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Status and habitat preferences of Uganda cheetahs: an attempt to predict carnivore occurrence based on vegetation structure

PAULE M. GROS[1,*] and MARCEL REJMÁNEK[2]
[1]*Department of Wildlife, Fish, and Conservation Biology, University of California, 1 Shields Avenue, Davis, CA 95616, USA;* [2]*Section of Evolution and Ecology, University of California, 1 Shields Avenue, Davis, CA 95616, USA;* **Author for correspondence (fax: (530) 752-4154; e-mail: ppgros@ucdavis.edu)*

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Abstract. In this paper we examine whether the occurrence of cheetahs (*Acinonyx jubatus*) in Uganda can be predicted from habitat characteristics extracted from a vegetation map. We first established the status of the cheetah in Uganda through field-interviews that Gros conducted in 1990. Cheetahs occurred almost exclusively in the Karamoja region where we estimated 53–310 individuals. Based on 216 sightings, the average number of adults in all-adults sightings was 1.65 + SD 0.95 and the average number of cubs in family groups 2.5 + SD 1.65. Compared to Graham and Parker's 1965 East African survey, average adult group size was slightly smaller in 1990 and large family groups were rarer. Comparison with Gros' 1990 survey showed considerably lower cub-to-adult ratio and percent of observations with cubs in Uganda than in Kenya. A Geographic Information System (GIS) analysis of vegetation structure in areas where cheetahs were observed and in those where none were reported suggested that cheetahs might favor habitats with 25–50% woody cover and grasses of medium height (50–100 cm). A discriminant analysis correctly classified 72.1% of 'used' habitats and 70.4% of 'no-report' habitats. A logistic regression analysis improved the correct allocation of 'used' habitats by 2.2%. Either the discriminant function or the logistic regression, which require only four easily obtainable vegetation characteristics, may help to pinpoint suitable cheetah habitats for conservation purposes. Our approach could be adapted for analyzing habitat suitability for other species of carnivores.

Key words: carnivore, cheetah, conservation, Geographic Information System, habitat modeling, habitat suitability, discriminant analysis, logistic regression, status, survey, Uganda, vegetation structure

Introduction

Historically, cheetahs in Uganda have been restricted to the north-eastern part of the country, mostly to Karamoja Region, a semi-arid thorn-bush ecosystem of 24,000 km^2 adjacent to Kenya and Sudan (Myers 1975, Figure 1). Karamoja was in an almost continuous state of instability between 1971 and 1989 as a result of country-wide civil wars and regional inter-tribal conflicts (Eu 1989). In particular, large scale game slaughter took place following the 1979 war when both soldiers and civilians entered the region's game reserves (Figure 1) armed with automatic rifles. This situation created international concern for the wildlife of Karamoja. In this paper we present

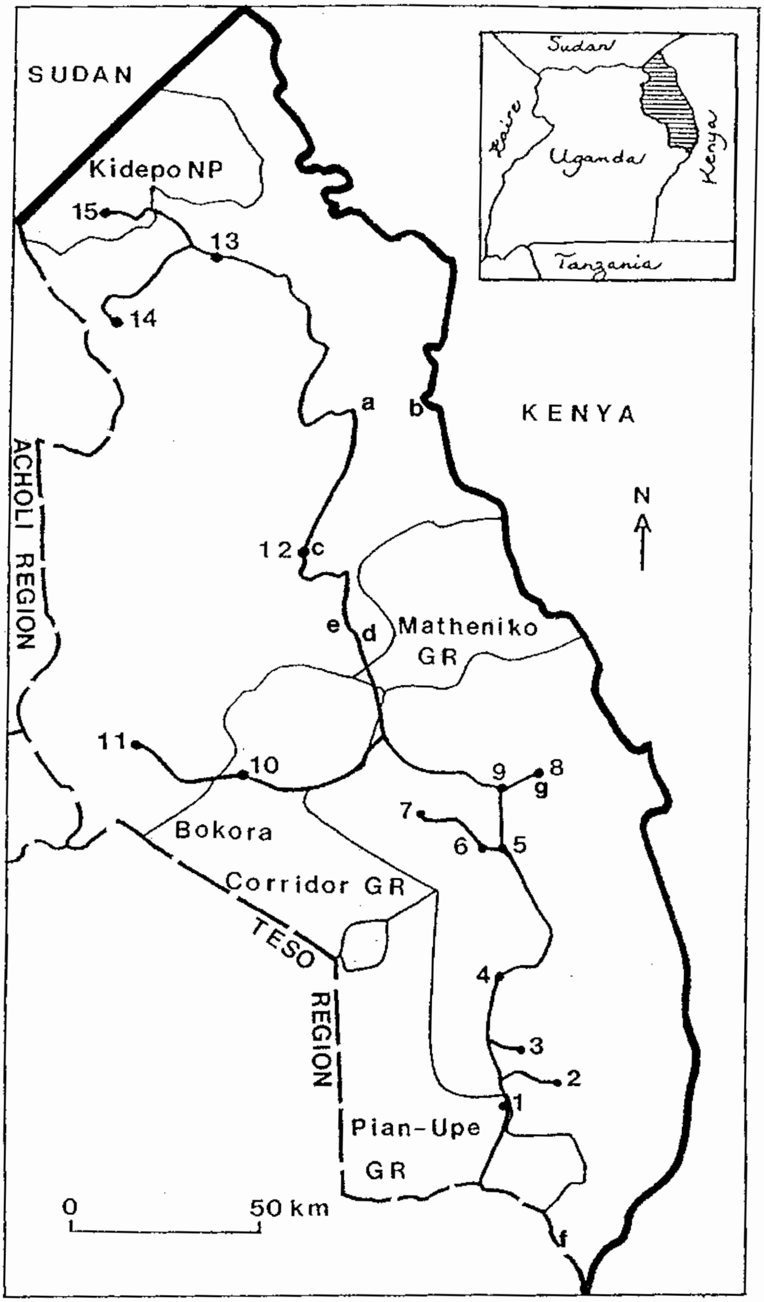


Figure 1. Geographical locations of Karamoja in East Africa, protected areas within Karamoja (N. P. stands for National Park, G. R. for Game Reserve), localities where interviews were conducted during this survey (1 Namalu, 2 Nakapiripirit, 3 Tokara, 4 Nabilatuk, 5 Lorengedwat, 6 Lotome, 7 Matany, 8 Moroto, 9 Nadunget, 10 Nyakwai, 11 Morulem, 12 Kotido, 13 Kapedo, 14 Karenga, 15 Kidepo National Park), and locations cited in the text (a Loyoro, b Torotukei, c Kotido, d Kaloserich, e Toror, f Kiriki, g Moroto).

the first data on the cheetah's status in Uganda since the early 1970's (Myers 1975). After discussing the distribution of the cheetah population, we estimate its size and some simple demographic parameters. In addition, we compare the cheetah's present status in Uganda to its past status in East Africa (Graham 1966) and its current status in Kenya (Gros 1998).

