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# MODELING THE SPATIAL DISTRIBUTION OF THE ECONOMIC COSTS AND BENEFITS OF ILLEGAL GAME MEAT HUNTING IN THE SERENGETI

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ABSTRACT. Illegal game meat hunting in the Serengeti National Park, Tanzania, and adjacent game reserves provides an important source of protein and cash income to local communities. We construct a profitability model that describes the spatial distribution of the economic costs and benefits of illegal hunting in the Serengeti during the late 1980s and early 1990s. Costs included capital investment in hunting weapons, $W_R$, and the opportunity cost of hunting, $W_O$, both held to be constants; and two spatially variable components, the logistic effort of traveling to hunting areas, $W_L$, and the penalties incurred if arrested, $W_P$. Benefit was the expected income from the sale of meat from resident wildlife species. The model suggests: (1) $W_R$ is the most important cost. (2) $W_L$ is the second most important cost and likely to determine the spatial distribution of hunting activity if hunters seek to minimize costs. (3) $W_O$ and $W_P$ are of minor importance, the former because alternative sources of income provide low pay, the latter because the overall chance of being arrested is low. (4) $W_P$ exceeds $W_L$ only in areas close to the boundary of protected areas. (5) Although resident wildlife contributes only a minor share of illegal offtake compared to the migratory herds, hunting resident wildlife is profitable in 68% of the area. This suggests that hunting of resident and migratory wildlife is highly profitable and may explain why the utilization of the target populations has become increasingly unsustainable.

KEY WORDS: Hunting, economics of hunting, optimality model, Serengeti, spatial heterogeneity.

**Introduction.** Prior to the establishment of the Serengeti National Park (SNP) and associated protected areas in northwest Tanzania, game-meat hunting within the Serengeti ecosystem was a component of the lives of many local communities (Turner [1987]). The establishment of the SNP effectively outlawed all hunting activity within the Park, whilst hunting in the protected areas adjacent to the Park was only legal if conducted under license (Campbell and Hofer [1995]). The level of illegal offtake by game-meat hunters has caused a dramatic decline in herbivore populations in certain areas within the SNP and associated protected areas (Campbell and Hofer [1995], Dublin et al. [1990]) and game-meat hunters can be considered to have a major predatory impact on both resident and migratory herbivores (Campbell and Hofer [1995], Hofer et al. [1996]). As a majority of game-meat hunters use the unselective hunting method of wire snares tethered to woody vegetation, populations of non-target species are also affected (Hofer et al. [1993]). Game-meat hunting provides both protein and cash income from the sale of dried meat for inhabitants in local communities. These and related benefits may have contributed to a significant increase in the density of the human population close to the boundary of the SNP between 1978 and 1988 (Campbell and Hofer [1995], Hofer et al. [1996]). This increase in human population is in part due to immigration into villages within 10 km of the protected area boundary from communities between 10–25 km from the boundary (Campbell and Hofer [1995], Hofer et al. [1996]).

Previous studies attempted to assess the magnitude of the problem of illegal hunting in the protected areas of the Serengeti ecosystem:

How many hunters operate inside conservation areas (Arcese et al. [1995], Campbell and Hofer [1995]), how many animals are taken out by hunters (Campbell and Hofer [1995], Hofer et al. [1996]), what impact hunting might have on the population dynamics of single species (Makacha et al. [1982], Dublin and Douglas-Hamilton [1987], Dublin et al. [1990], Hofer et al. [1993], Arcese et al. [1995], Mduma [1996]) and the community of herbivores as a whole (Arcese et al. [1995], Campbell and Hofer [1995], Hofer et al. [1996]). However, less attention has been paid to the assessment of the costs and benefits of hunting and the spatial distribution of hunting activities, both issues of considerable practical importance to the management of protected areas: How profitable is hunting? How are the costs and benefits distributed and thus where is hunting most likely to occur? Where should we expect to see the biggest impact of hunting on resident herbivores? Which locations should park rangers patrol in order to maximize the efficiency of their law enforcement efforts?

The problem of which location to choose for hunting is similar to the task that many animals face when searching for food. Optimal foraging theory (Stephens and Krebs [1986]) has been successfully used to describe rules that animals employ to solve foraging problems in an efficient manner. In optimal foraging theory, costs and benefits of foraging are ideally measured using the currency of Darwinian fitness. We have previously introduced two optimality models (Campbell and Hofer [1995]) in which a system of dimensionless indices describes a location in terms of its suitability for hunting to assess the pattern (space use) and extent (total area) of illegal hunting activity. In the current study we construct a new model of the spatial distribution of costs and benefits of illegal hunting during the late 1980s and early 1990s where costs and benefits were defined in monetary terms. The new model looks at the costs of hunting in terms of investment in hunting weapons, the opportunity cost of hunting, the penalties incurred if arrested, and the loss of income associated with time spent traveling to and from hunting areas. The benefit of hunting is calculated in terms of the expected income from the sale of meat from resident herbivores. We used this model to answer the following questions: How profitable is the hunting of resident wildlife? How important are the different cost components? Which cost component is likely to determine the distribution of hunting activity if hunters seek to

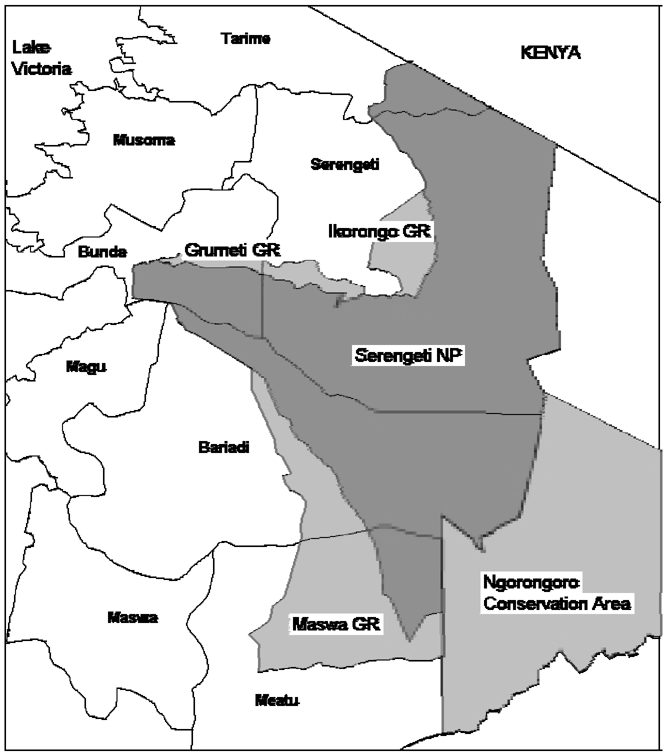


FIGURE 1. Location of the study area in northeastern Tanzania. The protected area (PA) in the Serengeti ecosystem includes Serengeti National Park (dark shading) and Ngorongoro Conservation Area and Maswa, Grumeti, and Ikorongo Game Reserves (light shading).

