Assessment of Effectiveness of Protection Strategies in Tanzania Based on a Decade of Survey Data for Large Herbivores

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Abstract: *Considerable controversy surrounds the effectiveness of strictly protected areas that prohibit consumptive resource use. For Tanzania we compared temporal changes in densities of large herbivores among heavily protected national parks and game reserves, partially protected game-controlled areas, and areas with little or no protection. Comparisons based on surveys conducted in the late 1980s and early 1990s versus the late 1990s and early 2000s showed three consistent patterns across the country. First, significant declines in the densities of large herbivores between these two snapshots in time overwhelmingly outnumbered significant increases in all protection categories. Second, more species fared well (increased significantly or showed no significant change) in strictly protected national parks than in areas with partial or no protection and in heavily protected game reserves relative to areas with no protection. Third, significantly more species fared poorly (densities declined or were too low to detect a decline) than fared well in areas with partial or no protection. Our results show that although heavy protection was generally more effective in maintaining large herbivore populations than partial or no protection, continued long-term monitoring is needed in Tanzania to inform managers whether large herbivores are experiencing declining population trends even within heavily protected areas.*

Keywords: conservation strategies, large herbivores, national conservation, population trends, protected areas, Tanzania

Evaluación de Efectividad de Estrategias de Conservación en Tanzania con Base en una Década de Datos de Muestreos de Herbívoros Mayores

Resumen: *Hay una controversia considerable en torno a las áreas protegidas estrictas que prohíben el uso directo de recursos. En Tanzania, comparamos cambios temporales en las densidades de herbívoros mayores en parques nacionales y reservas de cinegéticas estrictamente protegidas, en áreas cinegéticas parcialmente protegidas y en áreas con escasa o ninguna protección. Las comparaciones, basadas en muestreos realizados a fines de los 1980, inicio de los 1990 e inicios de los 2000, mostraron tres patrones consistentes en todo el país. Primero, las declinaciones significativas en las densidades de herbívoros mayores en dos instantáneas de tiempo fueron abrumadoramente más numerosas que los incrementos significativos en todas las categorías de protección. Segundo, un mayor número de especies estuvo bien (incremento significativo o ningún cambio significativo) en parques nacionales estrictamente protegidos en relación con áreas sin protección. Tercero, un mayor número de especies estuvo mal (declinación en la densidad o una declinación muy lenta que no se detectó) en áreas con protección parcial o nula. Nuestros resultados muestran que, aunque la protección estricta generalmente fue más efectiva que la parcial o nula para el mantenimiento de poblaciones de herbívoros*

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Paper submitted May 18, 2006; revised manuscript accepted January 22, 2007.

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DOI: 10.1111/j.1523-1739.2007.00705.x

mayores, se requiere continuar con el monitoreo a largo plazo en Tanzania para informar a los gestores si los herbívoros mayores están experimentando tendencias poblacionales negativas aun dentro de áreas fuertemente protegidas.

Palabras Clave: areas protegidas, conservación nacional, estrategias de conservación, herbívoros mayores, Tanzania, tendencias poblacionales

Introduction

Accelerating rates of resource extraction generate much concern worldwide. Despite a consensus that destructive processes such as habitat degradation, fragmentation, and overexploitation threaten natural resources, heated debate surrounds the issue of how to best conserve wild nature. A key factor in this on-going controversy is the degree to which biodiversity conservation is best achieved by either excluding or incorporating human use of natural resources (Kiss 2004; Borgerhoff Mulder & Coppolillo 2005).

Some conservationists (e.g., Oates 1997; Terborgh & van Schaik 2002; Struhsaker et al. 2005) argue that the best hope of protecting species lies in strictly protected areas with heavy restrictions on resource use and enforcement. Others note that strictly protected areas often ignore the needs and rights of rural people (Stevens 1997; Hackel 1999) and argue that hostility generated by this "fences and fines" approach will ultimately compromise protected-area success (Ghimire & Pimbert 1997).

Consequently, there are many different arguments for how to best alleviate the ongoing biodiversity crisis. These include calls to strengthen protected-area networks (Noss et al. 1999; Terborgh et al. 2002), mediate threats and offer local people benefits of protected areas via integrated conservation and development programs (McShane & Wells 2004), allocate funds to multiuse areas such as extractive or indigenous reserves (Schwartzman et al. 2000*a*, 2000*b*), and transfer land rights and decision-making power to local institutions (Ghimire & Pimbert 1997). This array of approaches reflects the debate over the degree to which conservation efforts should be allocated inside versus outside strictly protected areas (Borgerhoff Mulder & Coppollilo 2005).

A critical component in this discussion is how well protected areas fare in conserving an array of taxa. A lack of systematic monitoring efforts across a large sample of protected areas (Terborgh & Davenport 2002), however, hinders standardized assessments of how protected areas fare over large spatial or temporal scales. Large-scale analyses based on questionnaires administered to managers and scientists (Bruner et al. 2001; Struhsaker et al. 2005) suggest that species fare better in protected areas than in areas surrounding protected land, but few broad-scale studies have collected biological monitoring data for a suite of different taxa in different types of protected and unprotected areas over time. Such data could provide information on how well strict protection works relative to areas with no protection, other conservation schemes, or gradients in levels of resource restrictions (Borgerhoff Mulder & Coppolillo 2005).

Tanzania sanctions a suite of different protection categories or areas with different levels of legal restrictions on resource use. Protection categories include national parks (permit no resource extraction), game reserves (allow tourist hunting), and forest reserves (permit selective logging). The Ngorongoro Conservation Area (NCA) is similar to a national park but allows cattle grazing by pastoralists. Game-controlled areas and open areas permit extractive resource use only under license. Although ranger patrols guard national parks, NCA, and game reserves in Tanzania, onsite enforcement is generally absent in game-controlled areas, forest reserves, and open areas. Wildlife management areas, or protected areas intended to incorporate community efforts to manage wildlife, compose Tanzania's newest protection category and are increasingly replacing game-controlled areas.

