Changes in large herbivore populations across large areas of Tanzania

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Abstract

We collated aerial census data collected during the late 1980s to early 2000s for large herbivore populations in eight large census zones in Tanzania. Of the ungulate populations that showed significant changes in densities at the start versus end of this decade, most declined; very few populations increased significantly. Thomson's gazelle, Grant's gazelle, hartebeest, reedbuck, roan antelope, sable antelope, warthog and zebra, for example, declined in over 50% of the zones where they were surveyed. Interestingly, small-bodied species fared particularly poorly in many census zones, whereas elephant and giraffe generally fared well across the country. Most populations of all herbivores declined in some portions of the country (e.g. Burigi-Biharamulo, Katavi, Greater Ruaha and Tarangire census zones). These surveys suggest that, even in a country renowned for its protected areas and conservation commitment, some large herbivore populations need more conservation attention in order to remain stable.

Key words: aerial surveys, East Africa, large mammals, population dynamics

Résumé

Nous avons rassemblé les données récoltées entre la fin des années 1980 et le début des années 2000 lors de recensements des populations de grands herbivores dans huit vastes zones de Tanzanie. La plupart des populations d'ongulés qui présentaient des changements de densité significatifs entre le début et la fin de ces recensements avaient diminué; très peu avaient augmenté significativement. La gazelle de Thomson, la gazelle de Grant, le bubale, le cobe des roseaux, l'antilope rouanne, l'antilope sable, le phacochère et le zèbre, par exemple, avaient décliné dans plusieurs zones. Il est intéressant de remarquer que les espèces de petite taille avaient des résultats plutôt médiocres dans de nombreuses zones de recensement alors que les éléphants et les girafes s'en sortaient bien dans tout le pays. La plupart des populations de tous les herbivores ont baissé dans certaines parties du pays (ex. les zones de recensement de Burigi-Biharamulo, Katavi, le Grand Ruaha et Tarangire). Ces études montrent que, même dans un pays renommé pour son engagement envers ses aires protégées et la conservation, certaines populations de grands herbivores ont besoin d'une attention de conservation plus grande pour rester stables.

Introduction

Monitoring changes in population size over time is critical for effective conservation. Long-term monitoring data reveal how changing abiotic and biotic factors influence population dynamics, and therefore are of great help in allocating conservation efforts (Hafner & Fasola, 1997). Investigations that focus on the impacts of land development (e.g. Briggs *et al.*, 1996; McCarthy *et al.*, 1999), invasive species (Fitzgerald & Gibb, 2001), restoration projects (e.g. Luke & Zack, 2001), and sustainable harvest efforts (e.g. Forsyth, 1999) on native flora and fauna all reiterate the necessity for assessing long-term trends in populations. In a review of tools for managing diversity within forests, Lindenmayer (1999) noted that though a growing number of publications hint at the many advantages of long-term data, relatively few long-term monitoring programmes exist.

In Tanzania, a megadiversity country with an extensive network of reserves, herbivore populations have been

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monitored using aerial censuses since the early 1970s. The Serengeti Ecological Monitoring Programme (SEMP) was established specifically to identify population trends within Serengeti National Park, but during the 1980s this focus was expanded to include many other protected ecosystems within the country. In the early 1990s, the Tanzania Wildlife Conservation Monitoring (TWCM) Programme was created as a joint project between Serengeti Wildlife Research Institute [now known as the Tanzania Wildlife Research Institute (TAWIRI)], the Wildlife Division, Tanzania National Parks, Ngorongoro Conservation Area Authority and the Frankfurt Zoological Society. TWCM carried out systematic wet and dry season aerial surveys of herbivore populations throughout Tanzania. Today, the Conservation Information Monitoring Unit (CIMU), a division of TAWIRI, continues ecological monitoring of Tanzania's protected ecosystems and surrounding areas. Monitoring is seen as a key component of conserving the large mammal diversity of Tanzania as it can assist in identifying which populations are changing, and thus, what sorts of conservation efforts might offer the best protection. Similar analyses in the Masai Mara in Kenya were useful in pinpointing which species experienced the largest declines (Ottichilo *et al.*, 2000) and which abiotic and anthropogenic variables influenced population fluctuations (Ottichilo, de Leeuw & Prins, 2001).

In this paper, we compare data collected at the start versus finish of an approximately 10-year time span (late 1980s/early 1990s to late 1990s/early 2000s) for large herbivores in eight different census zones in Tanzania, defined as geographically distinct, repeatedly surveyed areas centred on a national park or game reserve and surrounding lands (with partial or no legal protection). We examine whether temporal changes tend to be increases or declines for most species in each census zone and for each species across the country. In addition, we test if population changes are most pronounced in large-bodied species, as these species are thought to be most preferable to bushmeat hunters (Arcese, Hando & Campbell, 1995), in species with large home range sizes, as they are most likely to be affected by encroachment around reserves (Woodroffe & Ginsberg, 1998), and in species with similar feeding preferences, as would be expected if changes in food availability is a primary driver of population changes. Our findings show which species and census zones are faring particularly well or poorly in a country viewed as a flagship conservation country in Africa.

Methods

We based analyses on aerial survey data collected by the SEMP, TWCM and CIMU monitoring teams using systematic reconnaissance flights (SRF; Norton-Griffiths, 1978). Monitoring teams conducted SRF surveys using a Cessna 182 or 185 aircraft that followed flight transects marked on 1:250,000 scale maps (Norton-Griffiths, 1978; Broten & Said, 1995; Campbell & Borner, 1995). Two rear seat observers recorded the numbers of animals seen between two parallel rods mounted on the wing struts of the aircraft as a front observer announced transect subunits (typically 30 s of flying time). Monitoring teams derived densities for each subunit based on the number of animals observed and the strip width of each transect (calibrated based on flight height). Survey teams also grouped subunits into a grid system of cells covering the area surveyed (Campbell & Borner, 1995). While observer identity did change between surveys, there was typically an overlap in observer personnel across surveys which provided important continuity in counting techniques.

