Factors affecting the availability of Yellow-toothed Mole-rats *Tachyorectes splendens* as prey for Augur Buzzards *Buteo augur* in the southern Lake Naivasha area, Kenya

Munir Z. Virani
The Peregrine Fund, 5668 West Flying Hawk Lane, Boise Idaho 83709 USA
Also Dept. of Biology, Leicester University LE1 7RH (UK) and Dept. of Ornithology, National Museums of Kenya, P.O Box 40658 Nairobi Kenya
munir.virani@bigfoot.com

Summary

A study of rainfall, temperature range, soil softness and grass height as factors affecting availability of mole-rats as prey for Augur Buzzards was made in three different land-use areas in southern Lake Naivasha, Kenya. Mole-rat indices were highest in Mundui and lowest in Hell's Gate where they only appeared to peak during cooler months. Grass height was the most important predictor of mole-rat availability in all three sites, although the other variables rainfall, temperature range and soil conditions maybe proximate in nature and their effects on mole-rats difficult to detect.

Key words: mole-rat, Augur Buzzard, prey availability, Buteo, south Lake Naivasha

Introduction

The importance of food abundance and availability for raptor population dynamics is well documented (e.g. Cave, 1968; Hagen, 1969; Southern, 1970; Newton, 1979). Disregarding the nest site and the nearest surrounding area, the habitats that a raptor lives in serve the main purpose of providing adequate food resources. Thus a major aspect of the quality of these habitats is prey availability. This in turn is a function not only of absolute prey density, but also of various habitat features influencing the accessibility of prey, and the time and energy needed for capture (Widen, 1994). A major change in plant cover density, such as habitat degradation, overgrazing, or sudden changes in land use patterns are likely to affect the availability of prey for raptors.

The Yellow-toothed Mole-rat *Tachyorectes splendens* (hereafter referred to as mole-rat) is abundantly distributed throughout the Rift Valley, central and western highlands of Kenya (Kingdon, 1974). The species is the principal prey of the Augur Buzzard *Buteo augur* as well as other medium sized raptors occurring within the mole-rat's distribution (Smeenk, 1974; Brown and Britton, 1980; Smart and Taylor, 1990; Virani, 1999). Cycles of rodent abundance in East Africa have mainly been studied in relation to crop pest situations (e.g. Delany and Roberts, 1978; Taylor and Green, 1976). According to Brown and Britton (1980), these studies have shown that rodents normally increase during the rainy seasons, sometimes reaching a peak of abundance well beyond the capacity of any socially-regulated raptor population to limit it. Most of the rodent-eating raptors breed during or after the rains, especially in the Lake Naivasha region, in Kenya's Rift Valley Province (Figure 1) where they have been recorded to breed during the long rains (March to May) and mid-year dry season (June to August) (Brown and Britton, 1980). These times of breeding are considered to coincide with peaks of rodent abundance as well as vegetative cover (Brown and Britton, 1980).

This paper examines factors affecting mole-rat availability as Augur Buzzard prey in three different land-use areas in the southern Lake Naivasha area, Kenya. Specific objectives were to a) understand seasonal trends of the factors that affect mole-rat availability. Four factors were looked at – rainfall, temperature range, soil softness and grass height; and b) to develop multiple regression models that best predicted mole-rat availability. Knowledge about prey dynamics in relation to predators can help in the formulation of effective conservation and management policies, especially in areas where land-use patterns are rapidly changing.

Materials and Methods

The study was conducted in the southern Lake Naivasha area (0° 45'S and 36° 20'E), in the eastern

Rift Valley of Kenya at an altitude of 1890 m (Figure 1). The three different land-use areas used as study sites were Hell's Gate National Park (hereafter referred to as Hell's Gate), Mundui and Sulmac-Oserian (Figure 2). The average rainfall in the area is less than 500 mm per year (Ambrose, 1984). However, rainfall is localised within different areas in the south Lake Naivasha area, with Hell's Gate being relatively drier than both Mundui and Sulmac-Oserian.