Using aerial census data from 1988 to 1991 (collected by the Serengeti Ecological Monitoring Programme and Tanzania Wildlife Monitoring Centre) Caro et al. (1998) found that large herbivore biomass is higher in national parks and game reserves than in areas with lower levels of protection and that large species benefit most. Thus, Caro et al.'s snapshot-in-time comparison of survey data shows that higher levels of protection are associated with higher wildlife densities. This finding is confounded, however, by the history of conservation in East Africa. National parks and game reserves were originally established in areas characterized by high wildlife numbers (Caro 2003). Thus, it is not clear whether wildlife densities are high in heavily protected areas because protection is successful or whether this is an artifact of such areas having higher initial densities.

A more informative way to assess the effectiveness of different protection schemes in conserving large mammals, therefore, is to examine changes in wildlife densities over time. Unfortunately, establishing long-term trends in densities is not only a critical task for gauging how populations are faring, but it is also difficult. Trends are sensitive to measurement errors and missing data and can be heavily influenced by the method of analysis (Thomas 1996). In addition, patterns can vary considerably when data from variable numbers of censuses are included

(Harris 1986). Detection of robust temporal trends in species' numbers over time therefore requires data from repeated, standardized surveys, yet surveys covering vast spatial scales are often limited.

Using aerial census data for 23 species of large herbivores in Tanzania, we compared information from surveys conducted in protected areas across the country in the late 1980s and early 1990s with data from surveys conducted approximately a decade later. Although these comparisons of wildlife densities at the start versus end of a 10-year period should be viewed as a precursor to a more rigorous long-term trend analyses, this method provides a crude indication of how species' densities differ across two widely separated snapshots in time. We examined changes in large herbivore densities in different protection categories (replicated across the country) and in all cases where this before-and-after approach indicated a significant increase or decline for a given species, we investigated whether all available surveys conducted during the survey period corroborated this change. Thus, we used monitoring data to assess how protected areas varying in intensities of resource use and onsite enforcement of restrictions influenced the persistence of large mammal populations at a nationwide scale.

Methods

We based our analyses on aerial survey data (systematic reconnaissance flights [SRF]; Nortan-Griffiths 1978) collected by the Serengeti Ecological Monitoring Programme, Tanzania Wildlife Conservation Monitoring, Conservation Information Centre, and Conservation Information Monitoring Unit (a division of the Tanzania Wildlife Research Institute) monitoring teams. Monitoring teams conducted SRF surveys in 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 observers in the rear seats of the aircraft recorded the numbers of animals seen between two parallel rods mounted on the wing struts of the aircraft, and a front observer announced transect subunits (typically 30 seconds of flying time). Monitoring teams derived densities for each subunit based on the numbers of animals observed and the strip width of each transect (calibrated based on elevation). Survey teams also assigned subunits to administrative localities and a series of cells within a grid system covering the area surveyed (Campbell & Borner 1995).

Species surveyed from the air included buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Gazella granti*), greater kudu (*Tragelaphus strepsiceros*), hartebeest (*Alcelaphus buselaphus* and *Sigmoceros lichtensteini*), impala (*Aepyceros melampus*), puku (*Kobus vardoni*), oryx (*Orxy gazella*), reedbuck (*Redunca* sp.), roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*), Thomson's gazelle (*Gazella thomsoni*), topi (*Damaliscus lunatus*), warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymus*), wildebeest (*Connochaetes taurinus*), and zebra (*Equus burchellii*). Although monitoring teams additionally recorded bushpig (*Potamochoerus larvatus*), bushbuck (*Tragelaphus scriptus*), duiker (*Sylvicapra grimmia*), and hippopotamus (*Hippopotamus amphibius*), the habitats and activity patterns of these species deem them particularly difficult to accurately count from the air. Therefore we performed analyses that included all 23 large herbivores and then repeated analyses after omitting the four species that are difficult to census.

We examined survey data from seven census zones (Table 1), defined as geographically distinct regions centered on a national park or game reserve (Fig. 1) over which surveys were conducted repeatedly. We examined census zones for which surveys had been conducted in the late 1980s and early 1990s and during the same season approximately 10 years later. We only examined census zones for which the surveyed area included not only a national park or a game reserve, but also the surrounding area, which allowed for comparisons among different protection categories.

The spacing of flight transects dictated the size of the 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 within a survey zone (Selous-Mikumi census zone) or over time (Greater Ruaha census zone), we examined grid cells of a standardized (10 × 10 km) size.

We assigned each grid cell within every census zone to a protection category (national park, game reserve, game-controlled area, or "other"). We considered national parks as strictly protected (no consumptive resource use), national parks, game reserves, and NCA as heavily protected (relatively heavy restrictions on resource use and ranger or game-scout patrolling), game-controlled areas as partially protected (some restrictions and no patrolling), and "other" areas as virtually unprotected (although these areas sometimes contained small portions of open areas with some restrictions). We based protection designations on a locality's protection status at the start of the survey period, as described in survey documentation and a map of Tanzania's protected areas (Leader-Williams et al. 1996). Wildlife management areas were therefore not included in our analyses because this protection category was not implemented during the majority of our study period. If a grid cell spanned two administrative localities with different protection status, we assigned it to the higher protection category. If the specific protection status of a cluster of grid cells was ambiguous (i.e., portrayed as a different protection category in different sources), we omitted these cells from analyses.

Table 1. Survey dates, size of survey grid cells, and average (SE) number of grid cells in each protection category for seven large-herbivore census zones in Tanzania.[a]

Census zone	*Survey dates*	*Cell size (km)*	*NP*	*GR*	*GCA*	*Other*	*In*[b]	*Out*[c]
Burigi-Biharamulo	W: Mar 90, D: Sep 90	5 × 5		126.5		153	126.5	153
	W: May 98			(2.5)[d]		(13.5)	(2.5)	(13.5)
	W: May 00, D: Sep 00							
Greater Ruaha	W: Mar 90, D: Sep 90	10 × 10	120	145.8		23.3	265.8	23.3
	W: Mar 93, D: Oct 93		(1.3)	(1.5)		(1.1)	(0.9)	(1.1)
	W: Apr 96, D: Nov 99 (early)							
Tarangire	W: May 88, D: Sep 90	5 × 5	106.3		34.2	55.7	106.3	398.7
	W: Mar 94, D: Oct 94		(2.3)		(1.6)	(4.8)	(2.3)	(9.7)
	W: Apr 97							
	D: Oct 99, W: May 01							
Katavi	W: Nov 91 (late)	5 × 5	80.5		185.8	60.8	80.5	424
	W: Dec 98, D: Oct 98		(2.6)		(1.1)	(0.5)	(2.6)	(2.9)
	W: May 01							
Serengeti	W: Apr 91	5 × 5	551	113	96.3	57	829	250.3
	W: Nov 96		(0.6)	(1.0)	(1.8)	(2.1)	(6.4)	(13.9)
	W: Apr 01							
Ugalla	W: Apr 91	5 × 5		201		92.4	201	92.4
	D: Oct 91, D: Oct 95			(1.1)		(3.0)	(1.1)	(3.0)
	W: Mar 95							
	W: Apr 99							
Selous-Mikumi	D: Sep 89	10 × 10	42.8	450.8	64	256.5	494.5	319.5
	D: Jun 91, D: Sep 94		(0.9)	(2.3)	(5.6)	(6.1)	(2.3)	(20.2)
	D: Oct 98							