We examined survey data for large herbivores in eight census zones (Table 1) centred on a national park or game reserve (Fig. 1) and the spacing of flight transects dictated the size of the survey grid cells in each census zone. Flight transects separated by 5 km, as in the Burigi-Biharamulo, Katavi, Serengeti, Tarangire, and Ugalla census zones, generated 5 × 5 km grid cells. When transect spacing varied between 5 and 10 km in a census zone (e.g, Selous-Mikumi) we examined grid cells of a standardized 10 × 10 km size. Similarly, when transect spacing switched from 10 km in earlier surveys to 5 km in later surveys (Greater Ruaha and Moyowosi-Kigosi census zones), we only examined data from transects spaced 10 km apart in all surveys to standardize comparisons over time.

We examined aerial census data for 25 species: buffalo (*Syncerus caffer*), bushpig (*Potamochoerus larvatus*), bushbuck (*Tragelaphus scriptus*), duiker (*Sylvicapra grimmia*), eland (*Taurotragus oryx*), African elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Gazella granti*), greater kudu (*Tragelaphus strepsiceros*), hartebeest [*Alcelaphus buselaphus* and *Sigmoceros lichtensteini* (combined)], hippopotamus (*Hippopotamus amphibius*), impala (*Aepyceros melampus*), lesser kudu (*Tragelaphus imberbis*), puku (*Kobus vardoni*), oryx (*Orxy gazella*), reedbuck (*Redunca* sp.), roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*), sitatunga (*Tragelaphus spekeii*), Thomson's gazelle (*Gazella thomsoni*), topi

Table 1 Survey documentation for eight census zones in Tanzania

Census zone	Survey dates	Size of surveyed grid cells	Mean number of grid cells
Burigi-Biharamulo	W[a]: Mar. 1990, D[b]: Sep. 1990 W: May 1998 W: May 2000, D: Sep. 2000	5 × 5 km	280
Greater Ruaha	W: Mar. 1990, D: Sep. 1990 W: Mar. 1993, D: Oct. 1993, W: Apr. 1996, D: (early) Nov. 1999	10 × 10 km	289
Tarangire	W: May 1988, D: Sep. 1990 W: Mar. 1994, D: Oct. 1994 W: Apr. 1997 D: Oct. 1999, W: May 2001	5 × 5 km	505
Katavi	W: (late) Nov. 1991 W: Dec. 1998, D: Oct. 1998 W: May 2001	5 × 5 km	504
Serengeti	W: Apr. 1991 W: Nov. 1996 W: Apr. 2001	5 × 5 km	1079
Ugalla	W: Apr. 1991 D: Oct. 1991, D: Oct. 1995 W: Mar. 1995 W: Apr. 1999	5 × 5 km	293
Moyowosi-Kigosi	D: Sep. 1990 W: Mar. 1994 W: May 1998 W: Sep. 2000	10 × 10 km	229
Selous-Mikumi	D: Sep. 1989 D: Jun. 1991, D: Sep. 1994 D: Oct. 1998	10 × 10 km	814

[a]'W' denotes wet season survey.
[b]'D' denotes dry season survey.

(*Damaliscus lunatus*), warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymus*), wildebeest (*Connochaetes taurinus*), and zebra (*Equus burchellii*). Bushpig, bushbuck, duiker and hippopotamus are found in many census zones but are particularly difficult to census from the air. Thus we conduct all analyses first including and then excluding these four species.

Analyses

For each species surveyed in a census zone, we compared densities in survey grid cells at the start versus end of a 10-year time period. We tested for significant differences ($P < 0.05$) between densities in start versus finish sets of survey grid cells using nonparametric Mann–Whitney tests due to the non-normal distribution of the densities across grid cells. We noted whether each species increased significantly, declined significantly or showed no significant change. If a species was observed in four or fewer grid cells in a given survey zone at both the start and end of the survey period, we considered the species as occupying too few cells to detect a significant change (based on results from mock Mann–Whitney tests).

Wildlife estimates are likely to fluctuate between counts performed in wet versus dry season months because many herbivores in East Africa congregate at water sources during the dry season and may be differentially difficult to detect between seasons. Thus, in start/finish comparisons of wildlife densities in grid cells, we compare data from sets of surveys that were conducted during the same season. In some census zones, available data enabled start/finish comparisons only during wet seasons (Katavi, Serengeti, Ugalla) or dry seasons (Moyowosi-