Cheetahs are rare by nature and endangered in an increasing number of countries (Nowell and Jackson 1996; Gros 1996). However, the ecological factors limiting cheetah populations are poorly understood. It has been reported that cheetahs avoid tall grass habitats (Graham and Parker 1965; Kingdon 1977), and that high grass ecosystems could restrict the species' distribution (Myers 1975). In addition, the cheetah's ability to exploit bushlands is being debated, and some conservationists worry about the possible consequences of bush encroachment in African savannas for the persistence of the species (Hamilton 1986). Clearly, a quantitative study of habitat preferences in cheetahs is still lacking. A better understanding of the habitat requirements of cheetahs would help to maintain and restore suitable habitat for the species, and to identify potential cheetah habitat for monitoring and survey purposes. It would also help to pinpoint appropriate areas for the translocations and reintroductions planned for this species (e.g. Bophuthatswana, Jackson 1995a; South Africa, Jackson 1995b; Zimbabwe, Atkinson et al. 1995). Here, we compare height of grass and proportion of woody vegetation cover in areas of Karamoja where cheetahs were observed with those in areas where no cheetahs were reported, using a Geographic Information System (GIS) approach. In addition, we explore whether cheetah occurrence can be predicted based on vegetation structure characteristics alone using both discriminant and logistic regression analyses.

Methods

Assessment of cheetah status

Gros surveyed the status of cheetahs using field interviews in August 1990 (see Figure 1 for interview locations). Interview survey has proven to be an accurate indirect method of assessing cheetah distribution and density (Gros et al. 1996). Ninety-six people provided cheetah sighting reports: 29 park or game reserve rangers, 14 wardens, 20 expatriates, 18 Karimojong pastoralists, and 15 drivers, traders, administrators, and mission workers.

Distribution of sighting reports

Respondents were asked to report all cheetah sightings that they could clearly remember. Location name, surrounding landmarks, and distance to nearest settlements were noted for each sighting. All sighting locations on Karamoja rangelands were plotted on a 1:1,250,000 map of Karamoja (adapted from Lutheran World Federation 1989), and the sightings made in Kidepo National Park were plotted on a 1:125,000 map (Department of Lands and Surveys 1972).

Demographic parameters
Respondents were asked to specify month and year of observation, and number of adults and cubs observed for each sighting. Based on these sightings, we computed average adult group size, average number of cubs accompanying their mother (termed 'litter size'), percent of all sightings that included cubs, and, cub-to-adult ratio (the total number of cubs divided by the total number of adults in all sightings).

Cheetah number estimates
(a) *Kidepo National Park.* Kidepo National Park is composed of the Kidepo and the Narus valleys, each occupying roughly one half of the total area of the park. While the rangers regularly patrolled Narus valley, they patrolled Kidepo valley only three times in 1990. Therefore we limited our population estimate to the Narus valley. To estimate numbers in the Narus valley, we added up the number of cheetahs in all sightings made there between October 1989 and October 1990. Potentially redundant sightings were discarded to avoid over-estimating cheetah density. For example, if a group of three males had been included in the count, additional sightings of three males, three adults, or three cheetahs were generally dismissed. The first exception to this rule was when groups of similar composition were observed the same day in locations separated by more than 5 km, the average distance cheetahs travel within a day (McLaughlin 1970). The second exception was when a group was unmistakably identifiable by either a particular physical characteristic of one of the cheetah, such as a kink in the tail or a torn ear, or by a difference in size among the group members. This method produces conservative estimates of cheetah density (Gros et al. 1996).

(b) *Karamoja rangelands.* We termed 'Karamoja rangelands' the savannas that cheetahs could potentially inhabit in the region outside of Kidepo National Park. This represents an area of 21,558 km^2: Karamoja area (24,000 km^2; Myers 1975) minus Kidepo National Park area (1442 km^2, Olivier 1992) and minus the rain forest areas that cheetahs cannot exploit (Kingdon 1977) (approximately 1000 km^2, from the map of Langdale-Brown et al. (1964)). We estimated a maximum number of cheetahs on Karamoja rangelands by multiplying the rangelands area by 0.0137 cheetah/km^2, the average density in two rangeland regions of Kenya (Gros 1998). A minimum number was obtained by adding up all cheetahs reported in August 1989–August 1990 sightings, after eliminating possibly redundant sightings. We also estimated a minimum number of cheetahs in the three game reserves of Karamoja, a subset of Karamoja rangelands (Figure 1), using the regression between 15–60 kg prey biomass and cheetah biomass ($y = 0.002x + 0.21$, $r^2 = 0.616$, $P = 0.007$, $N = 10$, Gros et al. 1996). Reserve sizes and prey densities were taken from Elthringham and Malpas (1993). This third method could not be used for the whole Karamoja rangelands because prey estimates were unavailable for areas outside game reserves.

Trend in cheetah numbers

Long term residents in a given area were asked if they thought that the number of cheetahs had increased, remained stable, or decreased over the 10-year period preceding the survey. Such perceived trends in cheetah numbers were found to reflect status estimators derived independently in other East African countries (Kenya, Gros 1998; Tanzania, Gros and Mtema under review). Moreover, long term residents' perceptions were consistent with actual population trends in other wild mammals (Magin and Greth 1994; Reynolds et al. 1994).

Analysis of vegetation structure in cheetah habitats

Locations of cheetah sighting reports (Figure 2) and the 1:500,000 vegetation map of Langdale-Brown et al. (1964) (Figure 3) were digitized in Universal Traverse Mercator coordinates and imported into the geographic information system ARC/INFO 7.04. The analysis of vegetation structure was carried out using ARCEDIT and GRID modules and ARC MACRO LANGUAGE programming. Outputs were generated with ARCVIEW 2.1.

We attributed a percentage of woody vegetation cover and a mean grass height to each of the 37 vegetation types recognized in Karamoja. These attributes represent potential values of vegetation cover and of grass height based on the floristic composition of each vegetation type. Actual values may differ from potential ones as a result of land use. Although the word 'potential' is not explicitly used to improve readability, it is implied hereinafter that we used potential values of grass height and woody cover as approximations of their actual values in our analyses. We took percentages of woody vegetation cover from Landgale-Brown et al. (1964). We computed grass heights by averaging mean heights of dominant grass species in each vegetation type using measurements given in the Flora of Tropical East Africa (Clayton 1970; Clayton et al. 1974; Clayton and Renvoizé 1982). Raw attribute figures were grouped into four woody vegetation cover classes (0–25%; 26–50%; 51–75%; 76-100% closed cover), and eight grass-height classes (25 cm classes from 0 to 200 cm). Thus each vegetation type had a woody vegetation cover attribute and a grass height attribute. Using these values, a woody vegetation cover coverage (Figure 4) and grass-height coverage were generated for Karamoja Region.

