hours)	\$ 14070*
Fuel (13 drums)	\$ 7020
Crew	\$ 3704
Support staff	\$ 3933
Logistical	\$ 9500
Consumables	\$ 1100
Analysis, reporting and administration	\$ 11789
Total	\$ 37,046 – 51,116
<i>6 vehicle transects 2014</i>	
Vehicle transects (6 X 25 km each driven twice)	300 km
Returning along each transect	300 km
Getting to start of transects from base (200 km total driven twice)	400 km
Diesel (@ 6.6 – 13.2 km/liter) used per year (76 – 152 liters @ \$ 0.89)	\$ 67-135
Engine oil	\$ 12
Vehicle repairs	\$ 50 - 100
Driver salary for 12 days	\$ 222
Driver per diem field rate for 12 days	\$ 111
Ranger salary for 12 days	\$ 222
Ranger per diem field rate for 12 days	\$ 111
Staff ecologist salary for 12 days	\$ 463
Staff ecologist per diem field rate for 12 days	\$ 111
Total	\$ 1,369 – 1,487

* assuming aircraft are hired

In theory, the time spent counting animals in the field and in subsequent analyses could be reduced by focusing on just a few species if their population trends represented population changes in many other herbivores, but I found no strong evidence for this. For the most promising species, warthog, population changes mirrored those of only six out of 15 other species (40%). Nonetheless, changes in both hippopotamus and reedbuck indices did mirror changes in combined megaherbivore, combined ungulate, and combined primate indices, suggesting they might be useful in drawing broad conclusions about trends in mammalian biomass over time. Nonetheless, counting all species of large herbivores seen during vehicle transects is the most cautious approach in all circumstances, particularly when effort and money have already been expended in setting up and driving transects.

To examine whether transects could be reduced in number, I looked at variation in species' densities among transects during a period of intensive study. There was great variation in densities among transects for nearly every species, except perhaps three, clearly showing that it would be very unwise to reduce the transect number. Short transects greatly underestimated species densities and should be dropped. A rule of thumb may be to drive a minimum of six transects, each 20 - 25km long, and critically, each must pass through several

different sorts of vegetation. Stratifying transect placement to run through representative habitats is very important for sampling species with different habitat and seasonal requirements.

The findings presented here are encouraging because they indicate that managers can obtain relatively accurate information about herbivore population trends using infrequent and hence cost-effective monitoring. Costs can be cut by reducing the number of times transects are driven per year as well as the frequency that they are driven between years. Managers are acutely aware of threats to protected areas [25] and vehicle transects provide them with an inexpensive means to monitor populations under their care [see also 26]. They may also embolden hunting authorities, such as the Wildlife Division in Tanzania, to start monitoring in game reserves and game controlled areas, places where they have been hitherto reluctant to monitor herbivore populations despite issuing hunting quotas [27].

The findings here pertain to species of large mammalian herbivores that are not under intensive pressure and whose population sizes are changing relatively slowly. Monitoring species that are under threat, however, such as lions (*Panthera leo*) [28], or whose populations are thought to be declining locally or nationally, such as elephants [29], requires different monitoring protocols. These may involve different sorts of surveys, in these cases through playback call-ins and aerial censuses respectively, and an increased frequency of monitoring, given the rapid decline of these populations throughout the continent.

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