[a]*Abbreviations: NP, national parks; GR, game reserves; GCA, game-controlled areas; Other, areas with virtually no protection; W, wet season survey; D, dry season survey.*
[b]*Total grid cells in national parks and game reserves (and Ngorongoro Conservation Area in Serengeti).*
[c]*Total grid cells in game-controlled areas and "other" areas.*

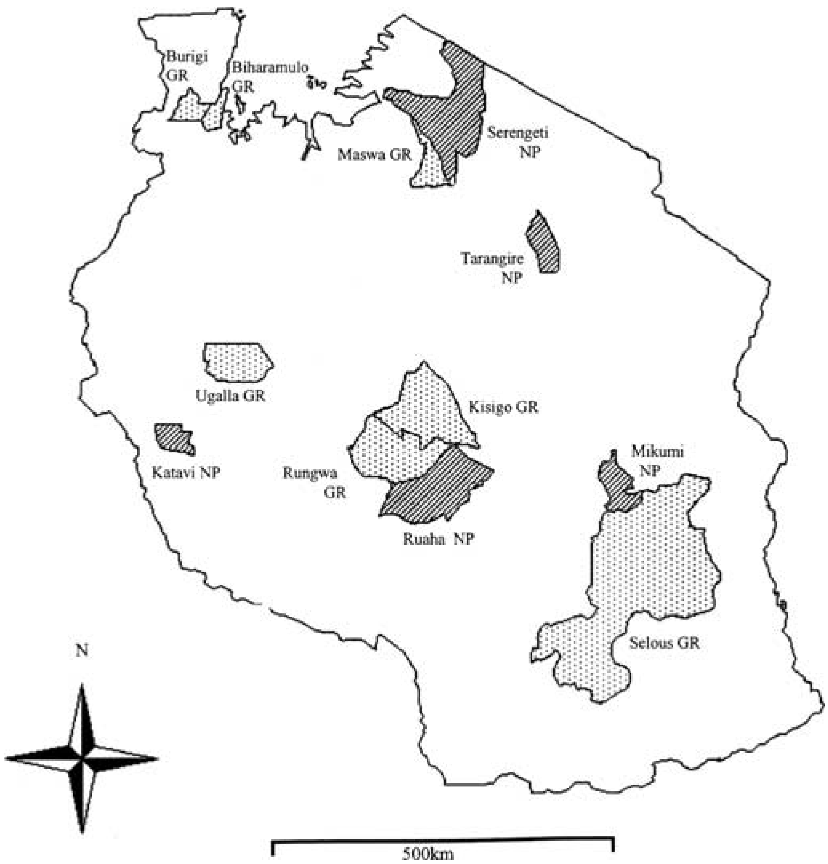

Figure 1. Tanzanian national parks (NP, hatched) and game reserves (GR, stippled) included in comparisons of changes in densities of large herbivores over time. Census zones (geographically distinct regions centered on a national park or game reserve over which surveys were conducted repeatedly) included Burigi-Biharamulo (Burigi GR, Biharamulo GR, surrounding areas), Katavi (Katavi NP, surrounding areas), Greater Ruaha (Ruaha NP, Rungwa GR, Kisigo GR, surrounding areas), Serengeti (Serengeti NP, Maswa GR, surrounding areas [including Ngorongoro Conservation Area]), Selous-Mikumi (Mikumi NP, Selous GR, surrounding areas), Tarangire (Tarangire NP, surrounding areas), and Ugalla (Ugalla GR, surrounding areas). Surrounding areas typically included partially protected game-controlled areas and "other" areas with virtually no protection.

We also coded all cells (including those that could not be placed into specific protection categories) according to their broader protection designation as either "in" a heavily protected area (all cells inside national parks or game reserves or NCA [Serengeti only]) or "out" (all cells inside game-controlled areas or "other" areas).

For each species surveyed in a given protection category of a census zone, we compared densities in grid cells at the start versus end of a 10-year time period. We tested for significant differences ($p < 0.05$) among densities in start versus end sets of survey grid cells with Mann-Whitney tests because of the non-normal distribution of the densities of large herbivores across grid cells. Using results of these start and end comparison results, we categorized each species in a given protection category as significantly increasing (showing significant increases in densities of wildlife in grid cells), not significantly changing, significantly declining, or having too few occupied grid cells to detect a significant decline.

To determine whether species occupied too few grid cells to detect a significant change, we first estimated the minimum number of occupied cells needed to detect a significant decline in each protection category. We ran mock Mann-Whitney tests with the number of occupied cells (with initial densities arbitrarily set at $1/km^2$) progressively increasing. We repeated this process until the number of occupied cells rose high enough to detect a significant difference between the initial mock survey and a terminal survey with all densities set to zero (to imitate a population crash). We classified species that occupied numbers of grid cells under this minimum cell requirement at both the start and finish of the survey period as likely to have occupied too few cells to detect a decline.

We calculated the percentage of species increasing, not significantly changing, declining, or occupying too few cells to detect a decline for every protection category within each census zone. When a species was classified as occupying too few grid cells to detect a decline in all protection categories in a census zone (as would be expected for species that are difficult to observe in that ecosystem), we excluded it from the pool of species contributing to total percentages (of species evaluated) for that zone.

To verify whether all surveys (not just those at the start and end) conducted during the 10-year time period supported the significant changes between beginning and end surveys, we also 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 & Rolf 1995). Thus, in every case where a species declined or increased significantly in a given protection category, we tested whether either the number of grid cells occupied or 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).