Circular buffer zones ($N = 179$) of 5 km radius (a total of 78.53 km^2) were drawn around cheetah sighting locations. McLaughlin (1970) found that cheetahs traveled on average 5 km daily in Nairobi National Park. Thus we assumed that each buffer approximated the area potentially available to a given cheetah on the day it was observed. For every buffer, areas occupied by each class of cover and grass height were computed. Figure 5 shows the buffers and the area in each of the four woody

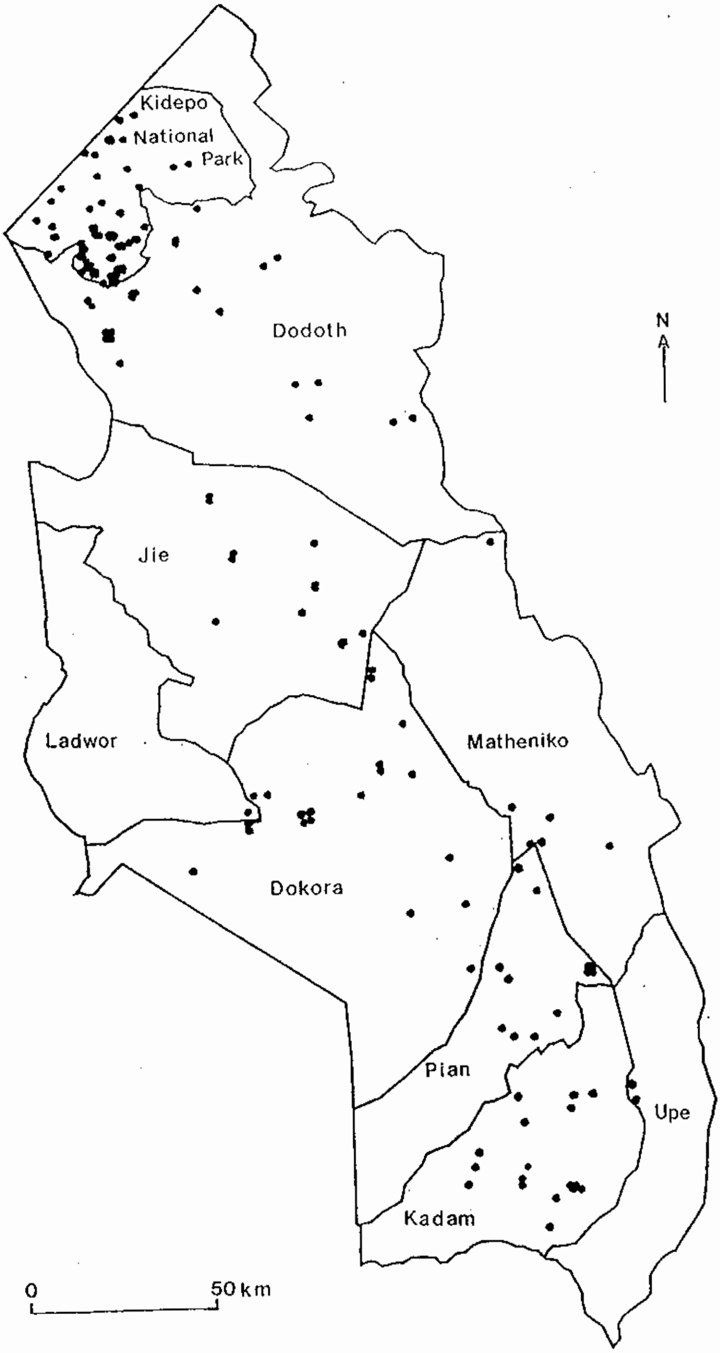


Figure 2. Distribution of locations where cheetahs have been observed by respondents interviewed in this study. Each dot represents one location (please contact the authors for more details).

vegetation cover classes within those buffers. To obtain an independent set of buffers where no cheetahs had been reported, we produced a map of Karamoja excluding the buffers surrounding cheetah sighting locations. After laying a grid over this new map, 179 new buffers were selected using random pairs of (x, y) coordinates as centers for the buffers, and excluding buffers which partially overlapped with cheetah sighting buffers.

We compared grass height and woody cover in buffers surrounding cheetah sightings (referred to as 'used buffers') and in buffers where no cheetah had been reported (referred to as 'no-report' buffers) to test if cheetahs were selecting specific structural characteristics of their habitat. We are using the term selection as in Johnson's (1980) third-order selection i.e. the use cheetahs make of differently structured habitats within their home ranges. We defined 'open habitats' as habitats with less than 50% woody vegetation cover. We compared percentages of open habitats in used and in 'no-report' buffers using a Mann–Whitney U test. To analyze the relationship between cheetah occurrence and grass height, we computed an overall grass-height value for each buffer. For example, a buffer with 40% of its area in the 0–25 cm class and 60% in the 125–150 cm was given an overall value of: $[12.5 \times 0.4] + [137.5 \times 0.6]$. We compared the medians of these overall value distributions for cheetahs and non-cheetah buffers using a Mann–Whitney test.

Data were further analyzed using a discriminant analysis (Huberts 1994; SPSS 1999) to determine if a predictive model of cheetah occurrence based on vegetation structure could be developed. For this analysis group one was defined as 'used habitat' and was composed of all buffers centered on cheetah observations ($N = 179$ sample units). Group two, defined as 'no-report' habitat, included the 179 buffers randomly chosen in parts of Karamoja where no cheetahs were reported. Defining used habitat based on observations of the species of interest tends to produce a conservative description of used habitats (Capen et al. 1986). However, cheetah observations reported in this study were made over a period of more than 10 years, which might reduce the probability of misclassifying 'used habitat' as 'no-report' habitat.