minimize costs? Although migratory herds contribute the major share of illegal offtake, and resident wildlife only a minor share (Hofer et al. [1996]), are expected benefits from resident wildlife species substantial enough to make hunting profitable, and if so, which locations would carry maximum expected profits?

**Study area.** The protected area of the Serengeti, (PA, Figure 1) referred to above includes the Serengeti National Park (SNP), Maswa, Ikorongo and Grumeti Game Reserves (GRs), and the Ngorongoro Conservation Area (NCA). No settlement, hunting or cultivation is permitted in the SNP. Licensed hunting but no settlement or cultivation is allowed in GRs. The NCA is inhabited by 26,900 people (1988 National Census, Bureau of Statistics [1988]), largely Maasai pastoralists with about 140,000 cattle and 184,000 sheep and goats (1987 aerial census estimates and data from 1988, Campbell [unpublished data], Homewood and Rogers [1991]). Hunting is prohibited. Although prohibited, some cultivation is practiced in the Ngorongoro Highlands. The human population in the six districts adjacent to the west of the protected areas (Figure 1) comprised 1,649,000 people at the time of the 1988 National Census (Bureau of Statistics [1988]). Cultural differences between the Maasai to the east of the PA and the agricultural and agro-pastoralist communities to the west result in major differences in human demands on wildlife within the PA, with illegal game meat hunting being chiefly conducted by hunters from the west (Campbell and Hofer [1995]). The PA constitutes the Tanzanian sector of the Serengeti ecosystem, and covers ca. 25,000 km$^2$.

**Methods.**

*Herbivore populations.* The more than 20 ungulate species in the Serengeti ecosystem (Swynnerton [1958]) are dominated by migratory species (wildebeest, *Connochaetes taurinus*, zebra, *Equus burchelli*, Thomson's gazelle, *Gazella thomsonii*, and eland, *Tragelaphus oryx*). During their annual migration, wildebeest, zebra and Thomson's gazelle move twice along a rainfall gradient, between their dry season (June–November) woodland refuges in the north and west of the ecosystem and the nutritious short-grass plains in the southeast (McNaughton and Banyikwa [1995].) For further details see Sinclair and Norton-Griffiths [1979]. Eight species constituted the majority of resident mammalian herbivore biomass (Campbell and Borner [1995]): African buffalo, *Syncerus caffer*, giraffe, *Giraffa camelopardalis*, Grant's gazelle, *Gazella granti*, impala, *Aepyceros melampus*, kongoni, *Alcelaphus buselaphus*, topi, *Damaliscus korrigum*, warthog, *Phacochoerus aethiopicus*, and waterbuck, *Kobus ellipsiprymnus.* Resident mammalian herbivores were concentrated in the hilly regions in the southwest, west, and north of the SNP, areas that received an average annual rainfall of greater than 800 mm and are covered by savanna or woodland. The flat, drier Serengeti Plains in the southeast of the Park have only low to very low densities of resident wildlife. Total mammalian herbivore population size exceeded 2 million animals. The distribution and population size of major mammalian herbivore species within the Serengeti ecosystem were taken from the most recently published (1988, 1989, 1991) aerial surveys (details in Campbell and Borner [1995]). Population estimates from aerial surveys were available for all four migratory and the eight key resident species. Other species, such as bushbuck, *Tragelaphus scriptus*, and Bohor reedbuck, *Redunca redunca*, are present in the ecosystem and are occasionally utilized by game meat hunters, but aerial censuses provided poor estimates of the distribution and size of their populations. Body mass and percent usable meat for each herbivore species were taken from Hofer et al. [1996].

*Local communities and hunting.* Information on details of hunting trips were derived from questionnaires of 571 individuals arrested and interviewed by law enforcement patrols between February 1992 and December 1993. These individuals represented a 43% sample of those arrested in SNP during this time. Numbers and proportion of each species killed per hunter were obtained from law enforcement patrol records from the same period (for details on questionnaires and patrol records, see Campbell and Hofer [1995] and Hofer et al. [1996]). For a sample of 81 patrols in 1992, law enforcement rangers recorded additional detailed information on individual patrol record cards on areas searched, the number of hunters seen and the number of hunters arrested on each occasion. This provided an estimate of the probability of apprehending hunters and the size of the area covered by a patrol. Information on the number of patrols conducted between 1986 and 1991 was available from monthly reports of the SNP authority, and from detailed patrol records in 1992–1993. This provided an estimate of patrolling rate.

Interviews conducted with 46 hunters arrested inside the SNP in 1988 provided data on the income that could be obtained from the sale of meat of resident wildlife (African buffalo, topi, giraffe). The mean value for each species was converted to a value per kg usable meat and averaged across all three species.

An estimate of the financial penalty incurred by hunters if arrested inside the PA was obtained from the records of the court cases against 29 of the 46 hunters interviewed in 1988. In two cases, the sentence comprised a prison term, in one case a fine, and in all other cases the sentence was expressed as a choice between a fine or a term in prison.

Interviews conducted with 94 hunters arrested in 1998 provided estimates of the costs of the types of weapons used by hunters and an estimate of the average number of weapons used per hunting trip. Capital expenditure on weapons was represented in the model by classifying arrows and snares as weapons that had to be replaced or obtained specifically for each hunting trip, and knives, spears, pangas (an all-purpose instrument similar to a machete), bows, and axes as general purpose weapons that were not specifically bought for hunting but would be confiscated by law enforcement rangers once arrested.