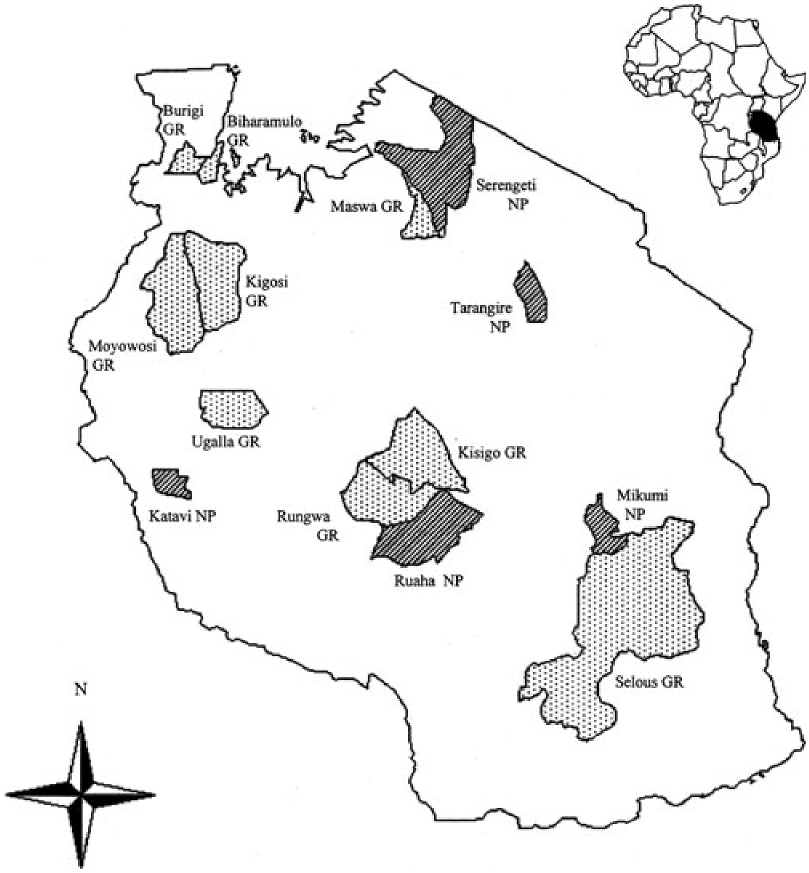


Fig 1 National Parks (NP) and Game Reserves (GR) in Tanzania. Census zones (geographically distinct regions centred on an NP or GR over which surveys were conducted repeatedly) included: Burigi-Biharamulo census zone (Burigi GR, Biharamulo GR and surrounding areas), the Katavi census zone (Katavi NP, Rukwa GR and surrounding areas), the Moyowosi-Kigosi census zone (Moyowosi GR, Kigosi GR, and surrounding areas), the Greater Ruaha census zone (Ruaha NP, Rungwa GR, Kisigo GR, and surrounding areas), the Serengeti census zone (Serengeti NP, Maswa GR, and surrounding areas), the Selous census zone (Mikumi NP, Selous GR, and surrounding areas), the Tarangire census zone (Tarangire NP and surrounding areas), and the Ugalla census zone (Ugalla GR and surrounding areas). 'Surrounding areas' typically included game-controlled areas and areas with no protection

Kigosi, Selous-Mikumi); survey data from Burigi-Biharamulo, Greater Ruaha, and Tarangire enabled comparisons of densities across wet season surveys (separated by 10 years) as well as dry season surveys. As vegetation growth during the wet season could reduce visibility, partitioning the data into wet and dry season surveys reduced this source of bias. Additionally, although differences in vegetation might be expected between years, vegetation greenness (as measured by satellite imagery) was relatively stable, increasing only slightly during the time frame that surveys were conducted (Pelkey, Stoner & Caro, 2000).

To verify whether all surveys (not just those at the start and finish) conducted during the 10-year time period supported the significant changes between start and finish, we additionally performed Kendall's coefficient of rank correlations. Kendall's rank correlation coefficient provides a nonparametric measure of association and tests the direction, but not magnitude, of a rank order of observations (Sokal & Rohlf, 2001). Thus, in every case where a species declined or increased significantly ($P < 0.05$; based on start/finish comparisons), we tested if either (i) numbers of grid cells occupied, or (ii) the average density of all occupied grid cells progressively changed across all surveys conducted over 10 years (as indicated by a one-tailed rank correlation test with $P \leq 0.05$).

We also tested whether species' traits were associated with the percentage change in grid cells occupied by each species (the difference in the number of cells occupied in a given census zone at the start versus finish of a decade, divided by the starting number). Information on species' (female) body size (kg), home range size (km^2) and food preference (predominately grazer, predominately browser, mixed grazer/browser, and all other diets) was primarily based on Estes (1991) and supplemented with Stuart & Stuart (1998). Analyses were conducted separately for individual census zones. When possible, associations were based on parametric tests and in most cases the dependent variable met normality assumptions after we applied an arcsin transformation. Body size and home range size variables were normalized by log transformation. If data did not meet the criteria for parametric tests, we applied nonparametric Mann–Whitney and Kruskal–Wallis tests.

Results

Census zones

Across all census zones, percentages of populations that experienced significant losses in densities within grid cells at the start versus finish of a 10-year period greatly outnumbered those experiencing significant increases (Table 2). Fewer than 10% of populations increased significantly in all census zones but Serengeti; indeed, no significant increases occurred in Greater Ruaha (wet season comparison), Tarangire (dry season comparison), or Burigi-Biharamulo (both seasons).

The percentage of increasing populations that additionally demonstrate a significant increasing trend (as determined by Kendall's rank correlation tests across all surveys) in either numbers of grid cells occupied or mean densities within occupied grid cells was similarly overwhelmed by high percentages of populations showing declines in all census zones but Ugalla (Table 2).

High percentages of significantly declining populations characterized four census zones in particular. More than 60% of species in Katavi (comparisons made across wet seasons), Tarangire (wet), Greater Ruaha (dry), and Burigi-Biharamulo (both seasons) experienced significant declines in comparisons with the start versus finish of a 10-year period (Table 2). In the latter three census zones, over 30% of species additionally experienced declining trends based on Kendall's rank correlations. After excluding difficult species that are difficult to census (Table 2), populations of large herbivores continued to fare worst in Katavi (wet), Tarangire (wet), Greater Ruaha (dry) and Burigi (both seasons) comparisons.