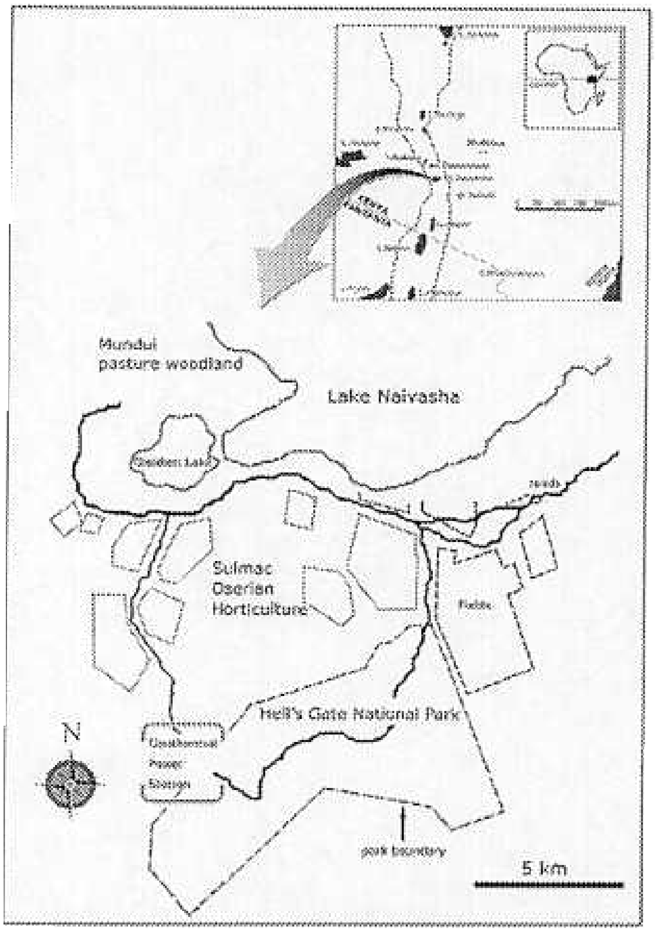


Figure 1. The core study area, land-use types and study sites in the southern Lake Naivasha area.

Hell's Gate

Hell's Gate is located about 2 km south of Lake Naivasha and covers an area of about 6825 ha. The main feature of Hell's Gate is the Ol-Njorowa gorge consisting of steep vertical cliffs. This is where the main study site was located covering an area of about 2920 ha. The vegetation is mainly scrubland dominated by an association of Leleshwe *Tarchonanthus camphoratus* and Whistling Thorn *Acacia drepanolobium* both of which rarely exceed 4 m in height, and open grasslands dominated by *Digitaria milanjiana*. The upland grasslands that occur on the cliff scree slopes and on cliff tops are dominated by tussock forming grasses. Characteristic trees include *Cussonia spicata*, *Schefflera abyssinica* and *Euphorbia magnicapsular*. Hell's Gate is a protected area with low human impact and moderate to extreme levels of wildlife grazing.

Mundui

Mundui is located in the area west of Lake Naivasha and covers an area of approximately 1460 ha (Figure 2). It comprises pockets of little to moderately grazed areas combined with minimal to moderate human settlement. The vegetation consists of *Acacia* woodland pastures made up of tall open-canopy Yellow Fever trees *Acacia xanthophloea* with open grasslands dominated mainly by *Digitaria scalarum*, *Themeda triandra* and *Indigofera tanganyikensis*. The *Acacia* woodlands are usually within close proximity of the lake shore where the canopy is often closed. As the woodlands stretch further inland, the canopy becomes more open. In this area, most of the land is privately owned with little land set aside for the development of residential property. Agricultural activities are limited to subsistence use, while domestic livestock grazing is minimal to moderate. Reasonable concentrations of mammalian herbivores exist, however overgrazing of the land is not considered a major problem.

Sulmac-Oserian

This study site is a combination of two different areas having similar land-use patterns. As a result, they were considered as one unit. Both are located along the Moi South Lake road running close to the lake's southern shoreline (Figure 2). Sulmac is closer to the lake shore while Oserian is further inland and once shared similar vegetation characteristics as Hell's Gate (Figure 2). The vegetation falls in Ecological Zone IV of Pratt *et al.*, (1966), a zone in which upland *Acacia* is common. The grasslands mainly comprise of tropical *Setaria* spp. which grades into the *Tarchonanthus camphoratus* bushland, typical of the Rift Valley floor (Litterick *et al.*, 1979).