The opportunity cost of hunting, the usual pay a villager might get for a day's work, was assessed by comparing several sources. The hunters interviewed in 1988 provided an estimate of their annual income equivalent to 0.46 US-\$ day$^{-1}$. The court penalties against a subsample of these hunters that were expressed as a choice between a fine and a term in prison provided an estimate of the earning potential of a villager as viewed by the legal system at this time of 0.17 US-\$ day$^{-1}$. These two estimates were compared with the published average annual total wage/salary of 0.80 US-\$ day$^{-1}$ paid in the food-processing industry in the Mara Region for 1988 by large companies (with more than 9 employees, Bureau of Statistics [1995]). Finally, an estimate of total annual household consumption of 0.23 US-\$ day$^{-1}$ (per person) and 1.41 US-\$ day$^{-1}$ (per household) was obtained from a national census of households carried out between December 1991 and November 1992 (Bureau of Statistics [1996]). This excludes the value of agricultural produce grown for home consumption by rural farm households because almost all hunters arrested inside the SNP came from rural farm households (Loibooki [1997]). Only 291 people were employed in large food processing factories in 1988 and thus this salary was higher than that obtained by the local population. As the cost of total household consumption per person exceeded the estimate based on the prison fine, the latter was considered too low. Thus, the value chosen was the estimate based on the annual income of hunters.

All monetary values were converted from the local currency (Tanzanian Shilling) to US-\$ equivalents at the appropriate average annual exchange rate for a given data set. Prior to 1993, the rates were those that one of us (KLIC) recorded on a monthly basis from a variety of sources in Tanzania. From 1994 onwards these were Interbank rates from OANDA [1999].

*The profitability model.* Profitability was defined as the difference between expected benefits, $W_B$, and total costs, $W_T$, profitability $= W_B - W_T$.

*Benefits.* Expected benefits from hunting were modeled in the conventional way (Clark [1990], Milner-Gulland and Mace [1998]) as

$$W_B = b_R \times E \times c_W \times M_R,$$

where $b_R$ is the average sales value of a kg of usable resident wildlife meat (Table 1), $E$ is the effort of hunting per person and hunting day (set to 1), $c_W$ is the catchability coefficient (the probability that an individual of a resident wildlife species is caught by a snare, Table 1), and $M_R$ is the total density of resident wildlife in a 5 km grid cell (see below) expressed in terms of mass of usable meat.

An estimate for $c_W$ was computed as $c_W = N_H/(N_S \times (t_B - t_T) \times N_R)$, where $N_H$ is the average number of wildlife caught per hunter during the time when he had his snares set (Hofer et al. [1996]), $N_R$ is the average of the total density of all resident wildlife species per grid cell in grid cells where hunters were caught, $N_S$ is the average number of snares per hunter, $t_B$ is the average number of days the hunter had spent in the PA, and $t_T$ is the average number of days of traveling from the nearest village to the grid cell where the hunter was arrested (the distance from the nearest village to the grid cell, $d_V$, divided by the speed of travel through the bush, $v_W$, Table 1).

The total usable meat for all resident wildlife in a 5 km grid cell, $M_R$, was summed over all 8 resident wildlife species as $M_R = \Sigma(N_i \times 25 \times m_i \times u_i)$, where $N_i$ is the density (in km$^{-2}$) for species $i$, $m_i$ is the average body mass of species $i$ and $u_i$ is the proportion of usable meat per individual.

Migratory wildlife were not incorporated into the model because of the unpredictable movements of these herds (Maddock [1979]).

TABLE 1. Estimates of constants used as parameters in the model.

| Parameter | Notation | Value | Units |
|---|---|---|---|
| Opportunity cost (pay for a villager's daily work) | $W_O$ | 0.46 | US-\$ day$^{-1}$ |
| Cost of weapons specifically obtained or replaced after each hunting trip | $W_R$ | 4.04 | US-\$ |
| Cost of equipment confiscated if arrested (not specifically bought for hunting) | $W_W$ | 2.43 | US-\$ |
| Cost of fine if arrested | $W_F$ | 110.26 | US-\$ |
| Total cost of penalties incurred if arrested | $W_J$ | 115.88 | US-\$ |
| Probability of apprehension if detected | $p_C$ | 0.666 | |
| Average sales value of usable meat (resident wildlife) | $b_R$ | 0.19 | US-\$ kg$^{-1}$ |
| A day's travel on foot in the bush | $v_W$ | 15 | km day$^{-1}$ |
| Catchability coefficient (of wildlife by hunters) | $c_W$ | 0.011 | – |
| Scaling constant to adjust the patrolling rate so that the mean of the modeled rates approximates the average empirical patrolling rate | $\beta_0$ | 0.014 | – |
| Scaling constant to reflect the patrolling rate of a grid cell as a function of its distance to the nearest ranger post | $\beta_1$ | -0.06765 | – |

The inclusion of migrants would change the measure of expected benefits from hunting and hence the measure of profitability of an area but would not affect the estimate of hunting costs (see below).

*Costs.* The total cost associated with a day's hunting in a particular grid cell was modeled as the sum of the capital investment in weapons specifically required for hunting, $W_R$, the opportunity cost of not earning an income in a different way, $W_O$, the cost associated with traveling to the grid cell, $W_L$, and the cost of penalties associated with an arrest by a law enforcement patrol, $W_P$,

$$W_T = W_R + W_O + W_L + W_P.$$

$W_R$, the cost of weapons specifically bought or replaced for each hunting trip, and $W_O$, the opportunity cost of hunting per day, were estimated as described above and set as constants (Table 1).