Species differences

Only three species, elephant, giraffe and hippopotamus, did not experience declines in over half of Tanzania's census zones in comparisons made across a decade in either wet or dry seasons (Table 3). In total, only eight significant increases (or increasing trends) in grid cell densities were seen across any census zones, seasons, and species, and six of these increases occurred in elephant populations (Table 4). Although giraffes did not significantly increase in any census zone, this species rarely declined (Table 3). Similarly, hippopotamus rarely showed significant changes, but this species is difficult to survey from the air and therefore data may be unreliable.

Several species tended to decline significantly in the census zones where they were observed. Thomson's and Grant's gazelles were only observed in sufficient numbers to detect any change in two wet season and one dry season comparison, but in all cases these species showed significant declines (Table 3). Bushbuck (difficult to census), hartebeest, reedbuck, roan antelope, sable antelope, warthog and zebra were commonly observed across the country and declined in at least 50% of census zones regardless of the season of comparison. Kendall's rank correlations based on either (i) numbers of occupied cells or (ii) mean densities of occupied cells across all surveys confirm declining trends in over half the surveyed populations of zebra and Thomson's gazelle (Table 3). Over 50% of populations of other species [e.g. buffalo, bushpig (difficult to census), duiker (difficult to census), eland, impala, lesser kudu, topi, and waterbuck] declined significantly in start/end survey comparisons made in one season, but this pattern was not consistent in comparisons in both seasons.

Species traits

Temporal changes in occupied grid cells (change in number of occupied cells at the start versus finish of a decade divided by number of cells occupied at the start) for each species in every census zone are plotted against species' traits in Fig. 2. Body size was positively correlated with increases in occupied grid cells in the Burigi-Biharamulo (wet season comparison: $F = 5.38$, $P = 0.0388$), Greater Ruaha (dry: $\chi^2 = 4.842$, $P = 0.028$), Selous-Mikumi (dry:

Table 2 Percentage of (large herbivore) species in each census zone that declined or increased over approximately a decade

							Excluding difficult to census species[d]	
Census zone	Season	N[a]	% species significantly declining[b]	% species also showing declining trend[c]	% species significantly increasing[b]	% species also showing increasing trend[c]	% species significantly declining[b]	% species significantly increasing[b]
Greater Ruaha	Wet	12 (4)	16.7	8.3	0	0	18.2	0
Ugalla	Wet	11 (8)	18.2	0	9.1	9.1	20	10
Moyowosi-Kigosi	Dry	14 (5)	21.4	0	7.1	0	18.2	9.1
Serengeti	Wet	16 (2)	37.5	18.8	12.5	12.5	42.9	14.3
Tarangire	Dry	15 (5)	46.7	20	0	0	46.2	0
Selous	Dry	18 (0)	50.0	0	5.6	0	42.9	7.1
Katavi	Wet	17 (3)	64.7	11.8	5.9	0	69.2	7.7
Tarangire	Wet	15 (5)	66.7	53.3	6.7	0	66.7	6.7
Greater Ruaha	Dry	13 (4)	69.2	30.8	7.7	0	72.7	9.1
Burigi-Biharamulo	Wet	14 (3)	71.4	42.9	0	0	69.2	0
Burigi-Biharamulo	Dry	12 (7)	83.3	41.7	0	0	80	0

[a]Number of species surveyed consistently in each census zone. Numbers in parentheses indicate additional species that were observed in too few grid cells to detect a significant decline and are omitted in calculations of percentages.
[b]Based on Mann–Whitney tests ($P < 0.05$) of densities in surveyed grid cells as the start versus finish of a decade.
[c]Based on Kendall's rank correlations of either (i) the number of occupied cells or (ii) the average density of occupied cells across all surveys conducted in a given census zone.
[d]Species that are particularly difficult to census from the air include bushbuck, bushpig, duiker and hippopotamus.

$F = 9.74$, $P = 0.007$), Serengeti (wet: $\chi^2 = 5.88$, $P = 0.015$), and Tarangire (wet: $\chi^2 = 3.86$, $P = 0.049$; dry: $F = 14.45$, $P = 0.002$) census zones. Although large home range size was associated with positive changes in occupied grid cells in Greater Ruaha (dry: $\chi^2 = 4.126$, $P = 0.042$) and Tarangire (wet: $\chi^2 = 3.02$, $P = 0.082$), results of these nonparametric tests are likely to be confounded by body size, which was a significant factor in both census zones (see above).

Feeding preferences were only associated with changes in occupied cells in the Katavi census zone (wet: $F = 4.82$, $P = 0.018$). Species that both browsed and grazed in the Katavi census zone fared significantly better than species that predominately grazed ($P = 0.004$), predominately browsed ($P = 0.009$), or with 'other' dietary preferences ($P = 0.020$). No traits investigated were associated with temporal changes in occupied cells in the Burigi-Biharamulo (dry comparison), Moyowosi-Kigosi (dry), Greater Ruaha (wet) or Ugalla (wet) census zones.

Discussion

Given its particularly diverse collection of species (IUCN, 1990) and increasing rate of human population growth (United Republic of Tanzania, 2003), Tanzania reflects the global challenge of maintaining megadiversity in the face of increasing demand for natural resources. Our analysis of aerial survey data across a decade suggests that many populations of large herbivores significantly declined in census zones across the country, whereas few populations significantly increased. This analysis also shows that population changes across vast areas (encompassing protected areas and surrounding lands) are most prominent for particular census zones and species.