The areas of greatest horticultural activity were in the Sulmac area (5230 ha) just north and northeast of Hell's Gate (Figure 2). Horticultural activities are concentrated either side of the road. Human settlement is moderate to extreme. The Sulmac area also has two large villages (Sulmac and DCK) which accommodate the nearly 10,000 employees of the major flower farms in the area (Ooko pers. comm.). Grazing pressure by domestic livestock is high. The major tree species include *Acacia xanthophloea*, where in some residential areas, particularly closer to lake's edge, a number of small open and closed canopy woodlands occur. Other trees include *Euphorbia candelabra* and *Eucalyptus* sp.

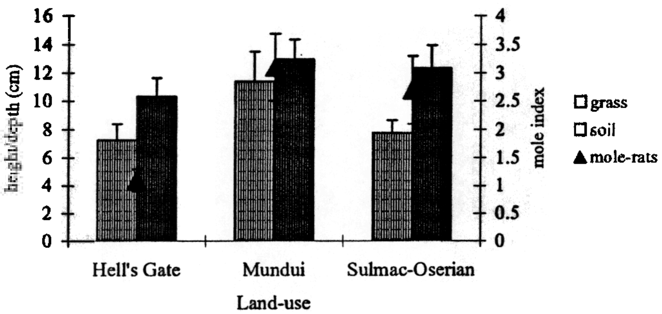


Figure 2. Mean soil softness, grass height and mole-rat index for the three different land-use areas in the southern Lake Naivasha area (January-September 1997).

Between Hell's Gate and Mundui is the Oserian area (Figure 2). This is another area of intensive horticultural activity that also extends further inland from the lake where the vegetation was once similar to Hell's Gate. The Oserian study site (2264 ha) consists of large-scale flower fields surrounded by undulating hills buffered by open *Acacia drepanolobium* – *Tarchonanthus camphoratus* scrubland. The steep gorges and slopes of these hills comprise pockets of *Euphorbia magnicapsular* trees. Other trees include *Cussonia spicata* and *Schefflera abyssinica*. This area also has moderate to high human settlement and is overgrazed by both domestic livestock and other mammalian herbivores.

Mole-rat sampling

The availability of mole-rats was estimated between January and September 1997 in 13 Augur Buzzard territories, covering three different land-use areas (4 in Hell's Gate, 2 in Mundui and 7 in Sulmac-Oserian). Mole-rats make conspicuous conical mounds on the ground as a result of their burrowing behaviour (Kingdon, 1974). The numbers of fresh mole-rat mounds emerging in an area per month can be used to indicate spatial and temporal variation in their activity (J. Jarvis, pers comm.). This indication can be extrapolated to assume that every fresh mole-rat mound constructed is potentially a hunting opportunity for a nearby perched Augur Buzzard.

Twenty transects per territory (260 total transects) were sampled at random by dividing each of the 13 territories into a 1 km by 1 km quadrant containing 100 grid squares and selecting 20 using random number tables. Non-foraging areas in the grid such as roads, water bodies, horticultural beds, green houses and residential units were removed before the final 20 were selected so that each grid square provided an equal opportunity to sample mole-rats. Starting points for each transects were selected by tossing a 6-inch nail in the air and walking in the direction it landed for either two or three minutes. The walking time was determined by tossing a coin (heads = 2 minutes, tails = 3 minutes). The end point of the walking time represented the starting point of a transect. This was repeated for each of the 20 grid squares until twenty transects were selected per territory. Each transect was 25 m long and 4 m wide (2 m either side of a transect). Sampling sessions were conducted between the middle and the end of each month, usually on bright sunny mornings from 09h00 onwards so the early morning dew had evaporated. Heavy rainfall on the night before a count made it impossible to differentiate between fresh and old mounds. All fresh mole-rat mounds found within the 4 m transect width were recorded. A mean mole-rat index per transect, defined as the number of fresh mounds per are (1 are = 100 m^2) was calculated monthly. At the beginning of each transect, the height of the grass and the softness of the soil was recorded. Soil softness was recorded as the penetration of a 0.5 cm circumference and 50 cm long calibrated metal rod inserted into the earth using the force of my left (weaker) hand.

Data analysis

Monthly mole-rat indices (the terms mole-rat availability and mole-rat index are used synonymously) were correlated with mean figures of rainfall, temperature, grass height and soil softness. Standard ANOVA was used to test for differences in mean soil softness, grass height and mole-rat availability between the three study sites. Correlation analysis was used to test for significant relationships between mole-rat availability and rainfall, temperature range, soil softness and grass height.