We also examined whether certain species tended to benefit more than others from heavy protection. We tallied the percentage of census zones in which each species fared well in the "in" category and subsequently the "out" category. Finally, we noted which species always fare well more frequently in heavily protected areas.

Results

Significant Population Increases and Decreases

Significant increases in densities of large herbivores occurred most frequently in higher protection categories (Fig. 2). In four of the five census zones with a significantly increasing species, for example, this increase occurred exclusively in a heavily protected national park or game reserve. No significant increases occurred in game-controlled areas in any of the four census zones encompassing these partially protected areas. A significant increase in large herbivores occurred in the "other" areas category (virtually no protection) in only one census zone (Selous-Mikumi).

Across all census zones, seasons, and protection categories, significant declines in species' densities nearly always dwarfed significant increases (Fig. 2). Significant declines were even prevalent among national parks and game reserves. In five out of seven census zones, for example, percentages of significant declines were higher in a national park or game reserve than in game-controlled areas or other areas. Significant declines (and increases) remained most common in these heavy protected categories after we omitted species that were difficult to census (bushpig, bushbuck, duiker, hippopotamus).

Species "Faring Well" in Different Protection Categories

Large percentages of species in protection categories showed either no significant changes in densities or occupied so few grid cells that a significant decline could not be detected (Fig. 2). Thus, in subsequent comparisons between different protection categories, we consider percentages of species that "fared well"—those that either increased significantly or maintained relatively high numbers of individuals (i.e., show no significant change) over the survey period.

More species fared well in areas with strict protection (national parks) than in the "other" category (no protection) in almost all census zones (Table 2). In the Selous-Mikumi census zone, however, slightly more species fared better in the other category than in the park category, although not as well as in the game reserve. More species fared well in game reserves than unprotected areas in all census zones, although percentages of species

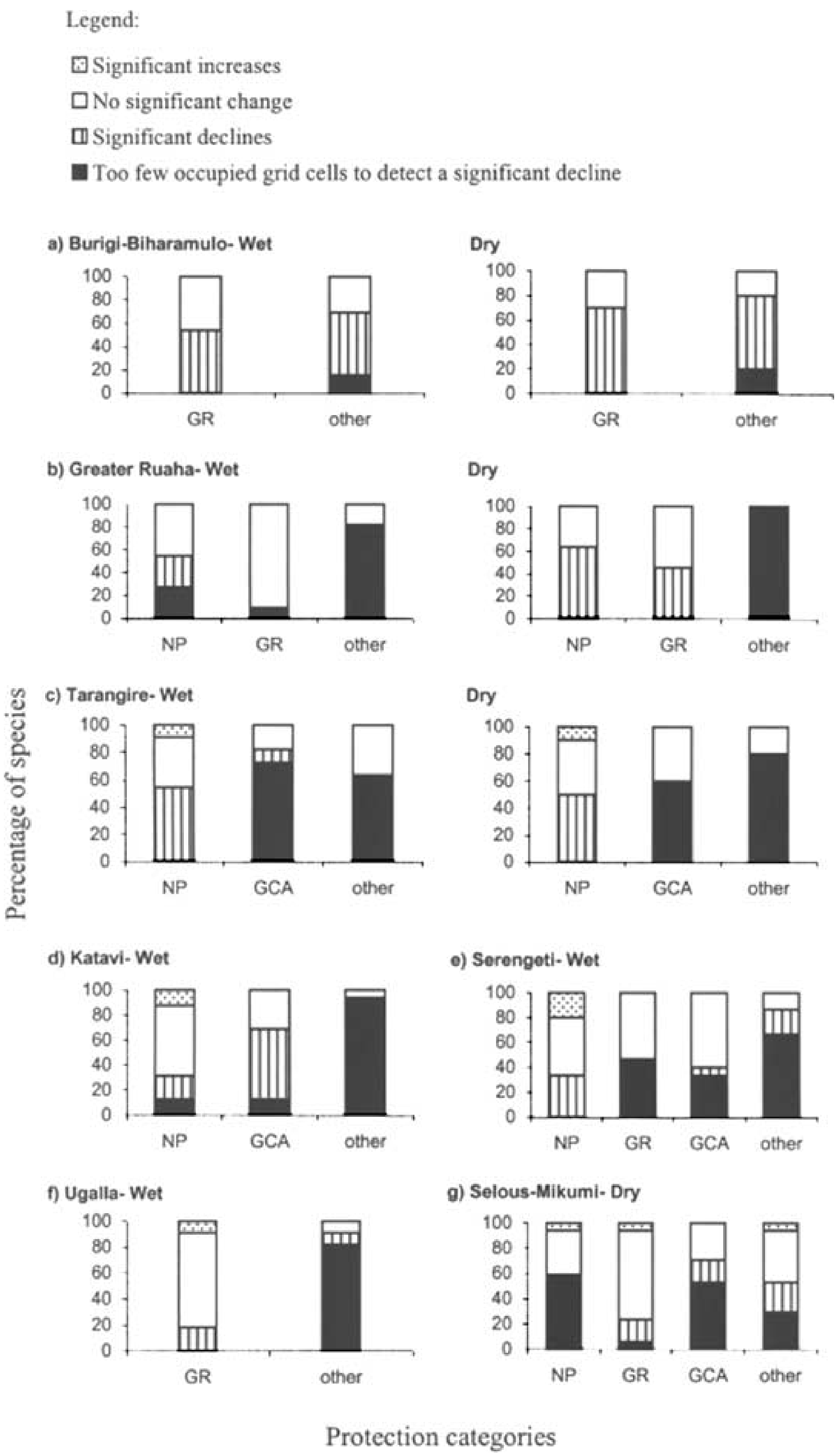

Figure 2. Percentage of species in national parks (NP), game reserves (GR), game-controlled areas (GCA), and "other" (no protection) categories that increased significantly, did not increase or decrease significantly (i.e., no change), declined significantly, and occupied too few occupied grid cells to detect a significant change in densities. "Wet" or "dry" refers to the season across which comparisons of densities at the start and finish of a decade were conducted.

faring well in these two categories were equal in the Burigi-Biharamulo dry-season comparisons after we omitted species that were difficult to census.

Comparisons of partially protected game-controlled areas with "other" areas in four census zones where they co-occur showed variable results. Species fared better in the game-controlled area category than the other category in Katavi and Serengeti zones and dry-season comparisons in the Tarangire zone, for example, but not in the Selous-Mikumi zone or Tarangire in the wet season (Table 2).