Our analyses suggest that large herbivores in the Burigi-Biharamulo census zone fared particularly badly over the time span of 1990–2000. This ecosystem has been plagued by difficulties including heavy burning, large groups of organized poachers, and lack ranger patrolling during the 1980s (WCMC, 1984). The large percentage (75–82%) of herbivore populations showing declines (in densities within surveyed grid cells) in this census zone and lack of species experiencing increases (Table 2) likely reflect the area having been inundated with refugees seeking escape from the Rwandan genocide in the mid-1990s. Although a programme has been initiated to revitalize the two game reserves in this ecosystem (GTZ, 2003), our analyses

Table 3 Percentages of changing populations for each species across census zones in Tanzania

Species	Season[a]	No. of census zones[b]	% census zones in which species declined[c]	% census zones in which species also show a declining trend[d]	% census zones in which species increased[c]	% census zones in which species also show an increasing trend[d]
Buffalo	Wet	5 (1)	40	0	20	20
	Dry	5 (0)	60	0	0	0
Bushbuck[e]	Wet	3 (3)	66.7	0	0	0
	Dry	5 (0)	60	0	0	0
Bushpig[e]	Wet	1 (3)	0	0	0	0
	Dry	1 (3)	100	0	0	0
Duiker[e]	Wet	1 (3)	0	0	0	0
	Dry	5 (0)	80	0	0	0
Eland	Wet	5 (1)	20	0	0	0
	Dry	4 (1)	75	25	0	0
Elephant	Wet	6 (0)	0	0	50	16.7
	Dry	4 (0)	0	0	75	0
Giraffe	Wet	6 (0)	16.7	0	0	0
	Dry	5 (0)	0	0	0	0
Grant's gazelle	Wet	2 (1)	100	0	0	0
	Dry	1 (0)	100	0	0	0
Greater kudu	Wet	0 (3)				
	Dry	1 (2)	0	0	0	0
Hartebeest	Wet	6 (0)	50	16.7	0	0
	Dry	4 (1)	50	0	0	0
Hippopotamus[e]	Wet	4 (1)	25	0	0	0
	Dry	2 (3)	0	0	0	0
Impala	Wet	6 (0)	33.3	33.3	0	0
	Dry	4 (1)	50	50	0	0
Lesser kudu	Wet	1 (2)	100	100	0	0
	Dry	1 (1)	0	0	0	0
Oryx	Wet	1 (0)	100	100	0	0
	Dry	0 (1)				
Puku	Wet	0 (1)				
	Dry	1 (0)	0	0	0	0
Reedbuck	Wet	6 (0)	50	16.7	0	0
	Dry	5 (0)	80	20	0	0
Roan antelope	Wet	3 (2)	100	0	0	0
	Dry	2 (1)	50	0	0	0
Sable antelope	Wet	4 (1)	50	25	0	0
	Dry	2 (3)	50	0	0	0
Sitatunga	Wet	0 (1)				
	Dry	2 (0)	100	0	0	0
Topi	Wet	4 (2)	25	25	0	0
	Dry	2 (2)	50	50	0	0
Thomson's gazelle	Wet	2 (1)	100	50	0	0
	Dry	1 (0)	100	100	0	0
Waterbuck	Wet	6 (0)	66.7	50	0	0
	Dry	3 (2)	33.3	33.3	0	0
Warthog	Wet	6 (0)	66.7	66.7	16.7	16.7
	Dry	5 (0)	60	40	0	0
Wildebeest	Wet	2 (0)	100	50	0	0
	Dry	2 (0)	50	0	0	0

Table 3 (Continued)

Species	Season[a]	No. of census zones[b]	% census zones in which species declined[c]	% census zones in which species also show a declining trend[d]	% census zones in which species increased[c]	% census zones in which species also show an increasing trend[d]
Zebra	Wet	5 (1)	80	60	0	0
	Dry	5 (0)	80	60	0	0

[a]Season across which comparisons were made for species' densities at the start versus finish of approximately a decade.
[b]Number of census zones in which each species was surveyed. Numbers in parentheses indicate additional census zones where the species was observed in too few grid cells to detect a significant decline.
[c]Significance based on Mann–Whitney tests ($P < 0.05$) of herbivore densities in surveyed grid cells at the start versus finish of a decade.
[d]Significance based on Kendall's rank correlations of either (i) the number of occupied cells or (ii) the average density of occupied cells across the dates of all surveys conducted in a given census zone.
[e]Species is particularly difficult to census from the air and therefore estimates are likely to be unreliable.

suggest that substantial conservation attention is needed for wildlife to recover.

Declines also characterized Greater Ruaha during the dry season and Tarangire during the wet season. These two ecosystems, like the Serengeti, are known for their seasonal migrations. Declines in the dry season in the Greater Ruaha census zone most likely reflect that the National Park's primary water supply during the dry season (the Ruaha River) is increasingly being diverted for cultivation in the Usangu plains (WWF, 2002; Sokile, Van Koppen & Lankford, 2003). Declines in the Tarangire census zone were prominent for most species during comparisons in the wet season when wildlife migrate out of the park. Declines in this census zones might merely reflect that the timing of seasonal surveys corresponded with different phrases of migration, but this cannot explain why a suite of species with small and large home ranges (including migratory species) tend to decline in comparisons made across time during both seasons. Perhaps these declines reflect intensifying competition for resources inside the park as migration routes surrounding Tarangire are increasingly severed by crop cultivation and settlements (Shemwetta & Kideghesho, 2000).