We initially used 12 vegetation structure measurements as potential predictor variables: the percentages of buffer area with (1) 0–25% woody vegetation cover, (2) 26–50% woody vegetation cover, (3) 51–75% woody vegetation cover, (4) 76–100% woody vegetation cover, (5) grass 0–25 cm high, (6) grass 26–50 cm high, (7) grass 51–75 cm high, (8) grass 76–100 cm high, (9) grass 101–125 cm high, (10) grass 126–150 cm high, (11) grass 151–175 cm high, and (12) grass 176–200 cm high. Although this data set did not achieve multivariate normality or equal covariation, we performed the analysis since the ratio of samples to variables was high, a characteristic which generally allows for some violation of the discriminant analysis assumptions (Brennan et al. 1986). Variables that best discriminated between 'used' habitats and 'no-report' habitats were determined using the SPSS 9.0 (SPSS 1999) stepwise selection method. The stability of the classification was checked by 200 cross-validation runs. Ninety (50%) of the locations from each habitat group were chosen randomly each time to construct a new discriminant function with which the remaining 50% of locations were classified. For this purpose, we modified a program for discriminant analysis in Ludwig and Reynolds (1988) and completed it with new sub-routines for random cross-validation (Tabachnick and Fidell 1989, Rejmánek and Richardson 1996). We used a kappa statistics (Titus et al. 1984) to test whether our classification results were significantly better than chance. As logistic regression analysis sometimes outperforms discriminant analysis, we also ran a stepwise multiple logistic regression (SPSS 1999) and compared the results of the two analyses.

Results

Cheetah status

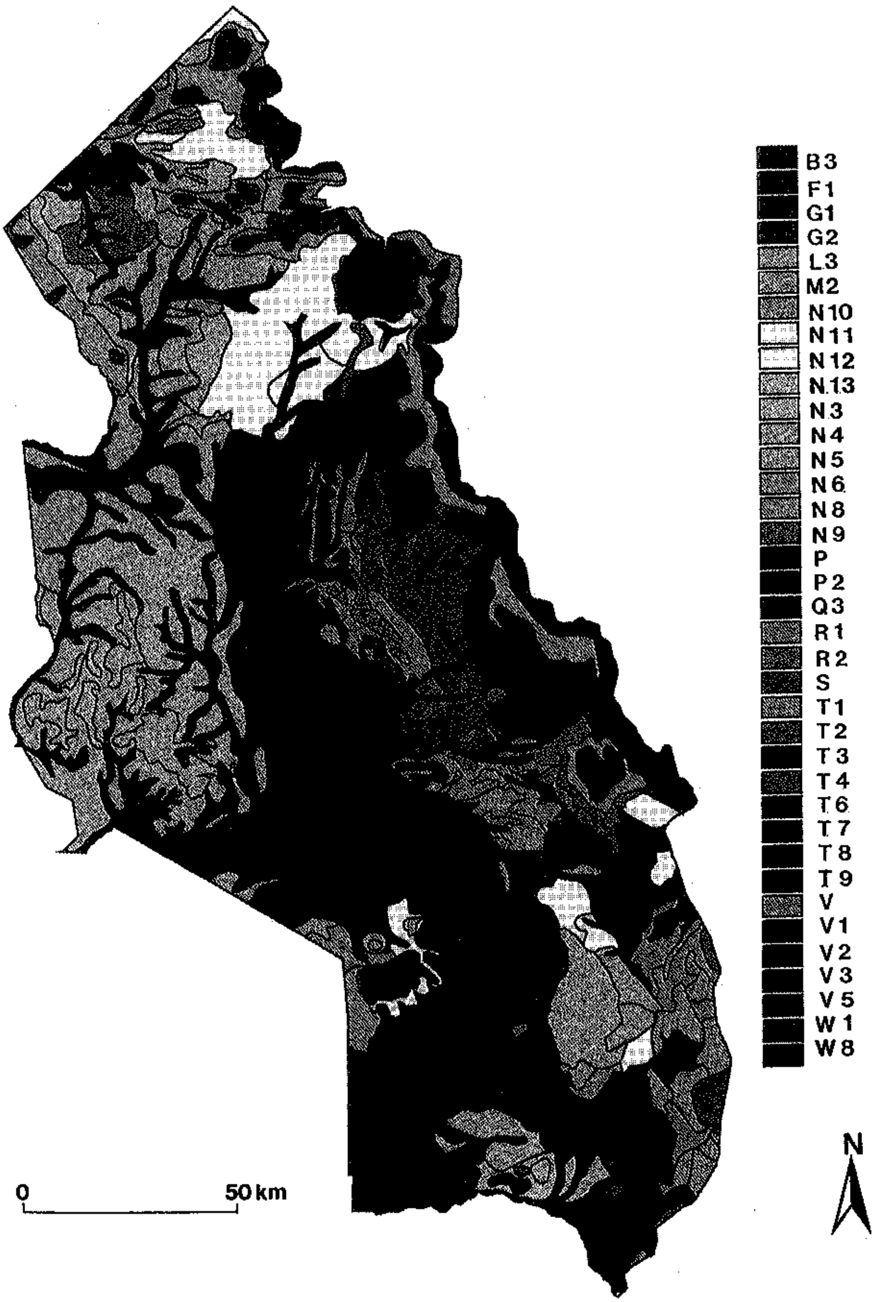
Cheetah distribution and demographic parameters

Two hundred and ten of the 216 sightings gathered were made in Karamoja. We were able to locate 179 of these precisely on a map (Figure 2). Sixty-seven percent of these 216 sightings occurred between 1985 and 1990 (40% in 1989 and 1990), 15% occurred in 1980–1984, 13% occurred in 1970–1979, and 5% occurred in 1960–1969. Respondents specified the number of cubs and adults in 141 sightings. In those detailed sightings, the average adult group size was 1.65 (SD = 0.97), and the average litter size 2.50 (SD = 1.65) (Table 1). Eighteen percent of sightings included cubs and the cub-to-adult ratio in all sightings was 0.25.

Population estimates

We estimated that 13 cheetahs lived in the Narus valley of Kidepo National Park (0.019 cheetah/km^2). One of the 32 respondents declared that cheetahs had declined