Even within the small sample of census zones containing both a national park and game reserve, neither protection type always held higher percentages of species that fared well (Table 2). Nevertheless, national parks maintained higher percentages of species faring well than did game-controlled areas across the census zones where they co-occurred, although this was not true in the Serengeti census zone after omitting species that were difficult to census. Species did not consistently fare better in game reserves versus game-controlled areas in the two census zones (Serengeti and Selous-Mikumi) that encompassed both of these protection categories (Table 2).

Overall, species generally tended to fare better in areas coded as “in” a heavily protected area (national park, game reserve, or NCA [Serengeti only]) than in areas coded as “out” (game-controlled areas and other areas) in most census zones, although not in Serengeti or Tarangire census zones (Table 2). After omitting species that were difficult to census, more species fared better “in” than “out” of heavily protected areas in all census zones but Burigi-Biharamulo, where equal percentages of species fared well in both categories in the dry-season comparisons.

Species Faring Well Versus Poorly in Each Protection Category

The percentage of species that fared well (averaged across all census zones) was not overwhelmingly higher than the percentage that fared poorly for any protection category (Fig. 3). In game-controlled areas percentages of species that fared poorly consistently outnumbered those that fared well, regardless of the season over which the comparisons are made. This difference is significant (Mann-Whitney, $p = 0.043$) if information from surveys of game-controlled areas in different census zones is pooled (Katavi [wet comparison], Serengeti [wet], Selous [dry], Tarangire [average of wet and dry comparisons]), although not after omitting species that are difficult to census. In “other” areas percentages of species faring poorly dwarfed those faring well in both wet- ($p = 0.004$) and dry-($p = 0.021$) season comparisons.

Species Differences

Only elephant densities increased significantly in more than one protection category or census zone (Table 3). All other species that experienced a significant increase (e.g., buffalo, bushbuck [difficult to census], impala, warthog) experienced many more significant declines in other areas. Four species—elephant, giraffe, hartebeest, and hippopotamus (difficult to census)—fared well in the “in” categories more frequently than “out” categories regardless of the season of the survey comparisons (Table 3).

Significant Changes Based on All Surveys Conducted during a Decade

Kendall’s rank correlations, based on either numbers of grid cells occupied by a species over time (in a protection category) or on the average densities of species within occupied cells over time, supported 38% (3/8) of the significant increases and 25% (20/79) of the significant declines detected with the start-end comparisons of herbivore densities in grid cells (Table 3). After omitting species that are difficult to census, 29% (2/7) of significant increases and 26% (18/69) of significant declines were supported by Kendall’s rank correlations.

Discussion

Researchers and managers in Tanzania have undertaken Herculean efforts to census wildlife across large areas, but to date virtually no temporal analyses have been carried out on the data over a nationwide scale. We compared data from aerial surveys conducted in the late 1980s

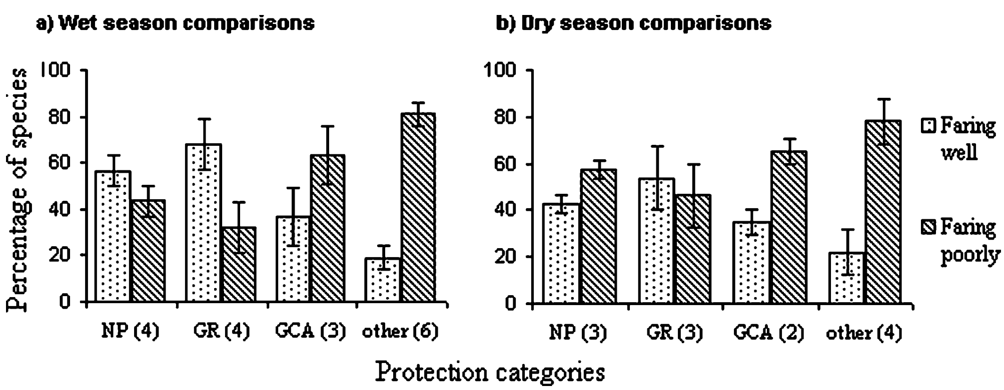

Figure 3. Average percentages of species faring well (increasing or showing no significant change) versus poorly (declining or occupying too few pixels to detect a decline) across (a) wet-season comparisons (Burigi-Biharamulo, Greater Ruaha, Tarangire, Katavi, Serengeti, Ugalla census zones) and (b) dry-season comparisons (Burigi-Biharamulo, Greater Ruaha, Tarangire, Selous-Mikumi). Abbreviations: NP, national parks; GR, game reserves; GCA, game-controlled areas; other, other areas with virtually no protection (number of zones surveyed in parentheses).

Table 2. Percentage of species that fared well (densities increased significantly or showed no significant change at the end of approximately a decade) in protection categories within seven large-herbivore census zones in Tanzania.

Census zone	*Season*[a]	n[b]	*National park*	*Game reserve*	*Game-controlled area*	*Other areas*	*In*[c]	*Out*[d]
Burigi-Biharamulo	wet	13		46.2		30.8	46.2	30.8
	dry	10		30.0		20.0	30.0	20.0
Greater Ruaha	wet	11	45.5	90.9		18.2	80.0	20.0
	dry	11	36.4	54.5		0.0	16.7	0.0
Tarangire	wet	11	45.5		18.2	36.4	38.5	46.2
	dry	10	50.0		40.0	20.0	41.7	83.3
Katavi	wet	16	68.8		31.3	6.3	68.8	37.5
Serengeti	wet	15	66.7	53.3	60.0	13.3	66.7	66.7
Ugalla	wet	11		81.8		9.1	81.8	9.1
Selous-Mikumi	dry	17	41.2	76.5	29.4	47.1	76.5	47.1

[a] *Season across which comparisons at the start and finish of a decade were conducted.*
[b] *Number of species in each census zone for which numbers of occupied pixels were sufficient to detect a significant decline in at least one protection category.*
[c] *Grid cells in national parks and game reserves (and Ngorongoro Conservation Area in Serengeti).*
[d] *Grid cells in game-controlled areas and other areas.*

and early 1990s and again in the late 1990s and early 2000s and found three consistent patterns in census zones across the country. First, in all protection categories, significant declines in the densities of large herbivores between the two snapshots in time far outnumbered significant increases. Second, higher percentages of species fared well in strictly protected national parks than in areas with partial protection (game-controlled areas), and species typically fared better in either national parks or game reserves than in other areas with virtually no protection. Third, percentages of species faring poorly in game-controlled areas and unprotected "other" areas were significantly larger than percentages of species faring well.