Based on wet season surveys, a large percentage of species declined in the Katavi census zone. Though we did not have survey data to compare populations across dry seasons, we suspect that these comparisons would similarly demonstrate wildlife declines because ground surveys suggest species do not migrate seasonally in this ecosystem (Caro, 1999). Caro (unpublished data) examined a suite factors impacting wildlife in this census zone, including rainfall and predation by carnivores, and concluded that local poaching is likely to be the most influential factor affecting herbivore populations in Katavi National Park. Our analysis did not detect that species of particular body size classes were most likely to lose occupied grid cells, as would be expected if hunters selectively target bigger species. Instead, species that were predominately browsers, grazers, or with 'other' diets fared worse than mixed browsers/grazers. Thus, food availability might play a role in the widespread declines observed in this census zones, because species with generalized diets tended to fare better than those with more selective food preferences.

In several census zones, increasing body size was correlated with positive changes in occupied grid cells (change in grid cell number at the start versus finish of a decade, divided by starting number of occupied cells). This is surprising because bushmeat hunters are assumed to prefer larger meat species (Arcese, Hando & Campbell, 1995; Caro, Rejmanek & Pelkey, 2000) and large-bodied species typically have difficulties recovering from overharvesting because they typically have long gestation periods (Purvis, 2001). Widespread increases in elephants, reflecting a recovery in the population after implementation of the Ivory Ban, surely contributed to this trend (Table 4). Giraffe, another large-bodied species also fared unusually well in most census zones and maintained stable populations across the country. Although they cannot be harvested legally, it is puzzling that giraffe did not experience more declines, as did smaller species, because they are hypothesized to be one of the key species targeted by poachers in some ecosystems (e.g. Katavi; Caro, unpublished data).

Although some smaller species (Thomson's gazelle, Grant's gazelle, hartebeest, reedbuck, roan antelope, sable

Table 4 The status of large herbivores in eight census zones in Tanzania

Census zone	Season[a]	Overall decline[b]	Decline between start and finish[c]	No change[c]	Increase between start and finish[c]	Overall increase[b]	Observed too rarely to detect a decline[d]
Burigi Biharamulo[e]	Wet	Impala Sable (antelope) Topi Warthog Waterbuck Zebra	Bushbuck[f] Eland Hartebeest Roan (antelope)	Buffalo Elephant Giraffe Reedbuck			Bushpig[f] Lesser kudu Sitatunga
Burigi-Biharamulo	Dry	Impala Topi Warthog Waterbuck Zebra	Buffalo Bushbuck[f] Duiker[f] Reedbuck Sitatunga	Eland Giraffe			Bushpig[f] Elephant Hartebeest Hippopotamus[f] Lesser kudu Roan Sable
Greater Ruaha[g]	Wet	Impala	Buffalo	Eland Elephant Giraffe Hartebeest Hippopotamus[f] Reedbuck Sable Warthog Waterbuck Zebra			Bushbuck[f] Bushpig[f] Roan Topi
Greater Ruaha[h]	Dry	Impala Eland Warthog Zebra	Buffalo Duiker[f] Reedbuck Roan Sable	Bushbuck[f] Giraffe Hartebeest	Elephant		Bushpig[f] Hippopotamus[f] Topi Waterbuck
Tarangire	Wet	Hartebeest Lesser Oryx Reedbuck Thomson's gazelle Warthog Wildebeest Zebra	Grant's gazelle Waterbuck	Buffalo Eland Giraffe Impala	Elephant		Bushbuck[f] Bushpig[f] Duiker[f] Greater kudu Topi
Tarangire	Dry	Reedbuck Thomson's gazelle Zebra	Bushbuck[f] Eland Grant's gazelle Hartebeest	Buffalo Duiker[f] Elephant Giraffe Impala Lesser Warthog Wildebeest			Bushpig[f] Greater kudu Oryx Topi Waterbuck
Katavi	Wet	Warthog Waterbuck	Buffalo Bushbuck[f] Giraffe Hartebeest Hippopotamus[f] Reedbuck Roan Sable Zebra	Bushpig[f] Duiker[f] Eland Impala Topi	Elephant		Greater kudu Puku Thomson's gazelle

Table 4 (Continued)

Census zone	Season[a]	Overall decline[b]	Decline between start and finish[c]	No change[c]	Increase between start and finish[c]	Overall increase[b]	Observed too rarely to detect a decline[d]
Moyowosi-Kigosi	Dry		Buffalo[f] Duiker[f] Sitatunga	Bushbuck[f] Giraffe Hartebeest Hippopotamus[f] Reedbuck Roan Topi Warthog Waterbuck Zebra	Elephant		Bushpig[f] Eland Greater kudu Impala Sable
Selous	Dry		Bushbuck[f] Bushpig[f] Duiker[f] Eland Hartebeest Reedbuck Warthog Wildebeest Zebra	Buffalo Giraffe Greater Hippopotamus[f] Impala Puku Sable Waterbuck	Elephant		
Serengeti	Wet	Warthog[i] Waterbuck[i] Zebra[i]	Grant's gazelle Thomson's gazelle Wildebeest	Bushbuck[f] Eland Giraffe Hippopotamus[f] Impala Hartebeest Reedbuck Topi		Buffalo[i] Elephant[i]	Duiker[f] Roan
Ugalla	Wet		Reedbuck Roan	Elephant Giraffe Hartebeest Hippopotamus[f] Impala Sable Topi Waterbuck		Warthog	Buffalo Bushbuck[f] Duiker[f] Eland Grant's gazelle Greater kudu Lesser kudu Zebra

[a]Season over which comparisons of grid cell densities at the start versus finish of an approximately 10 year period (late 80s/early 90s to late 90s/early 2000s) were conducted.

[b]Species showing significant changes (based on Mann-Whitney tests) between start/finish sets of grid cells and additionally show a trend (based on Kendall's rank correlations) in either: i) numbers of occupied cells or ii) mean densities of occupied cells over all surveys conducted.