Figure 3. Digitized map of the plant communities of Karamoja adapted from Langdale-Brown et al. (1964). B3 = *Juniperus-Podocarpus* Dry Montane Forest; F1 = High altitude Forest/Savanna Mosaic; G1 = Undifferentiated Semi-deciduous Moist Thicket; G2 = Riparian Moist Thicket; L3 = *Butyrospermum* Savanna; M2 = Palm Savanna, N3 = *Combretum-Cymbopogon* Dry Savanna; N4 = *Combretum-Oxytenanthera-Hyparrhenia* Dr Savanna; N5 = *Combretum-Acacia-Hyparrhenia* Dry Savanna; N6 = *Combretum-Acacia-Lasiurus* Dry Savanna; N8 = *Combretum-Acacia-Themeda* Dry Savanna; N9 = *Combretum-Acacia-Commiphora* Dry Savanna; N10 = *Boswellia-Fagara-Heeria* Dry Savanna; N11 = *Acacia-Combretum* Dry Savanna; N12 = *Acacia-Heeria-Terminalia* Dry Savanna; N13 = *Lannea-Combretum-Lonchocarpus* Dry Savanna; P = Dry *Acacia* Savanna; P2 = *Acacia-Hyparrhenia-Themeda* Dry Savanna; Q3 = Dry *Hyparrhenia* Grass Savanna; R1 = *Acacia* Tree and Shrub Steppe; R2 = *Lannea-Acacia* Tree and Shrub Steppe; S = *Chrysopogon* Dry Steppe; T1 = *Acacia mellifera* Bushland; T2 = *Acacia-Commiphora-Lannea* Bushland; T3 = *Acacia-Commiphora Bushland*; T4 = *Acacia reficiens-Commiphora* Bushland; T6 = *Lannea-Acacia-Balanites* Bushland; T7 = *Acacia-Albizia-Dichrostachys* Bushland; T8 = *Acacia mellifera* Bushland; T9 = *Acacia seyal-A. nilotica-Pennisetum mezianum*; V = Dry Thicket; V1 = Undifferentiated Deciduous Dry Thicket; V2 = *Acacia-Euphorbia* Dry Thicket; V3 = *Acacia-Commiphora* Dry Thicket; V5 = *Acacia mellifera* Dry Thicket; W1 = *Echinochloa* Grassland; W8 = *Acacia-Setaria* Savanna.


B3
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P2
Q3
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R2
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Figure 4. Computerized map of woody vegetation cover in Karamoja.

Figure 5. Distribution of habitats with various percentages of woody vegetation cover (0–25; 26–50; 51–75, and 76–100%) within 5 km radius buffers drawn around the locations where cheetahs have been reported.

Table 1. Composition of the 141 detailed cheetah sighting reports in the 1990 Uganda survey.

All-adult sightings						
Number of adults	1	2	3	4	8	
Number of sightings ($N = 115$)	62	40	8	4	1	
Sightings including cubs						
Number of cubs per litter	1	2	3	4	5	6
Number of sightings ($N = 26$)	8	10	2	2	1	3

in the park since 1980, the others felt they encountered cheetahs too rarely to form an opinion. For the entire Karamoja rangelands we estimated a minimum of 40 cheetahs based on sighting reports. Extrapolating from densities on Kenya rangelands, the maximum figure was 295 cheetahs for the same area. Finally, we predicted at least 44 cheetahs in Karamoja Game Reserves (Bokora Corridor, Matheniko, and Pian-Upe, Figure 1) using the prey–cheetah biomass model. All of 21 respondents thought that cheetah numbers had declined on Karamoja rangelands between 1980 and 1990.

Comparison with other surveys

Average adult group size was higher in the 1965 East African survey than in the 1990 Uganda survey (Table 2). This result is probably due to a higher proportion of groups of three or more adults in 1965 (190 of 972 groups vs. 13 of 115 groups; $\chi^2 = 4.601$; $df = 1$; $P = 0.032$). Although average litter sizes were similar in the two surveys, there were fewer large litters in 1990 (eight out of 26 with more than three cubs) than in 1965 (136 out of 252 with more than three cubs) ($\chi^2 = 5.08$, $df = 1$; $P = 0.024$). Cub-to-adult ratio and percent of observations with cubs did not differ significantly between the two surveys (Table 2).

Average adult group sizes and average litter sizes were not significantly different in the 1990 Kenya and Uganda surveys (Table 2). However, percentage of sightings including cubs and cub-to-adult ratio were nearly twice as high for Kenya than for Uganda (Table 2).

Table 2. Cheetah demographic parameters in Uganda 1990, East Africa 1965, and Kenya 1990 surveys.

Survey	Adult group size	Litter size	Cub-to-adult ratio	Percent of observation with cubs
Uganda 1990	1.65 ($N = 115$)	2.50 ($N = 26$)	0.29 ($N = 285$)	18.44 ($N = 141$)
East Africa 1965	1.85 ($N = 972$)	2.72 ($N = 252$)	0.33 ($N = 2,784$)	20.65 ($N = 1,225$)
Kenya 1990	1.77 ($N = 249$)	2.56 ($N = 120$)	0.51 ($N = 910$)	32.52 ($N = 369$)
Uganda 1990 compared to East Africa 1965	†$Z = 1.970$; $P = 0.049$	*$U = 2,585$; $P = 0.065$	•$\chi^2 = 0.972$; $P = 0.324$	•$\chi^2 = 0.381$; $P = 0.537$
Uganda 1990 compared to Kenya 1990	†$Z = 1.018$; $P = 0.310$	*$U = 1,369$; $P = 0.342$	•$\chi^2 = 13.295$; $P < 0.001$	•$\chi^2 = 9.899$; $P = 0.002$

†Z test, *Mann–Whitney U, •χ^2 test.

Vegetation structure in cheetah habitat

Results of the spatial analysis

The distribution of percentages of area in different woody vegetation cover across all buffers is contrasted for 'used' and 'no-report' habitats in Figure 6. On average, used buffers ($N = 179$) included a larger proportion of open habitats (median of the distribution = 100%) than 'no-report' buffers ($N = 179$, median = 85%) (Mann–Whitney U test; $U = 10983$; $P < 0.0001$).

Figure 7 shows the distributions of percentages of buffer area occupied by habitats with different grass-heights in all used and all 'no-report' buffers. Overall grass height values were significantly lower in used buffers than in 'no-report' buffers ($N = 179, 179$; Medians = 87.7 vs. 103.1 cm; $U = 8576$, $P < 0.01$).