A major limitation of our study is that we relied on comparisons based on two snapshots in time. Although these two snapshots are separated by approximately a decade, it need not be the case that differences between two points in time reflect an overall trend in wildlife densities. Nonetheless, Kendall's rank correlations, based on sequential changes in either the number of grid cells occupied by a given species over time or the mean density of these occupied cells over time, corroborate just over a quarter (26%) of the changes indicated in the comparison of the first and last survey. This support is not as low as it might seem because near-perfect sequential declines or increases are particularly conservative indicators of change. Such sequential changes are especially unlikely if small numbers of wet- and dry-season surveys are pooled together, as they were in this case due to limited survey data, because many species fluctuate in population size across seasons. Clearly, long-term trends are best reflected from repeated, frequent surveys that are standardized across the country.

Can findings gleaned from comparing densities at the start versus finish of a decade reliably point to which protection categories are most effective? Data from census zones surveyed in both wet and dry seasons at the start and end of approximately 10 years suggest percentages of species faring well tend to vary by season, but general patterns between protection categories remained fairly consistent (Fig. 2). Similarly, average percentages of species faring well were higher in the wet season (especially for national parks and game reserves), yet the same general pattern of species faring well in national parks versus game reserves versus game-controlled areas versus other areas was maintained across comparisons made during both seasons (Fig. 3). Thus, although the percentage of species faring well appeared to be sensitive to seasonal effects, comparisons made between the percentages of species faring well in different protection categories showed relatively consistent results.

As in previous analyses based on large-scale surveys administered by managers and researchers (Bruner et al. 2001; Struhsaker et al. 2005), our analysis of aerial survey data for large herbivores in Tanzania suggests that heavily protected areas are more successful in conserving natural resources than are nearby areas with no protection. The few significant increases observed for species over a decade were most common in national parks and game reserves. In addition, the percentage of species faring well was generally higher in national parks and game reserves than in areas with no legal protection.

Such comparisons of heavily protected areas with areas of no protection are telling, but a more useful question is how such strictly protected areas fare in comparison with other approaches that represent a gradient of human use (Borgerhoff Mulder & Coppollilo 2005). Some researchers argue that generally little association exists between World Conservation Union categories and conservation effectiveness and therefore local people should be allowed to live in and use resources in protected areas (Shepard 2005). Others argue that the effectiveness

Table 3. Results of comparisons of densities of large herbivores in grid cells at the start versus finish of a decade in different protection categories.[a]

		Census zone and protection category																						
		Burigi-Biharamulo		*Greater Ruaha*			*Tarangire*			*Katavi*			*Serengeti*[b]				*Ugalla*		*Selous-Mikumi*					
Species	*Season*[e]	*GR*	*other*	*NP*	*GR*	*other*	*NP*	*GCA*	*other*	*NP*	*GCA*	*other*	*NP*	*GR*	*GCA*	*other*	*GR*	*other*	*NP*	*GR*	*GCA*	*other*	*In*[c]	*Out*[d]
Buffalo	wet	0	0	D	0	*	D	*	*	0	D[f]	*	I	0	*	*							60	60
	dry	D	0	D	0	*	0	*	*										0	0	D	0	50	50
Bushbuck[b]	wet	D	0										I	*	*	*							50	50
	dry	0	0																*	D[f]	*	*	100	100
Bushpig[b]	wet									*	D	*											0	100
	dry																							
Duiker[b]	wet									I[g]	*	*											100	100
	dry	0	D	D	D	*													*	0	*	D	50	25
Eland	wet	D	*	D	0	*	0	*	*	0	0	*	0	*	0	*							80	60
	dry			D	0	*	D	*	*										0	0	*	D	0	33
Elephant[i]	wet			0	0	*	I	*	*	I	0	*	I	*	0	*	0	*					100	60
	dry			0	0	*	I	*	*										I[f]	I	0	0	100	67
Giraffe[i]	wet	0	*	0	0	0	0	0	0	0	D[f]	*	0	0	0	0	0	*					100	50
	dry	0	*	0	0	*	0	0	0										*	0	*	*	75	25
Grant's gazelle	wet						0	*	*				D	*	0	*							50	50
	dry						D	*	*														0	100
Greater kudu	wet																							
	dry																		*	0	*	*	100	0
Impala	wet	0	D	D[f]	0	0	D	0	0	0	0	*	0	0	0	D	0	*					67	50
	dry	D	D	D[f]	D	*	D	0	*										0	0	*	I	25	50
Hartebeest[i]	wet	D	D	*	0	*	D[f]	D[f]	*	0	D	0	0	0	0	D	0	*					60	20
	dry			0	0	*	D	0	*										*	D[f]	0	0	33	0
Hippopotamus[b,i]	wet			0	*	*				0	D[g]	*	0	*	*	*	0	D					100	0
	dry																		*	0	D	0	100	0
Puku	wet																							
	dry																		*	*	0	*	0	0
Oryx	wet						D	*	*														0	0
	dry																							
Reedbuck	wet	0	D	*	0	*				D[f]	D	*	0	0	*	*	D	*					60	0
	dry	D	D																*	D	0	*	0	33
Roan antelope	wet	D	D							D	*	*					D	*					0	0
	dry			D	D	*																	0	0
Sableantelope	wet	0	0	*	0	*				*	0	*					0	*					75	0
	dry			0	0	*													*	0	*	0	50	50
Thomson's gazelle	wet						D[f,g]	*	0				D	*	D	*							0	0
	dry																							
Topi	wet	D[h]	D							0	0	*	0	0	0	*	0	0					75	75
	dry	D[h]	D																				0	0
Warthog	wet	D[h]	D	0	0	*	D[f]	*	*	D	D[f]	*	D	0	*	0	I[f]	*					33	33
	dry	D[h]	D	D	D	*	0	*	*										0	0	D	D	50	25

continued

Table 3. (continued)