Two best-fit stepwise-multiple regression models were developed to predict the influence of rainfall, temperature range, soil softness and grass height on mole-rat availability. Model 1 used rainfall, temperature range, soil softness and grass height as potential predictors while Model 2 used the same predictors but excluded temperature range. Rainfall and temperature data for 1997 were used because data on soil softness, grass height and mole-rat availability were also collected in that year.

Climate data were kindly provided by Sulmac Ltd from their automatic weather station located at Sulmac. The southern Lake Naivasha area experiences short-term differences in local weather patterns especially in rainfall, but within-area differences over longer periods are negligible (J. Juma, J. Root pers comm.). Four types of data were collected – mean monthly rainfall, mean monthly rainfall over a three-year period (1995 – 1997), mean monthly temperature range and mean monthly temperature range over a three-year period (1995 – 1997).

Results

The mean mole-rat index was highest in Mundui (3.10 [se = 0.59] mounds per are), whilst for Hell's Gate and Sulmac-Oserian they were 1.10 (se = 0.19) and 2.70 (se = 0.60) mounds per are respectively (Figure 3). These means were significantly different (ANOVA, df = 26, F = 4.86, p < 0.01).

The grass in Mundui was significantly higher compared to grasses in Hell's Gate and in Sulmac-Oserian (ANOVA; df = 26, F = 6.53, p < 0.01) (Figure 3). The mean soil softness between the three areas were not significantly different (ANOVA; df = 26, F = 1.02, p > 0.05) (Figure 3).

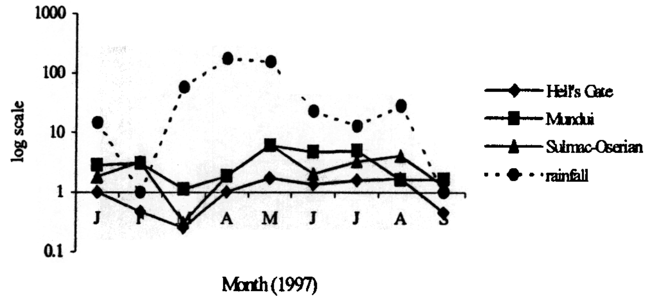


Figure 3. Trends in mean monthly rainfall and mean monthly mole-rat index for Hell's Gate, Mundui and Sulmac-Oserian for 1997.

Influence of rainfall and temperature

Monthly rainfall trends in the southern Lake Naivasha area show a bimodal distribution (peaks in April and November) (Virani 1999). Temperature ranges drop from January to April followed by a consistent period of low temperature ranges until July, after which they begin to increase (Virani 1999). Neither mean monthly rainfall for 1997 nor mean of mean monthly rainfall for 1995 to 1997, was correlated with mole-rat availability in each of the three land-use areas (Table 1). Both mean monthly temperature range (1997) and mean of mean monthly temperature range (1995-97) were negatively correlated with mole-rat availability (Table 1), significantly in the case of Hell's Gate (Table 1).

Although there were no statistically significant correlations between rainfall patterns and mole-rat availability, there was an apparent visual trend in that an increase in rainfall was followed approximately one month later by an increase in mole-rats in all three different land-use areas (Figure 4).