Results of the discriminant analysis

Four vegetation variables contributed significantly ($P < 0.001$) to the Fisher's linear discriminant function: the percentage of buffer area with 26–50% woody vegetation cover (W1) which accounted for 36.5% of the total multivariate distance, the percentage of buffer area with 51–100% woody vegetation cover (W2; negative contribution; 8.3%), the percentage of buffer area with 51–100 cm tall grass (G1; 49.1%), and the percentage with 100–150 cm tall grass (G2; negative contribution; 6.1%). Although the relationship between species' occurrence and environmental factors is often non-linear (Meenst et al. 1983; Brennan et al. 1986), power and

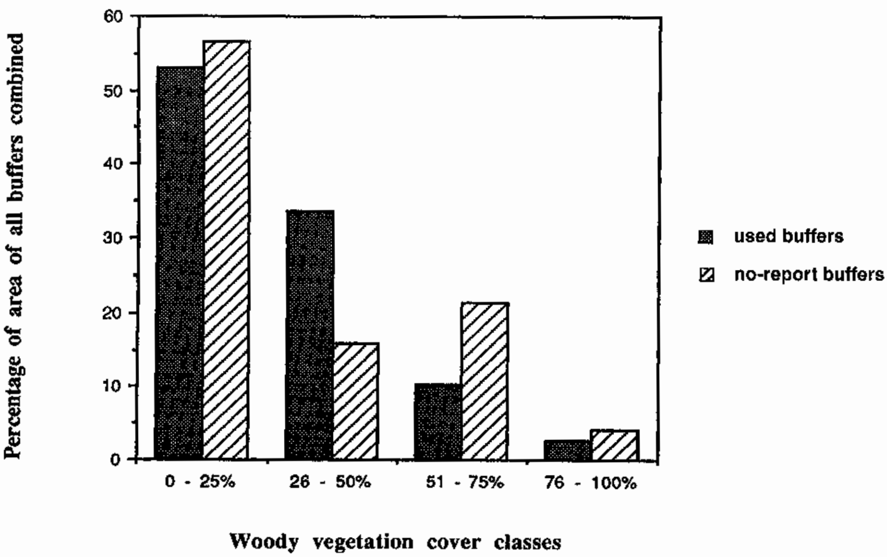

Figure 6. Percentages of the combined area of all 'used' buffers representing the four classes of woody vegetation cover (gray pattern), and corresponding percentages for 'no-report' buffers (hatched pattern).

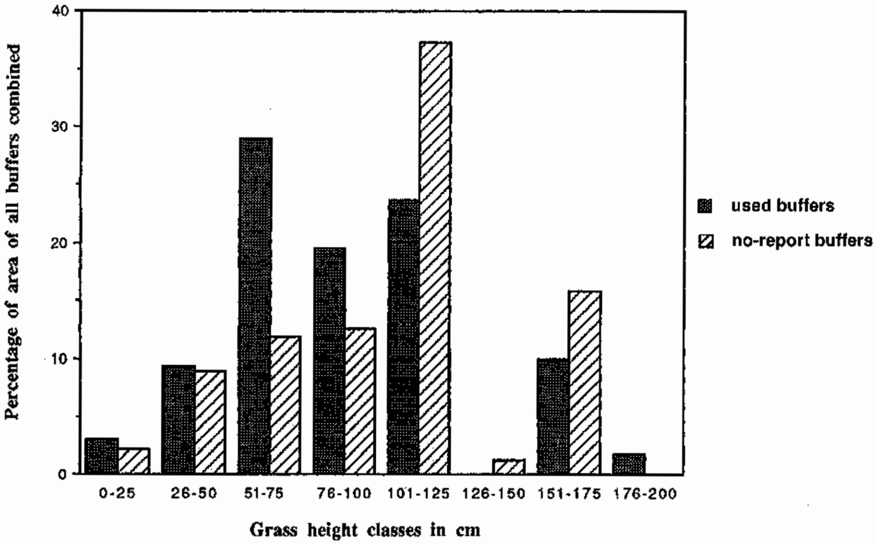

Figure 7. Percentages of the combined area of all 'used' buffers representing the various classes of grass height (gray pattern), and, corresponding percentages for 'no-report' buffers (hatched pattern).

square root transformations of the variables did not improve the results. The resulting discriminant function was:

$$Z = -1.023 + 2.18\,\mathrm{W1} - 0.65\,\mathrm{W2} + 2.12\,\mathrm{G1} - 0.52\,\mathrm{G2};\ F = 23.39,\ \ P < 0.001$$
$$\text{Mahalanobis distance} = 1.05, \text{dividing point}(0.0)$$

This function classified correctly 71.2% of the original buffers, with a slightly better allocation success for used habitats (Table 3). Moreover, only used habitats could reach Z values above 1.5 (Figure 8). The classification was 42.5% better than chance (kappa = 0.425; approximate standard error = 0.052; normal curve deviate = 8.034; $P < 0.0001$). This value of kappa indicates a 'moderate' strength of agreement between the classification based on the discriminant function and the actual buffers' membership (Everitt 1992).

The percentage of correctly classified habitat buffers in the random cross-validation procedure (Table 3) showed that the classification was rather stable. The mean percentage of correctly classified cases was only slightly worse than the original classification when the whole data set was used (Table 3; mean kappa = 0.406). Moreover, even the worse of the 200 random cross-validations (36.5% of cases incorrectly classified) was still 27% better than chance (kappa = 0.269, normal curve deviate = 3.59, $P < 0.0006$).

Table 3. Classification matrix showing actual habitat buffer membership, and, predicted habitat buffer membership by the discriminant function and by the logistic regression distinguishing habitats used by cheetahs from those with no cheetah reports.

	Actual group membership	Predicted group membership	
		Used	No-report
Discriminant function	Used	72.1	27.9
	No-report	29.6	70.4
Means of 200 random cross-validations using 50% of the data	Used	71.6	28.4
	No-report	31.1	68.9
Logistic regression	Used	74.3	25.7
	No-report	30.7	69.3

Figures are percentages of habitat buffers classified in each category.

The logistic regression analysis provided results very similar to those of the discriminant analysis. It used the same variables as the discriminant function. The probability [0,1] that an area was used by cheetahs was expressed as:

$$\text{Prob(used)} = 1/(1 + e^{0.972}e^{-2.11(W1)}e^{0.593(W2)}e^{-2.00(G1)}e^{0.486(G2)})$$

The logistic regression classified correctly 71.8% of the original buffers (cut value = 0.5; Table 3), a very slight improvement over the discriminant function. However, correct allocation of used buffers was 2.2% better with the logistic regression function.

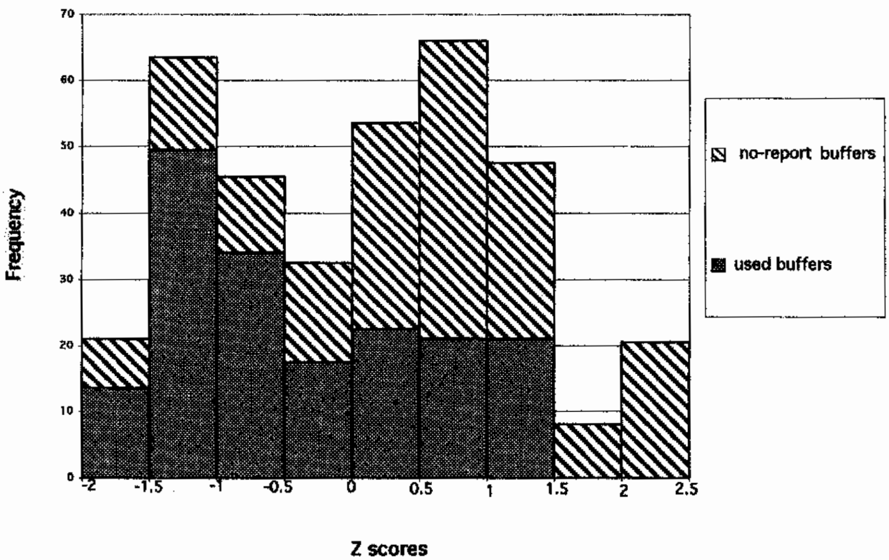

Figure 8. Frequency of 'used' buffers (gray pattern) and 'no-report' buffers (hatched pattern) along the discriminant function Z.