[c]Significant ($P < 0.05$) based on Mann-Whitney tests performed across grid cell densities at the start versus finish of ten years.

[d]Species were observed in too few survey grid cells to detect a significant decline (based on Mann-Whitney tests).

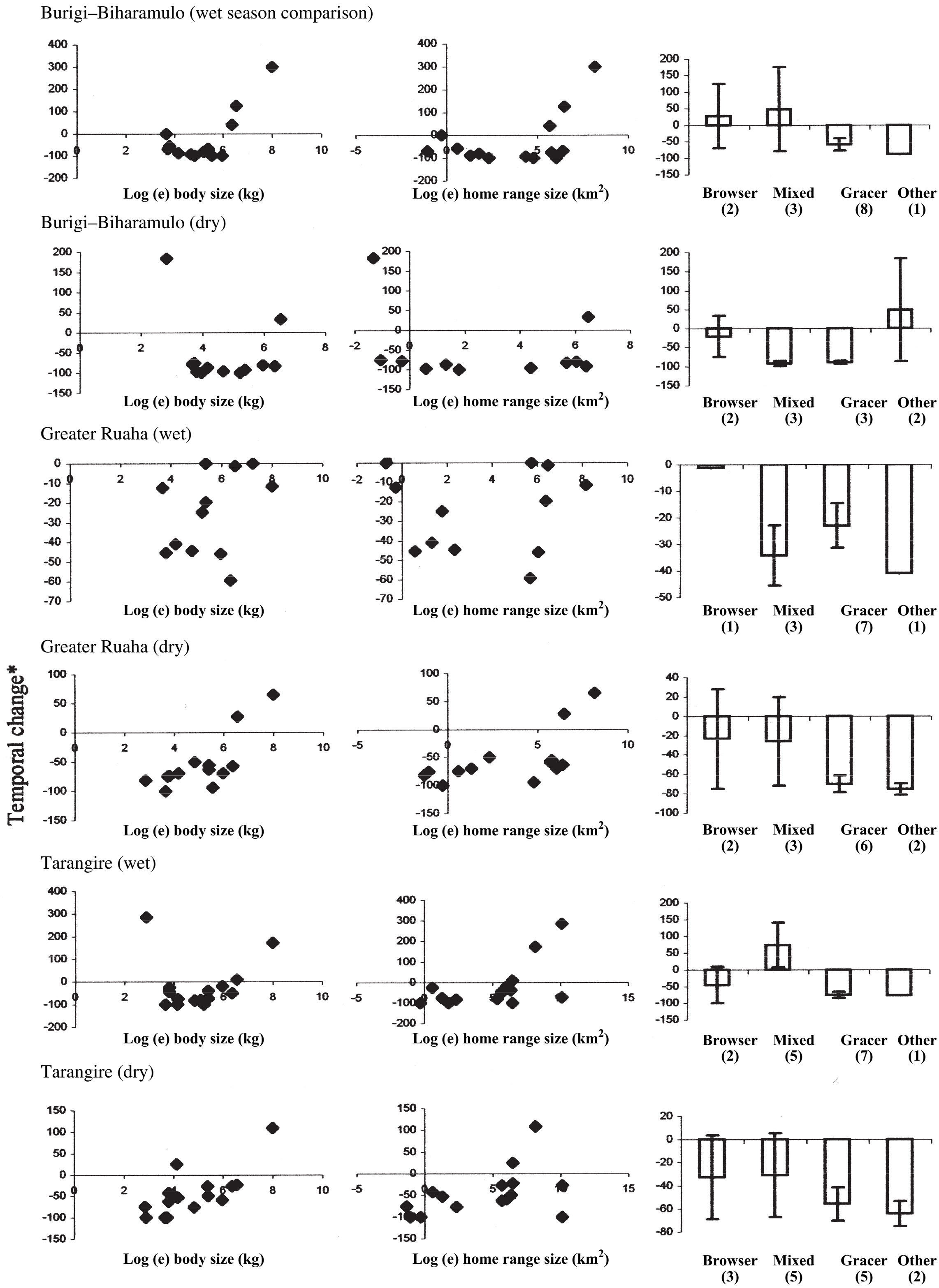
[e]Duiker and hippopotamus are present but some survey information for these species is missing.

[f]Species are particularly difficult to census from the air and therefore estimates are likely to be unreliable.

[g]Duiker, Greater kudu and lesser kudu are present but some survey information for these species is missing.

[h]Greater kudu and lesser kudu are present but some survey information for these species is missing.

[i]Kendall's rank correlations could not be performed (due to insufficient numbers of surveys in this census zone) but species demonstrate sequentially changing numbers of occupied cells across all surveys conducted.


Burigi–Biharamulo (wet season comparison)
Log (e) body size (kg)
Log (e) home range size (km2)
Browser (2)
Mixed (3)
Gracer (8)
Other (1)
Burigi–Biharamulo (dry)
Log (e) body size (kg)
Log (e) home range size (km2)
Browser (2)
Mixed (3)
Gracer (3)
Other (2)
Greater Ruaha (wet)
Log (e) body size (kg)
Log (e) home range size (km2)
Browser (1)
Mixed (3)
Gracer (7)
Other (1)
Greater Ruaha (dry)
Temporal change*
Log (e) body size (kg)
Log (e) home range size (km2)
Browser (2)
Mixed (3)
Gracer (6)
Other (2)
Tarangire (wet)
Log (e) body size (kg)
Log (e) home range size (km2)
Browser (2)
Mixed (5)
Gracer (7)
Other (1)
Tarangire (dry)
Log (e) body size (kg)
Log (e) home range size (km2)
Browser (3)
Mixed (5)
Gracer (5)
Other (2)