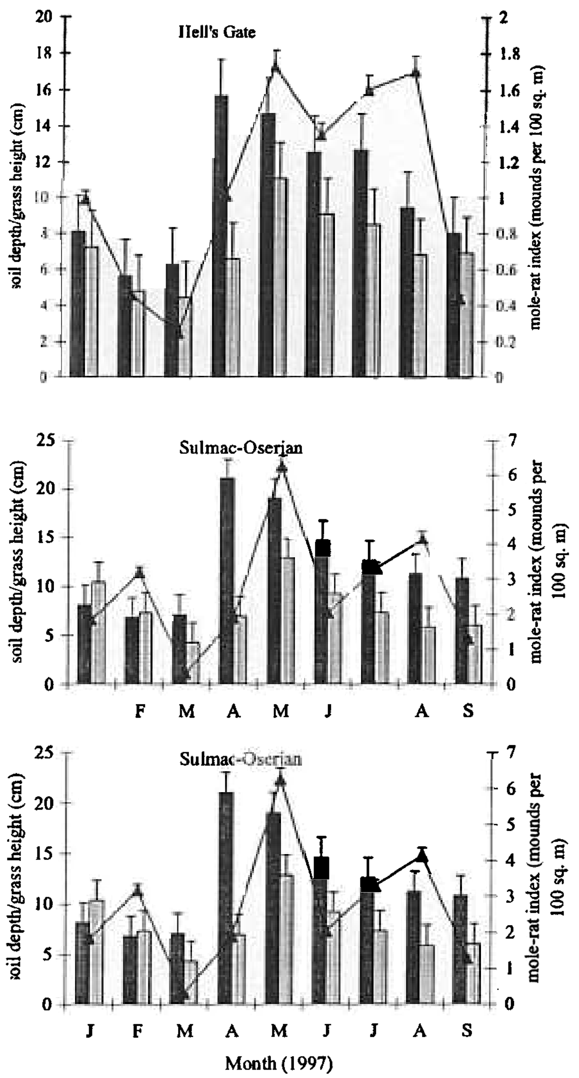


Figure 4. Trends in soil softness, grass height and mole-rat index for Hell's Gate, Mundui and Sulmac-Oserian (January to September 1997).

Influence of soil softness and grass height

Soil softness in all areas increased rapidly between March and April and then gradually declined until September (Figure 5). Soil softness was positively correlated with mole-rat index in Hell's Gate ($r = 0.69$, $p < 0.05$) but only weakly correlated in Sulmac-Oserian ($r = 0.41$, $p > 0.05$). There was no relationship between soil softness and mole-rat index in Mundui ($r = 0.01$, $p > 0.05$).

The grass heights in all areas showed a negative trend between January and March (Figure 5). Between March and May, the grass more than doubled in height, but this was subsequently followed by a gradual decrease between June and September (Figure 5). Grass height was positively correlated with mole-rat index in Hell's Gate ($r = 0.79$, $p < 0.01$) and in Mundui ($r = 0.72$, $p < 0.05$). There was also a positive correlation between grass height and mole-rat index in Sulmac-Oserian, but the relationship was not significant ($r = 0.63$, $p = 0.071$).

Mean mole-rat indices in Hell's Gate dropped from 1.0 in January to approximately 0.2 in March (Figure 5). This was then followed by an eight-fold rise between March and May, where the mole-rat index stabilized until August thereafter dropping to 0.4 in September (Figure 5). In Mundui and Sulmac-Oserian, mole-rat indices rose gently in February but dropped to minimum levels in March (Figure 5). Between March and May, mole-rat indices in these two areas rose sharply to peak levels of approximately 6.0 mounds per are. In Mundui, mole-rat indices remained high until July, after which they dropped to an index of 1.5 (Figure 5). In Sulmac-Oserian however, mole-rat indices dropped steeply in just one month by two-thirds to just above an index of 2.0 in June, after which they rose again to 4.0 by August, before finally dropping to just above 1.0 in September (Figure 5).

Additive effect of rainfall, temperature, soil and grass on mole-rat availability

The inter-correlations of rainfall, temperature range, soil softness and grass height for each of the different land-use areas are given in Tables 2 (Hell's Gate), 3 (Mundui) and 4 (Sulmac-Oserian). Mean monthly rainfall for 1997 was positively correlated with soil softness in all three land-use areas, while mean of mean monthly rainfall (1995 – 1997) was only strongly positively correlated with soil softness in Sulmac-Oserian. Neither rainfall variable was correlated with grass height. Mean monthly and mean of mean monthly temperature range were negatively correlated with soil softness in both Hell's Gate and Sulmac-Oserian but not in Mundui. Temperature variables were not correlated with grass height. Soil softness and grass height were positively correlated in Hell's Gate, but only weakly correlated in Sulmac-Oserian.

For Model 1, mean monthly temperature range (in Hell's Gate) and grass height (in Mundui) were the most important predictors that best fitted the multiple regression models to predict mole-rat availability

(Table 5). For Sulmac-Oserian, Model 1 resulted in no predictors. For Model 2, grass height in all three land-use areas was the most important predictor that best fitted the multiple regression models to predict mole-rat availability (Table 5). However the p value for the model in the Sulmac-Oserian was 0.071 (Table 5).