		Census zone and protection category																						
		Burigi-Biharamulo		*Greater Ruaha*			*Tarangire*			*Katavi*			*Serengeti*[b]				*Ugalla*		*Selous-Mikumi*					
Species	*Season*	*GR*	*Other*	*NP*	*GR*	*Other*	*NP*	*GCA*	*Other*	*NP*	*GCA*	*Other*	*NP*	*GR*	*GCA*	*Other*	*GR*	*Other*	*NP*	*GR*	*GCA*	*Other*	*In*[c]	*Out*[d]
Waterbuck	wet	D[f]	0							0	D	*	D	0	0	*	0	*					50	50
	dry	D[f]	*																*	0	*	0	50	50
Wildebeest	wet																							
	dry						0	*	*										0	0	*	0	100	100
Zebra	wet	0	D	0	0	*	0	*	0	0	D[f]	*	D	*	0	D							80	20
	dry	D	D	D	D	*	D	0	0										0	0	0	D	25	25

[a] *Abbreviations and symbols: NP, national parks; GR, game reserves; GCA, game-controlled areas; other, areas with virtually no protection; I, significant increase; 0, no significant change; D, significant decline; *, too few occupied grid cells to detect a significant decline.*
[b] *Kendall's rank correlations were not carried out for species in the Serengeti census zone due to insufficient numbers of surveys conducted within a decade.*
[c] *Percentage of census zones in which species either significantly increased or experienced no significant change in the "in" category (in all grid cells coded as either national parks, game reserves, or Ngorongoro Conservation Area [Serengeti only]).*
[d] *Percentage of census zones in which species either significantly increased or experienced no significant change in the "out" category (in all grid cells coded as either game-controlled areas or "other" areas).*
[e] *Season during which surveys were conducted.*
[f] *Supported by Kendall's rank correlations based on the number of occupied cells over time (across all surveys conducted during the approximately 10-year period).*
[g] *Supported by Kendall's rank correlations based on the average densities of occupied cells over time.*
[h] *Data from species that are difficult to census may not be reliable.*
[i] *Species that fared better inside the "in" category (vs. "out" category) regardless of the season of the surveys.*

of strictly protected areas depends on the social context of a region but that areas prohibiting resource use offer the best hope of conserving biodiversity (Terborgh et al. 2002).

Our comparisons of species faring well under different levels of legal resource use showed some support for both arguments. Although only a few direct comparisons among the varying levels of protection were possible, even within this small sample size no protection category consistently showed the highest percentages of species faring well over time (Table 2). This may be due to the extent to which different census zones incorporate the home range of large mammals. For example, Tarangire National Park is the dry season range for many species of large ungulates, whereas large ungulates in Selous live within the game reserve all year round. Nevertheless, when national parks were compared with game-controlled areas (that allow some resource use and do not have onsite enforcement), the strictly protected area consistently held higher percentages of species experiencing significant increases or no change. The game-controlled area category could only be compared with unprotected areas in a handful of census zones, but nonetheless these comparisons showed variable results: game-controlled areas maintained higher percentages of species faring well than unprotected areas in some, but not all, census zones. In short, differences in conservation success among protection categories with relatively similar restrictions on resource use were difficult to detect (due to limited sample sizes), but strictly protected national parks in Tanzania were clearly more effective than multiuse areas with fewer restrictions on resource use and no onsite enforcement.

Our investigation of how particular species fare under different protection categories also showed that few species unanimously fared well in heavily protected areas. Elephants were unique in that they experienced many significant increases in density, particularly in national parks and game reserves. Only four species (giraffe, elephant, hippopotamus [difficult to census], and hartebeest) fared well more frequently inside the "in" category (all national park and game reserve grid cells) than in the "out" category (all game-controlled areas and other area grid cells) regardless of the season. Although large species are hypothesized to benefit most from protection because they are sought by hunters elsewhere (Caro et al. 2000), some large species such as buffalo and eland did not consistently fare better inside national parks and game reserves.

If more species fare well in heavily protected areas than in partially protected or unprotected land (as our analysis suggests), yet many species are still faring poorly in these areas (as long-term trends are needed to confirm), what does this reveal about the status of conservation in Tanzania? First, such a pattern would corroborate similar findings in Kenya, where research by Norton-Griffiths (1998) indicates that large mammals have fared better inside versus outside protected areas yet still are in a long-term decline. Such findings hint that parks, potentially the best hope for conserving large mammals in this region, are protecting only some species. In addition, these findings illustrate that it is difficult to assess the effectiveness of parks as a means to halt or reverse population decline, and therefore it is essential to assess how these areas compare with a suite of alternative conservation strategies (Borgerhoff Mulder & Coppolillo 2005). Our analysis for Tanzania compared government-regulated strict versus partially protected areas, but how do species under these protection schemes fare relative to other conservation projects with varying levels of community participation?

Compiling long-term trends across Tanzania is a challenging task. Logistical difficulties associated with each survey limit the numbers of regularly repeated surveys in each zone and lead to variability in the frequencies of surveys across different zones. Nonetheless, continued and frequent surveys, standardized as much as possible across the country, would greatly facilitate the process of deriving long-term trends. Such a data set is valuable in gauging the status of species, especially because our analysis suggests many large herbivores may be declining even within heavily protected areas. These data can provide equally important information on the responses of populations to management changes in protected areas, such as the recent upgrading or expansion of heavily protected areas, or efforts to bring local people the benefits of protected areas, such as the current trial implementation of community-based wildlife management areas. Standardized monitoring efforts can therefore provide conservation authorities with information on the success of conservation efforts targeted inside and outside heavily protected areas. Despite debates surrounding how to best conserve biodiversity, all camps agree that monitoring of resources under different protection strategies is essential.