A logistical problem for hunters results from the travel distance to the hunting area. Greater distances require more time and energy and may increase the cost of carrying dried meat out of the PA. Investment of time in travel to a hunting area thus decreases time that can be allocated to the generation of income by alternative means. Hence, $W_L$ was modeled for each grid cell as the time it takes to do a round trip to this grid cell multiplied by the opportunity cost of traveling,

$$W_L = W_O \times (2d_V/v_W).$$

$W_P$ was modeled for each grid cell as $W_P = r_A \times W_J$, where $r_A$ is the rate of arrest in that grid cell per day and $W_J$ the penalty incurred if arrested. $W_J$ was modeled as $W_J = 7W_O + W_F + W_W$, where $7W_O$ is the opportunity cost associated with the average time spent under arrest until charged, $W_F$ is the fine set by the court, and $W_W$ is the cost of those weapons not specifically bought for hunting that were confiscated by law enforcement rangers if arrested. $W_F$, $W_W$ and hence $W_J$ were empirically derived and set as constants (Table 1).

The spatial distribution of the rate of arrest, $r_A$, was considered to be dependent on the rate per day at which law enforcement rangers patrolled a grid cell, $r_P$, the probability of being detected by such a patrol in the grid cell given that the grid cell is being patrolled, $p_D$, and the probability of being caught once detected, $p_C$.

$p_C$ was estimated from the detailed records of patrols in 1992 and set as a constant (Table 1). The rate at which a grid cell was patrolled, $r_P$, was considered to be highest near ranger posts and to decline with increasing distance $d_R$ from such posts. We used an exponentially decaying function with two scaling constants $\beta_0$ and $\beta_1$,

$$r_P = \beta_0 e^{-\beta_1 d_R}.$$

As it requires two days to travel 30 km on foot, in addition to the time patrols devote to searching for hunters, and patrols rarely lasted more than one day, we set $\beta_1$ (Table 1) in such a way that the probability of patrolling was 100% at the ranger post and 10% at $d_R$ of 30 km. The parameter $\beta_0$ (Table 1) was introduced to adjust the rate of patrolling so that the mean of the modeled rates of patrolling across grid cells approximated the average empirical rate of patrolling per grid cell and day. The average empirical rate of patrolling per grid cell and day was estimated as follows. The mean number of patrols per day throughout the PA between 1986 and 1991 was 1.28. The detailed records of patrols in 1992 suggested that each patrol covered on average 3.09 grid cells per day. This implied an average rate of patrolling of 0.0045 patrols per grid cell and day.

The probability of detection, $p_D$, was considered to depend on relief and habitat structure, and hypothesized to being greatest in flat open areas, and least in rocky and densely vegetated areas, particularly near rivers. $p_D$ was set as $p_D = 1 - c_T$ where $c_T$ was the maximum of (1) relief (variance in elevation per grid cell), (2) percent total woody canopy cover, (3) closeness to major rivers and drainage lines and (4) percent rocky and stony ground, all factors scaled between 0 and 1 where 1 is equivalent to the maximum value of each variable. Closeness to rivers replaced the percentage of riparian habitat in a preliminary version of the model (Campbell and Hofer [1995]). Discussions with law enforcement personnel confirmed that an increase in the value of any of these factors would be expected to make the detection of hunters by patrols more difficult.

*Data analysis.* All spatially referenced data were summarized by 5 km grid cells and analyzed using the Idrisi (Eastman [1993]) Geographic Information System (details in Campbell and Hofer [1995]). Because the analysis aimed to examine the impact of hunting inside the PA, statistical tests were confined to grid cells within it. Statistical analyses were performed using Systat 8.0 (Wilkinson [1998]). $P$-values are two-tailed unless specified otherwise.

We explored whether spatial data deviated from a random distribution in space, i.e., whether they exhibited spatial autocorrelation. If spatial autocorrelation is present, then the effective sample size and degrees of freedom differ from the actual sample size and degrees of freedom, and $P$-values of test statistics need to be modified (Cliff and Ord [1981], Haining [1990]). All data sets were significantly spatially autocorrelated (as indicated by Moran's $I$ as coefficient of spatial autocorrelation under the assumption of randomization), and therefore the $P$-values of test statistics were adjusted following

TABLE 2. Basic statistics for model parameters averaged across 680 grid cells covering the protected area of the Serengeti ecosystem.

| Parameter | Dimensions | Minimum | Maximum | Mean | SD | CV | Median |
|---|---|---|---|---|---|---|---|
| Distance to nearest ranger post ($d_R$) | km | 1.9 | 40.1 | 16.8 | 8.3 | 0.50 | 15.8 |
| Distance to nearest village ($d_V$) | km | 2.0 | 81.4 | 29.4 | 18.2 | 0.62 | 25.0 |
| Patrolling rate ($r_P$) | grid cell$^{-1}$day$^{-1}$ | 0.0006 | 0.01 | 0.005 | 0.003 | 0.58 | 0.004 |
| Probability of detection ($p_D$) | – | 0 | 1.0 | 0.8 | 0.2 | 0.23 | 0.8 |
| Rate of arrest ($r_A$) | grid cell$^{-1}$day$^{-1}$ | 0 | 0.008 | 0.002 | 0.002 | 0.64 | 0.002 |
| Cost of penalties ($W_P$) | US-$ grid cell$^{-1}$day$^{-1}$ | 0 | 0.91 | 0.28 | 0.17 | 0.64 | 0.2 |
| Cost of traveling ($W_L$) | US-$ grid cell$^{-1}$day$^{-1}$ | 0.12 | 4.95 | 1.79 | 1.11 | 0.62 | 1.52 |
| Total costs ($W_T$) | US-$ grid cell$^{-1}$day$^{-1}$ | 4.75 | 9.62 | 6.56 | 1.12 | 0.17 | 6.22 |
| Benefits ($W_B$) | US-$ grid cell$^{-1}$day$^{-1}$ | 0 | 2132.12 | 78.40 | 214.91 | 2.74 | 17.63 |
| Profitability ($W_B - W_T$) | US-$ grid cell$^{-1}$day$^{-1}$ | -9.62 | 2123.94 | 71.84 | 214.93 | 2.99 | 10.91 |

procedures recommended by Bivand [1980] and Haining [1990].

**Results.** Empirical estimates of some model parameters set as constants are listed in Table 1. Basic statistics for $d_R$, $d_V$, and model parameters that included spatial components ($r_P$, $p_D$, $r_A$, $W_P$, $W_L$, $W_T$, $W_B$, and profitability, $W_B - W_T$) are presented in Table 2.