Discussion

Status of the cheetah in Uganda

The current distribution of the cheetah in Uganda is apparently limited to Karamoja, where it remains widespread. Earlier reports indicated the presence of cheetahs in the east of the Acholi and Teso Regions (Graham and Parker 1965; Myers 1975). We, however, did not collect any sighting dated after 1973 for Acholi, nor did we obtain any sighting for Teso. Thus cheetahs may have become extremely rare or extinct outside of Karamoja. Within Karamoja, we found that, in 1990, cheetahs were still present throughout the range described in Kingdon (1977) as well as in four of the five areas described by Graham and Parker. We obtained sighting reports in Kidepo National Park (see Figure 1 for locations), around Loyoro and Torotukei (area 2), south east of Kotido around Kaloserich and Toror (area 3), and one respondent mentioned regularly seeing cheetahs north of Kiriki (area 4). We did not get any sighting report north of Moroto (area 5), an area where cheetahs were present until at least 1973 (Wilson 1973). Interestingly, we collected 64 sightings made after 1980 outside of Graham and Parker's five areas, and 19 sightings in the southwest of Karamoja classified by Kingdon as cheetah's former range. This probably stems from methodological differences between surveys rather than from cheetah re-colonization of previously lost habitats. For example, Graham and Parker used written questionnaires which typically produce less complete distribution data than interviews (Gros 1998).

We estimated a density of 0.019 cheetah/km^2 in the Narus Valley of Kidepo National Park which falls within the range of informed guesses for this protected area (1985: 0.018 cheetah/km^2, W. Labongo, personal communication; 1990: 0.036 cheetah/km^2, D. Okech, personal communication. This density is low by Kenya standards (0.016–0.098 cheetahs/km^2, $N = 8$ protected areas, Gros 1998), but close to the average cheetah density reported for protected areas in Africa outside Kenya (0.021 cheetah/km^2, $N = 13$, Gros et al. 1996). Edroma (1984) reported that in the 1970's cheetahs were poached for skins and their prey killed for meat and trophies in Kidepo National Park. Comparing aerial surveys conducted during 1970–1990 in Kidepo (Ross et al. 1976; Edroma 1980; Olivier 1992) suggests that poaching activity seriously depleted herbivore populations and interrupted seasonal migrations between Narus and Kidepo valleys. Among other species Bright's gazelles (*Gazella granti brighti*), a prey favored by cheetahs (FitzGibbon 1988), might have been driven to extinction (Olivier 1992). Although cheetahs could survive on smaller prey such as hare and ground birds (Labuschagne 1979), they were certainly affected by the reduction of herbivore biomass in the park and by the spatial curtailment of wildlife to the Narus Valley. Moreover, cheetah observations shifted from 'unremarkable' occurrences (Bere 1975) to 'rare' ones (this study and Olivier 1992). In sum, the size of the 1990 cheetah population of Kidepo was probably below the maximum possible number in the park. Leakey' s (T. Butynski, personal communication) 1998 aerial survey results should cast some light on the most recent changes in wildlife and cheetah numbers in Kidepo National Park.

We estimated 40–295 cheetahs on Karamoja's rangelands. The figure of 40 was obtained by counting all individuals reported in sightings that were clearly non-redundant, and is certainly an underestimate. Conversely, the figure of 295 derived by generalizing densities on Kenya rangelands to Karamoja is probably too high, because the two Kenya regions which served as references for cheetah density had higher rainfall and less poaching than Karamoja. We think that Karamoja Game Reserves alone could hold at least 44 cheetahs under adequate conservation management. This number is most likely a minimum because we generated it from a cheetah–prey biomass model which tends to underestimate real cheetah numbers by 37% on average (Gros et al. 1996), and we used prey counts (Eltringham and Malpas 1993) dating from the height of the prey slaughter period. The effects of human activity were probably more extreme on the rangelands of Karamoja than in Kidepo Valley National Park. Despite the fact that Karamoja remained lightly populated and almost exclusively devoted to extensive cattle raising to the present (Oloka-Onyango et al. 1993, LWF 1985), the prevalence of modern weapons posed a serious threat to the local wildlife (Dietz 1987). Thus it is likely that cheetah numbers decreased as prey density dropped during the lawless 1970's and early 1980's (Eltringham and Malpas 1993; W. Labongo, personal communication). Moreover, armed pastoralits probably shot cheetahs either to defend livestock, for their skins, because they mistook them for dangerous animals, or spitefully. Respondents' perceptions that cheetah numbers had dropped between 1980 and 1990 corroborate the thesis of a decline. In conclusion, cheetah numbers probably decreased on Karamoja rangelands over the last 40 years but the extent of their decrease cannot be evaluated. However habitat loss, which is often the foremost cause of large cat populations decline, is not to be blamed here. The cheetah population of Karamoja rangelands could be expected to recover if safety conditions improved in the region.

Comparisons with past surveys of the cheetah's status in Uganda do not provide evidence for a change in cheetah status through time. Cub-to-adult ratio and proportion of sightings including cubs were comparable in 1965 (Graham and Parker 1966) and in 1990 (this study). Large adult and family groups were significantly less common in 1990, however. This could reflect a decrease in cheetah group size, at all ages, in Uganda between 1965 and 1990. We bracketed an overall population of 53 to 308 cheetahs in Karamoja while Myers (1975) guestimated 100–250 cheetahs for all of Uganda. These figures are inconclusive for assessing a change in number over time, however they provide an estimate of magnitude for the Karamoja population. Based on these numbers the Karamoja cheetah population, considered alone, might not be viable (Lande and Barrowclough 1987). However, other populations occur in adjacent Turkana District, Kenya, and in southern Sudan (Merz 1986), and the Karamoja population probably contributes to increase the survival odds of a regional cheetah population complex.