Acknowledgments

We thank members of Conservation Information Monitoring Unit, Tanzania Wildlife Research Institute, Tanzania Wildlife Conservation Monitoring, Serengeti Ecological Monitoring Programme, Serengeti Wildlife Research Centre, Deutsche Gesellschaft fuer Zusammenarbeit, Ngorogoro Conservation Area Authority, Frankfurt Zoological Society, Tanzania National Parks, and the Wildlife Division who collected and processed the data used in this study. In particular, we thank R. Baldus, J. Balozi, G. Bigurube, K. Campbell, I. Douglas-Hamilton, H. Dublin, B. Farm, J. Hando, K. Hirji, S. Huish, A. Kaigili, A. Kajuni, E. Kapela, B. Kawasange, B. Kibonde, C. Kibwe, S. Kihaule, N. Kuwai, J. ole Kuwai, R. Lamprey, I. Lejora, J. Liani, B. Lyimo, J. Magombi, G. Makumbule, H. Maliti, M. Masota, B. Mbano, C. Mdoe, J. Mhina, S. Mhina, W. Minja, G. Mng'ong'o, D. Mnyagatwa, L. ole Moirana, L. Mollel, L. Morou, F. Msoffe, C. Mufungo, H. Mwageni, B. Mwasaga, H. Mwinyijuma, W. Ngowo, H. Nkya, I. Lejora, S. Lelo, M. Obed, L. Patterson, V. Runyoro, M. Stanley-Price, C. Seeberg, C. Seeber-Elverfeldt, E. Severre, J. Silkiluwasha, A. Songorwa, L. Stephan, W. Summay, M. Tarimo, S. Tham, R. Tibanyenda, C. Trout, S. Wood, B. Woodworth, P. Viljoein, and M. Zacharia. H. Frederick, R. Woodroffe, M. Schwartz, S. Thirgood, C. Schelten, and two anonymous reviewers provided helpful comments on the manuscript.

Literature Cited

Borgerhoff Mulder, M., and P. Coppolillo. 2005. Conservation: linking ecology, economics, and culture. Princeton University Press, Princeton, New Jersey.

Broten, M. D., and M. Said. 1995. Population trends of ungulates in and around Kenya's Masai Mara Reserve. Pages 169–193 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago.

Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. B. da Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. Science **291:**125–127.

Campbell, K., and M. Borner. 1995. Population trends and distribution of Serengeti herbivores: implications for management. Pages 117–145 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago.

Caro, T. M. 2003. Umbrella species: critique and lessons from East Africa. Animal Conservation **6:**171–181.

Caro, T. M., N. Pelkey, M. Borner, K. L. I. Campbell, B. L. Woodworth, B. P. Farm, J. Ole Kuwai, S. A. Huish, and E. L. M. Severre. 1998. Consequences of different forms of conservation for large mammals in Tanzania: preliminary analyses. African Journal of Ecology **36:**303–320.

Caro, T. M., M. Rejmanik, and N. W. Pelkey. 2000. Which mammals benefit from protection in East Africa ? Pages 221–238 in A. Entwistle and N. Dunstone, editors. Has the panda had its day? Future Priorities for the Conservation of Mammal Biodiversity. Cambridge University Press, Cambridge, United Kingdom.

Ghimire, K. B., and M. P. Pimbert. 1997. Social change and conservation: an overview of issues and concepts. Pages 1–45 in K. B. Ghimire and M. P. Pimbert, editors. Social change and conservation, environmental politics, and impacts of national parks and protected areas. Earthscan, London.

Hackel, J. D. 1999. Community conservation and the future of Africa's wildlife. Conservation Biology **13:**726–734.

Harris, R. B. 1986. Reliability of trend lines obtained from variable counts. Journal of Wildlife Management **50:**167–171.

Kiss, A. 2004. Making biodiversity conservation a land-use priority. Pages 98–123 in T. McShane and M. Wells, editors. Getting biodiversity projects to work: toward more effective conservation and development. Columbia University Press, New York.

Leader-Williams, N., J. A. Kayera, and G. L. Overton. 1996. Community-based conservation in Tanzania. Occasional paper of the IUCN Species Survival Commission, no. 15. World Conservation Union, Gland, Switzerland.

McShane, T., and M. Wells 2004. Getting biodiversity projects to work: toward more effective conservation and development. Columbia University Press, New York.

Norton-Griffiths, M. 1978. Counting animals. 2nd edition. Handbook no. 1. Techniques in African wildlife ecology. African Wildlife Foundation, Nairobi, Kenya.

Norton-Griffiths, M. 1998. The economics of wildlife conservation policy in Kenya. Pages 279–293 in E. J. Milner-Gulland and R. Mace, editors. Conservation of biological resources. Blackwell Science, Malden, Massachusetts.

Noss R., E. Dinerstein, B. Gilbert, M.Gilpin, B. J. Miller, J. Terborgh, and S. Trombulak. 1999. Core areas: where nature reigns. Pages 99–128 in M. E. Soulé and J. Terborgh, editors. Continental conservation: scientific foundations of regional reserve networks. Island Press, Washington, D.C.

Oates, J. F. 1997. Myth and reality in the rainforest: how conservation strategies are failing in West Africa. University of California Press, Berkeley.

Shepard, G. 2005. Poverty and forests: sustaining livelihoods in integrated conservation and development. Pages 340–371 in T. McShane and M. Wells, editors. Getting biodiversity projects to work: toward more effective conservation and development. Columbia University Press, New York.

Schwartzman, S., A. Moreira, and D. Nepstad. 2000*a*. Rethinking tropical forest conservation: perils in parks. Conservation Biology **14:**1351–1357.

Schwartzman, S., D. Nepstad, and A. Moreira. 2000*b*. Arguing tropical forest conservation: people versus parks. Conservation Biology **14:**1370–1374.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. 3rd edition. W.H. Freeman, New York.

Stevens, S. 1997. Conservation through cultural survival: indigenous peoples and protected areas. Island Press, Washington, D.C.

Struhsaker, T. T., P. J. Struhsaker, and K. S. Siex. 2005. Conserving Africa's rainforests: problems in protected areas and possible solutions. Biological Conservation **123:**45–54.

Terborgh, J., and C. Van Schaik. 2002. Why the world needs parks. Pages 3–14 in J. Terborgh, C. van Shaik, L. Davenport, and M. Rao, editors. Making parks work: strategies for preserving tropical nature. Island Press, Washington, D.C.

Terborgh, J., C. van Shaik, L. Davenport, and M. Rao. 2002. Making parks work: strategies for preserving tropical nature. Island Press, Washington, D.C.

Terborgh, J., and L. Davenport. 2002. Monitoring protected areas. Pages 395–408 in J. Terborgh, C. van Shaik, L. Davenport, and M. Rao, editors. Making parks work: strategies for preserving tropical nature. Island Press, Washington, D.C.

Thomas, L. 1996. Monitoring long-term population change: why are there so many methods? Ecology **77:**13–27.