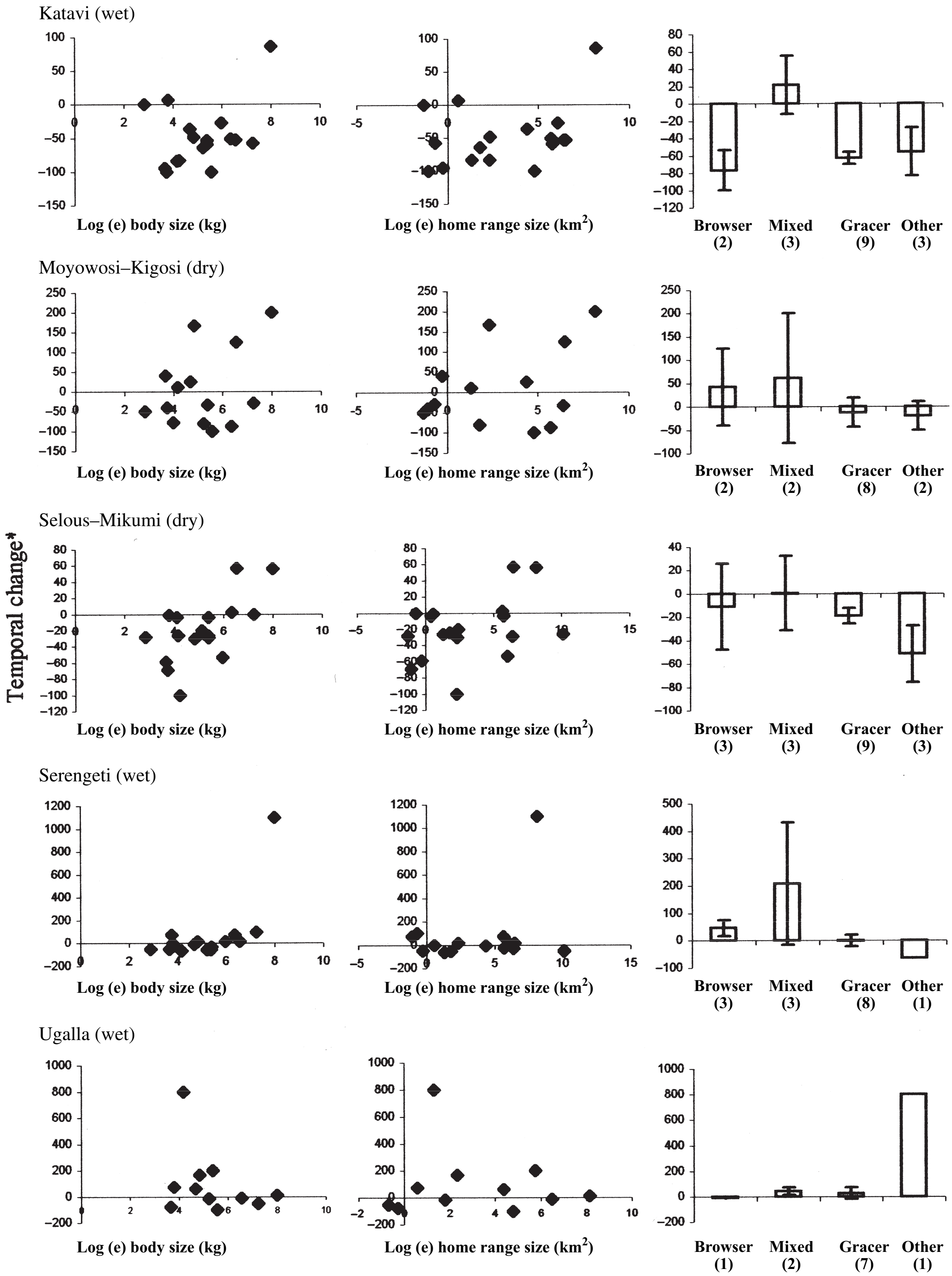


Fig 2 Change in occupied grid cells [(number of occupied grid cells at finish of decade − number of occupied cells at start)/number at start] for every census zone plotted against species' traits. *Difference in number occupied cells at the start versus finish of a decade divided by starting number

antelope, warthog and zebra) commonly declined in census zones where they were surveyed (Table 3), most species fared well in some census zones but poorly in others. Of the 21 species surveyed in at least two census zones, for example, eight showed no significant population change in at least 50% of both wet and dry season comparisons. This pattern probably reflects the fact that most species did not decline or increase consistently across the country, but rather are influenced by local idiosyncrasies including habitat, rainfall, protection regimes or anthropogenic disturbance

Overall, our analyses suggest that population declines tend to outnumber population increases for herbivores across Tanzania, but declines are most prevalent for particular census zones and species. Though comparisons of two snapshots in time might be a particularly liberal test of change, nearly 30% of declines based on comparisons of grid cell densities at the start versus finish of a decade were corroborated by very conservative rank correlations (based on all surveys conducted during this time; Table 4).

When performed across limited numbers of surveys, as was the case in most census zones, such rank correlations highlight rapid and sequential declines. These findings based on only a decade of survey data may reflect either short-term anomalies in population behavior or longer-term declining trends, but they hint at the need for continued, standardized monitoring that will enable formal trend analyses. If some large herbivores are characterized by declines across large spatial and temporal scales, as this preliminary analysis suggests (see Table 4), these populations may need considerably greater conservation attention to persist.

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