Cheetahs seem to fare better in Kenya than in Uganda based on the results of Gros' 1990 interview surveys in the two countries (Table 2). Average litter and adult group sizes were comparable suggesting a similar social organization of cheetah populations in Uganda and Kenya. Yet cub-to-adult ratio and percent of observations with cubs were 1.75 times higher in Kenya. Such an outcome could stem from a sex ratio more biased towards females or a higher cub rearing success in Kenya. Nevertheless, a higher proportion of cubs in the Kenya population could also reflect higher cheetah densities. Several pieces of evidence support this latter interpretation. First, a strong and highly significant correlation exists between percentage of observations with cubs and population density in Tanzania (Gros and Mtema, under review). Second, cub-to-adult ratio and population density appear positively associated in cheetahs. Bowland (1993), found that cub-to-adult ratio increased with cheetah density in the cheetah sub-populations he studied in the Kruger National Park, South Africa. Likewise, cub-to-adult ratio tended to correlate with estimated cheetah density in protected areas in Kenya (Gros 1998). Third, the population density estimated for Kidepo Valley National Park was low for a protected area by Kenya standards. Finally, while all Karamoja respondents thought that cheetah numbers were declining on range lands, 62% of interviewees ($N = 122$) felt that cheetah numbers were stable or increasing in Kenya (Gros 1998). These data all seem to indicate that cheetah populations may be more threatened in Uganda than in Kenya.

Vegetation structure in cheetah habitats

Our results should be interpreted with caution. We paid particular attention to reduce the potential biases resulting from the use of indirect methods rather than actual measurements of cheetah occurrence and vegetation structure. Nonetheless, those biases cannot be completely eliminated. Although we interviewed a large number of well informed people, some cheetahs might have occurred in parts of Karamoja where none were reported. Despite the fact that we analyzed habitat structure in buffers surrounding sighting locations, rather than at the exact area where cheetahs were seen, our analysis might still overestimate the importance of open and short grass habitat. More cheetah sightings could have been made in those habitats because cheetahs were more conspicuous there (Brennan et al. 1986). Therefore, we consider the results discussed below as preliminary indications that will need to be fully confirmed by independent field data.

In Karamoja, cheetahs appeared to use habitats with differing vegetation structures in a manner that was disproportionate to their availability. This can be interpreted as selection for habitat structure (Poole et al. 1996). Cheetahs apparently favored open habitats (0–50% open) and grass of medium height (50–100 cm). The significantly larger proportion of habitats with less than 50% woody cover in cheetah buffers seemed driven by a cheetah's preference for semi-open habitats (26–50%) (Figure 6). Burney (1980) described a similar pattern of habitat preferences in Masai

Mara National Reserve, Kenya, where cheetahs spent more time in bush grasslands than in any other habitat, and in grasslands with medium-sized grass than in either short or tall grasslands.

Previous qualitative studies showed that cheetahs use bushlands and thickets (Burney 1980; Whateley and Brooks 1985), and that populations exist, sometimes at high density, in landscapes dominated by closed vegetation (Myers 1975). Therefore, it was proposed that bushlands were good cheetah habitats (Hamilton 1986) rather than sub-optimal ones as generally stated (Myers 1975). Our results, however, suggest that cheetahs use open habitats more than closed habitats when both are available.

Cheetahs could be attracted to semi-open habitats because these habitats support higher prey density. Intermediate in their vegetation structure, semi-open habitats accomodate species of both close and open habitats; for example Kirk's dikdiks (*Madoqua kirkii*), which are thicket specialists, and oribis (*Ourebia ourebi)* which favor open and thinly bushed country (Kingdon 1982a, b). Alternatively, semi-open habitats could be preferred to very open ones because they offer better concealment opportunities. Cheetahs use cover for stalking their prey (Shaller 1968) and abandon their hunt when detected by the prey (FitzGibbon 1989). Semi-open habitats may also afford some protection against weather and competing predators.

Although our results suggest that cheetahs may favor semi-open habitats and medium-sized grass, it is important to bear in mind that they could only choose among the habitat structures available to them in Karamoja. The availability of habitats different from those existing in Karamoja, or, of the same habitats present in different proportions, may influence the preference rating of semi-open habitat and medium sized grass (Chesson 1978; Johnson 1980). Therefore, we need to test our method in other African savanna habitats to assess the generality of our conclusions.

The discriminant analysis confirmed that the vegetation structure in habitats used by cheetahs was different from the vegetation structure in habitats where no cheetah was reported. Used and 'no-report' habitats could be best segregated by the proportion of area covered in 50–100 cm grass and the proportion of habitat with 25–50% woody vegetation cover. The discriminant power of the latter variable suggests that cheetahs use semi-open habitats as inferred earlier from the data distribution in Figure 5. Grass-height variables contributed to 55.2% of the multivariate distance between groups. Thus, grass layer height seems to slightly supersede bush cover density for determining cheetahs' occurrence in Karamoja. Grass of the appropriate height for a cheetah might be more limiting than appropriate bush cover in the region. Alternatively, cheetahs might be restricted to a narrow range of grass heights but more versatile with regard to bush cover. Cheetah hunting behavior provides an explanation for the importance of 51–100 cm high grass in 'used habitats'. After locating potential prey by sight, cheetahs typically stalk until they are within 20–50 m of their target before rushing at it (Schaller 1968). With eyes set 60–70 cm above the ground while moving (after Williams 1967; Dorst and Dandelot 1970), cheetahs might experience diminishing return when hunting in grass exceeding this height. On the other hand, FitzGibbon (1990) showed that cheetah hunts were three times less successful in vegetation lower than 30 cm than above that threshold, probably due to lack of appropriate cover for stalking.

In the future, several lines of research could be explored to test and refine the approach presented in this paper. We could first elaborate on the correspondence between remotely obtained data on vegetation structure and actual measurements of vegetation structure in the field. We could test the performance of vegetation maps and that of other remote sensing resources. A second improvement would be to gain a better appreciation of habitat use by cheetahs. This could be done by measuring the time actually spent by individuals in the different habitat types available to them. We could proceed either through direct observation of focal animals (Burney 1980) or by analyzing the distribution of radio-collared individuals (Chapin et al. 1998). Either method would also indicate if cheetahs avoided some of the habitats available to them. Finally, we could assess the generality of our predictions by testing them outside of Karamoja (Capen et al. 1986). If adequate vegetation data were obtained, we could run our analyses for Kenya and for Tanzania savannas for which cheetah distribution data are available (Gros 1998; Gros and Mtema, under review). It would be particularly interesting to test our predictions in the savannas of Botswana (Gros, unpublished data), Southern Africa, which greatly differ from those of East Africa in their floristic and faunistic compositions.

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