Capital investment, $W_R$, comprised 61.5%, $W_L$ 27.2%, $W_O$ 7.0% and $W_P$ 4.3% of the average total costs of hunting. The total cost of penalties incurred if arrested, $W_J$, was substantial and equivalent to 252 days of normal villager's earnings. However, the daily patrolling rate and hence the modeled daily rate of arrest were low. As a consequence, $W_P$, which incorporates the likelihood of being arrested, was substantially and significantly (Wilcoxon test, $z = 22.21$, $p < 0.0001$) lower than $W_L$ (Table 2).

Across the PA, a day's hunting produced an average profit equivalent to 156 days of normal villager's earnings. Benefits based on hunting of resident wildlife exceeded costs in 68.2% of grid cells.

*Spatial distribution of benefits.* The spatial distribution of expected benefits, $W_B$, from hunting resident wildlife is illustrated in Figure 2. The highest expected benefits occurred in the Western Corridor, the southwestern area of the SNP and in central to northern sections of the SNP.

*Spatial distribution of costs.* The spatial distribution of modeled $W_L$ is shown in Figure 3. $W_L$ was highest in the eastern and southeastern sectors of the PA, particularly the short-grass plains. The spatial distribution of the probability of detection, $p_D$, a function of the distribution of the topographic and habitat features is shown in Figure 4. $p_D$ was high along the boundaries of the Western Corridor and on the short-grass plains in the southeast of SNP. The spatial distribution of the rate of arrest, $r_A$ is shown in Figure 5. Since $W_P$ is simply $r_A$ multiplied by a constant, Figure 5 also illustrates the spatial distribution of $W_P$. Figure 6 illustrates that the 41 grid cells where $W_P$ exceeded $W_L$ were distributed along the boundaries of the PA. The spatial distribution of $W_T$ is shown in Figure 7. Total costs were lowest in the central parts of Maswa GR, and high throughout most of Grumeti and

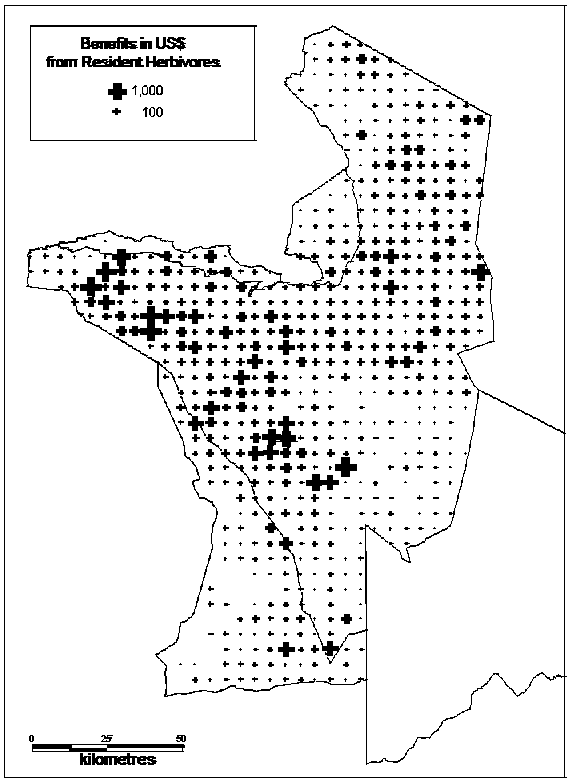


FIGURE 2. Spatial distribution of the expected benefit, $W_B$, (in US-\$) from hunting resident herbivores in the protected area of the Serengeti.

Ikorongo GRs. Substantial areas with lower total costs also occurred inside SNP south of the Grumeti GR, east of the Ikorongo GR, in the northwest, and in the west and southwest of the PA. The short-grass plains in the southeast of SNP were the locations with the highest total costs.

*Spatial distribution of costs versus benefits.* The spatial distributions of $W_B$ and $W_L$ were not linked (Spearman's $\rho = -0.065$, NS), whereas $p_D$ significantly declined with increasing values of $W_B$ ($\rho = -0.226$, $p < 0.001$). $r_A$ and consequently also $W_P$ were not linked to benefits

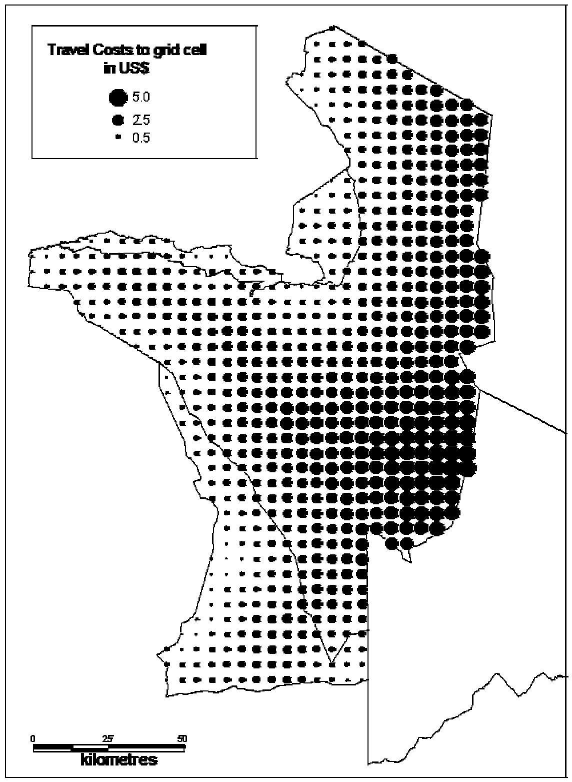


FIGURE 3. Spatial distribution of modeled traveling cost, $W_L$, (in US-$) from the nearest village outside the boundaries of the protected area of the Serengeti to each grid cell.

($\rho = -0.075$, NS). Total costs $W_T$ were also not linked to benefits ($\rho = 0.076$, NS), i.e. there was no obvious general trade-off between total costs or several of its components and benefits.

*Spatial distribution of profitability.* The spatial distribution of profitability is shown in Figure 8. Hunting was modeled to be most rewarding in the western sector of SNP, and less rewarding in areas beyond an arc extending from southeast of the Ikorongo GR to the mid-point of the border between SNP and Maswa GR. Campbell and Hofer [1995]

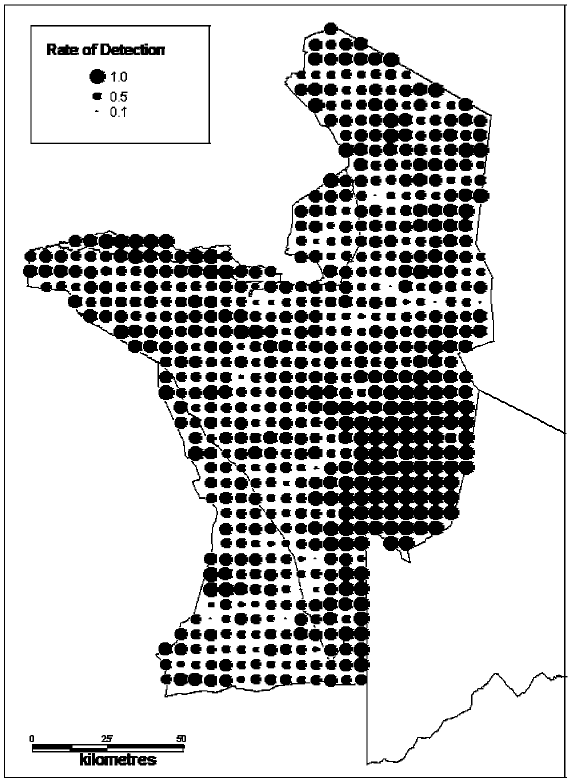


FIGURE 4. Spatial distribution of the modeled probability of detection, $p_D$, of hunters by law enforcement rangers per grid cell in the protected area of the Serengeti, given that the cell is patrolled by law enforcement rangers.

had classified grid cells into five "risk zones" by comparing the modeled suitability of hunting of the area modeled as a series of dimensionless indices with the density of resident wildlife as an index of potential hunting benefits. For instance, grid cells were described as "already overexploited" if they had a high suitability for hunting but a low density of resident wildlife. There was a highly significant difference between risk zones in their average profitability as calculated by the current model (Kruskal Wallis test, $H = 214.82$, $df = 4$, $p < 0.001$). The risk zone with the highest median profitability of US-\$ 51.38 ($n = 119$) was

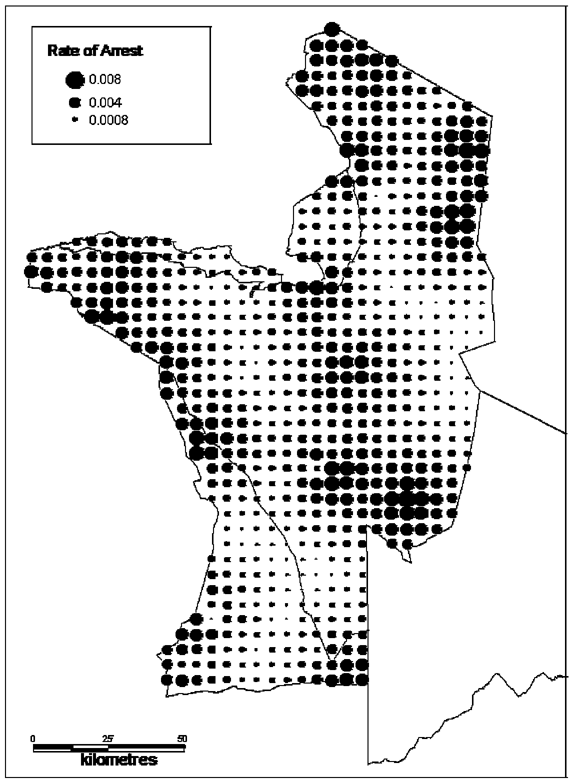


FIGURE 5. Spatial distribution of the modeled rate of arrest, $r_A$, of hunters by law enforcement rangers in the protected area of the Serengeti. $r_A$ was computed as the modeled rate of a grid cell being patrolled, $r_P$, multiplied by the modeled probability of detection in that cell given that the cell is patrolled, see Figure 4, $p_D$, multiplied by the estimated probability of apprehension in that cell given that the hunter was detected, $p_C$.

the zone where "escalated conflicts" were predicted to be most likely between law enforcement rangers and hunters, followed by the "endangered" zone (median US-\$ 35.30, $n = 64$) and the "future expansion" zone (median US-\$ 12.48, $n = 293$). The "untouched" zone and the "already over-exploited" zones both had negative median profitabilities (US-\$ $-4.78$, $n = 110$; and US-\$ $-3.72$, $n = 94$, respectively).

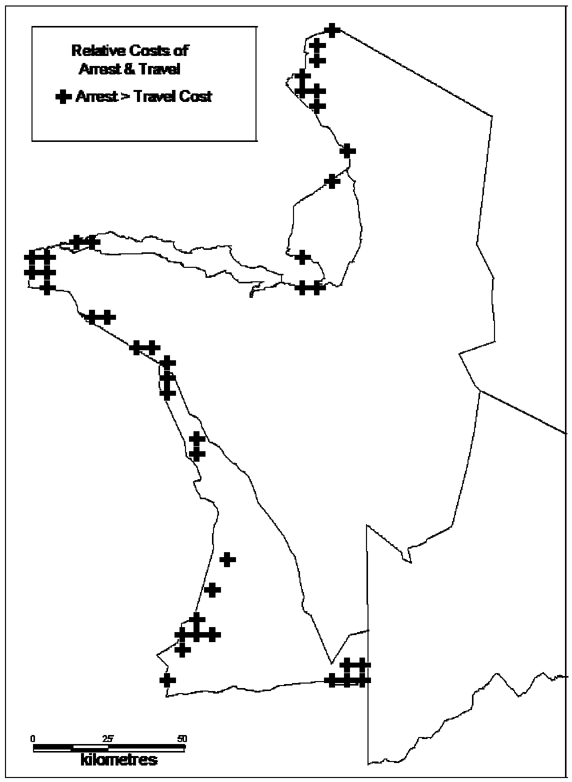


FIGURE 6. Spatial distribution of grid cells in the protected area of the Serengeti where the modeled cost of penalties incurred if arrested, $W_P$, was higher than the modeled cost of traveling to that grid cell, $W_L$. Costs were expressed in US-$.

**Discussion.** Game-meat hunting plays an important role in the economy of villages close to the PA boundary and is an important driving force in the dynamics of the Serengeti ecosystem (Hofer et al. [1993], Campbell and Hofer [1995], Arcese et al. [1995], Hofer et al. [1996]). Our aim in this study was to answer the following questions: How profitable is hunting of resident wildlife? How important are the different cost components? Which cost component should determine the distribution of hunting activity if hunters seek to minimize costs? Which locations would carry maximum expected profits? In summary,

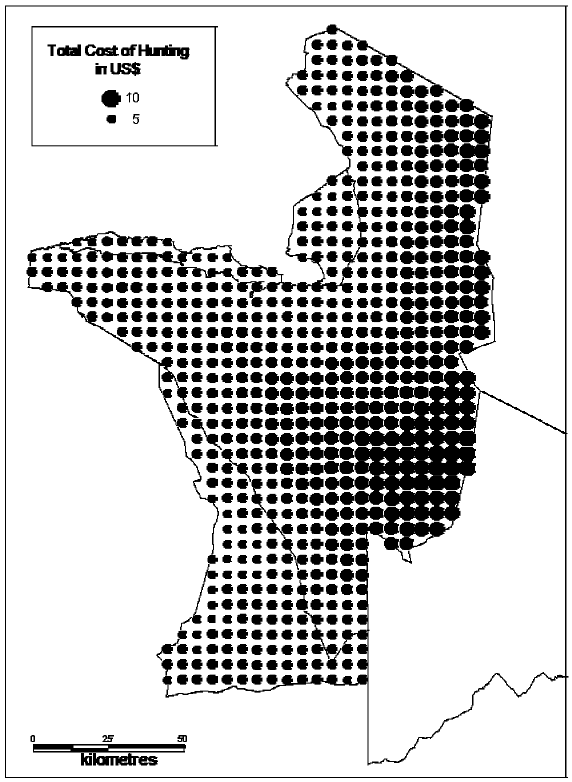


FIGURE 7. Spatial distribution of the modeled total cost, $W_T$, in US-\$ of hunting in the protected area of the Serengeti.

hunting of resident wildlife was profitable (and substantially so) in more than two thirds of the protected areas of the Serengeti. There was no overall trade-off between the costs and benefits of hunting, and the most profitable areas for hunters were located in the west and southwest of the SNP. The most important cost was the capital investment in specific hunting weapons. If hunters seek to minimize costs, the cost of traveling was more likely to determine the distribution of hunting activity than the cost associated with penalties.

*Model assumptions and limitations.* Aerial survey results usually

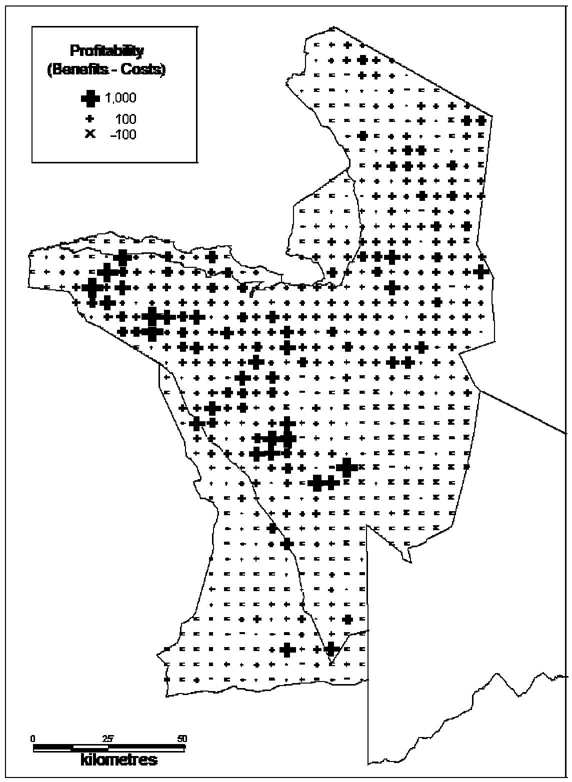


FIGURE 8. Spatial distribution of the modeled profitability of hunting (benefits from resident wildlife minus total costs) in US-$ in the protected area of the Serengeti.

underestimate true wildlife population numbers (Caughley [1974]), so recorded densities on which expected hunting benefits were based are likely to underestimate true benefits. This suggests that the model estimates of benefits and profitabilities are conservative and the true returns of daily hunting of resident wildlife may be even higher than the already substantial value of five months of normal earnings.

The model did not consider migratory wildlife. These mobile resources were not considered because the movements of herds are unpredictable, may vary substantially between years (Maddock [1979]) and because we had no data on the dry season movements of the migratory herds during the study period. In future it might be possible to incorporate migratory wildlife densities in benefit models for specific years, if the dry season distribution of migratory wildlife is known for that year. Alternatively, it might be possible to use remote sensing as an indicator of migratory wildlife densities, if a calibration study demonstrates that these can be modeled from remotely sensed parameters.

The cost of traveling from the home village of a hunter to the village closest to the PA boundary was ignored. This cost is likely to be less than that within the PA. It is also possible that hunters that travel long distances to reach the Park are most likely to operate during the dry season (June–November) when there is little agricultural activity in their home villages and the returns from hunting are significantly increased by the presence of migratory herds near or beyond the boundaries of the PA. If the cost of traveling outside the PA was included, the relative importance of the cost of traveling is likely to increase further compared to the cost of penalties.

The model did not consider the cost of being arrested while traveling to hunting areas within the PA. Because many hunters travel at night, their chance of being arrested is reduced and thus this cost is unlikely to be high. The model also ignored the cumulative cost of penalties that increase additively with every day of hunting inside the PA. Given an average number of 3.5 days that hunters spent in the PA before being arrested (Hofer et al. [1996]), including a day of traveling, the average total cost of penalties $W_P$ per hunting trip is likely to be two to three times the mean value of $W_P$ listed in Table 2. This would still leave the cost of traveling to be more than twice as high as $W_P$.

The data used to construct the model came from different study years. Most data used to model the costs of hunting were collected in 1988. Data on the densities of resident herbivores were available from 1988, 1989 and 1991. Data on details of hunting trips, period of stay in the park and other parameters were available from interviews of arrested hunters conducted in 1988, 1992 and 1998. To reconstruct the distribution of costs and benefits of illegal hunting during the late 1980s and early 1990s, these data were used with the assumption that the US-$ values did not change or changed little. This is an assumption that is justified for at least some of the parameter estimates. For instance, the assessment of the sales value of resident wildlife species had changed little from US-\$ 0.19 $kg^{-1}$ in 1988 (this study) to US-\$ 0.21 in 1995 as assessed by a group of hunters interviewed then (M. Maige [pers. comm.]).

The annual incomes quoted by hunters were comparatively low, and were likely to include income acquired through legal activities outside the PA but exclude illegal income from game-meat hunting. The comparison of several methods of assessing the opportunity cost of hunting showed that the annual income quoted by hunters was likely to be of the correct order of magnitude.

*Testing the model.* This model could be tested with data on the spatial distribution of hunting activity. This would permit elucidation of the rules by which hunters operate, e.g., whether in the parlance of optimal foraging theory hunters maximize the rate at which they acquire benefits, minimize costs, and/or operate risk-averse, risk-prone or risk-insensitive tactics. The current model suggests that hunters should be sensitive to logistical considerations but quite insensitive to spatial variation in the costs of penalties incurred that are associated with being arrested.

*Spatial heterogeneity.* In part, the value of the model relies on the explicit acknowledgment of spatial variation in the density of wildlife populations and costs of hunting. Campbell and Hofer [1995], who used a series of dimensionless indices to describe the suitability of an area for hunting, and classified grid cells as "already over-exploited" if they had a high suitability for hunting but a low density of resident wildlife, showed that these grid cells experienced a significant decline in all major resident herbivore populations over the short period between 1989 and 1991, a period for which suitable census data existed (Campbell and Hofer [1995], Campbell and Borner [1995]). This is compatible with the results from the current model where the median profitability of these grid cells was negative, based on the average of the three aerial censuses of resident wildlife in 1988, 1989 and 1991. In contrast to overexploited grid cells, areas classified as "endangered" and "escalating conflict" had the highest median profitabilities in this study, experienced non-significant population increases between 1989 and 1991 (Campbell and Borner [1995]) and must be considered the most interesting target areas for hunters in years from 1991 onwards. The results of the current model predict that more recent wildlife survey data should show a decrease in densities of resident herbivores in these areas. These analyses suggest then that current densities of resident wildlife species may be strongly influenced by current as well as past exploitation pressures rather than by intrinsic factors alone.

*Predicting future developments.* Illegal hunting within the protected areas needs to be viewed within a complex and dynamic framework. Large travel distances outside the park increase time and energy costs associated with hunting. Extended travel inside the Park increases the probability of encountering law enforcement patrols. Both of them increase the costs of hiring porters to carry meat out of the park. Changes in population distribution and numbers and in market forces may result in modified patterns of demand for wildlife products. Hunting itself clearly has an impact on targeted species and is likely to result in a reduced supply of a product for which there is increasing demand. The average annual rate of population increase between 1978 and 1988 within 10 km of the PA boundary was substantially higher than the national average. This is likely to have been due in part to migration from villages located between 10–25 km from the PA boundary, where rates of increase were below the regional averages (Hofer et al. [1996]). Offtake of game meat from the Serengeti ecosystem is clearly linked to the potential market for this product. As a result, the rapidly growing human population close to the PA boundary will inevitably lead to an increasingly unsustainable utilization of both resident and migratory wildlife, as well as increased mortality of non-target species. When this occurs, hunters will be forced to use less profitable sites, such as those further inside the PA, and sites where the chances of encountering a law enforcement patrol are greater. This is likely to result in several interrelated developments:

- an escalation of conflict between law enforcement units and hunters operating within the PA;
- an increased use of more powerful weapons by hunters to assist them in evading arrest;
- as hunting becomes less efficient and less profitable, viable alternative means of generating income or obtaining meat may be more readily

adopted. However, if suitable alternatives are not available, hunters are likely to substantially increase their investments in hunting activities in an attempt to compensate for its increased costs.

Increased law enforcement is clearly needed for the protection of wildlife, but in itself is unlikely to provide a viable long-term solution. The current study suggests that investments in law enforcement would have to be substantial before costs associated with penalties are likely to have such an impact on the overall cost of hunting that alternative sources of income become more attractive. As long as there is continuing demand for game meat, hunters will continue to supply that demand. The published estimates of wildlife offtake (Campbell and Hofer [1995], Hofer et al. [1996]) suggest that alternative sources of the products from hunting, namely meat and cash income, are either not available or that available sources are unable to meet the rising demand.

The evident need for the products of hunting strongly suggests that one of the highest priorities should be to develop cost-effective, viable and attractive alternatives to wildlife meat as well as alternative sources of disposable income, employment and new opportunities for generating income in locations adjacent to the protected areas. We suggest that the value of both conservation education and extension services would be greatly enhanced by such programs.

**Conclusions.** The model presented in this paper makes predictions that can be tested with empirical data. If model predictions and data match, then the model is useful for identifying rules by which hunters might operate. Hence, such models are of practical, strategic use to wildlife managers and development planners as they facilitate optimal allocation of limited resources, in particular when making decisions about the placement of new ranger posts or how best to direct law enforcement patrols. We emphasize that law enforcement is unlikely, by itself, to prevent over-exploitation of wildlife within the SNP. Viable, alternative sources of meat or income to those provided by game meat also need to be developed if utilization of wildlife is to be kept within sustainable limits and conflict between wildlife managers and local communities is to be minimized.

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