Discussion

Grass height emerged as the most important factor that best predicted mole-rat availability in all three sites, where it peaked in May, two months after the long rains in April, following an increase in grass height. Grazing by herbivores (in Hell's Gate and Mundui) and domestic livestock (in Mundui and Sulmac-Oserian) from May onwards reduces grass cover hence making prey more visible and available to predators. This could account for the decrease in mole-rat density in all areas. The sudden decrease in their densities in Sulmac-Oserian after a peak in May may be explained by human activities. Mole-rats (and other rodents) are considered pests by farmers and horticulturalists, and in the Naivasha area, staff are employed by farms solely to kill mole-rats (S. Higgins; J. Root; pers. comm.; pers obs.). This can have negative impacts on Augur Buzzard breeding performance.

There was no significant correlation between rainfall and mole-rat availability, although there was a clear trend that an increase in rainfall resulted in a subsequent (month later) increase in mole-rat availability. Jarvis (1969) suggested that breeding in mole-rats coincided with optimum food supply (grass roots and shoots) and soil conditions, both of which are linked with local rainfall patterns. Kiringe (1990) showed that primary production in the grasslands in Hell's Gate coincided with rainfall amount and availability, and concluded that rainfall was the main limiting factor for primary production of grasses. Strugnell and Pigott (1978) working in Ruwenzori National Park, Uganda, Onyeanusi (1983), working in Masai-Mara, Kenya and Kinyamairo (1987) working in Nairobi National Park also in Kenya found that primary production was correlated with rainfall. My Augur Buzzard study did not measure primary production but used grass-height as an index for it. Although I did not find any significant correlation between rainfall and grass-height, the general trend was that peak rainfall in April was followed by vegetation growth, mainly grasses, which led to abundance in mole-rats, and possibly other rodents. Delaney and Roberts (1978) found that breeding in small rodents such as *Arvicanthis niloticus* and *Otomys angoniensis* (both relatively common in the Naivasha area) in the Rift Valley of Kenya was maximal in the wet season (April-May) resulting in highest rodent densities occurring in the dry season (June-August).

High mole-rat availability in Hell's Gate coincided with cooler temperatures. In hot and dry areas (such as Hell's Gate), various species have evolved behavioural adaptations (e.g. aestivation) to conserve body water. It is possible that mole-rats in Hell's Gate (and surrounding areas of similar climatic and vegetation regimes) may become more active (and hence peak) only when weather conditions are generally cooler (such as in May to August). Another reason may be that in the absence of higher moisture content and density dependent factors, coupled with apparently high predation pressure by virtue of the park harbouring a large number of avian and terrestrial predators (Virani, 1999), mole-rats in Hell's Gate may be responding to subtle temperature regimes. This in turn may trigger their breeding activity and hence their availability. In both Mundui and Sulmac-Oserian, the weather is generally cooler from landward breezes and horticultural irrigation sprinklers which probably create a microclimate conducive to mole-rat activity.

Although I found a correlation between grass height and mole-rat indices, other variables such as rainfall, temperature range and soil conditions may be proximate in nature and their effects on mole-rats may have been difficult to detect. For example, an increase in soil softness in all three areas was followed by an increase in mole-rat densities. Greater soil softness probably enable easier burrowing for mole-rats and hence increased activity resulting in greater mole-rat availability. Newton (1998) suggested that different limiting factors can sometimes act in concert to influence numbers but their effects are not always straightforwardly additive. One factor might enhance the effect of another, so that their combined impact on populations is greater (or less) than the sum of their individual effects (Newton 1998).

This study has shown that grass-height is an important factor in determining prey availability for Augur Buzzards. Grazing by livestock and wild ungulates creates more conducive habitats for Augur Buzzards. This is mirrored in the fact that Augur Buzzards tend to be more common in agricultural and livestock areas such as the central highlands and the wheat belt of Kenya. Future studies should focus on the impacts of overgrazing on prey availability for Augur Buzzards and other raptors.

Acknowledgements

Permission to conduct this research was kindly granted by the Office of the President in Kenya and the Kenya Wildlife Services. This study formed part of my PhD. thesis, and was supported mainly by a grant from The Peregrine Fund (USA). Additional support came from the Aga Khan Foundation and The Earthwatch Institute. I am grateful to Rick Watson, David Harper, Simon Thomsett and Leon Bennun for their supervision, guidance and advice. Thanks are also due to the staff of Elsamere Conservation Centre, Leicester University and the National Museums of Kenya. Members of the Lake Naivasha Riparian Association granted me permission to access their land. Numerous Earthwatch Institute volunteers assisted during the study. I am also thankful to Maureen and Kathy Harper, Pradeep Ratnam, Barry Shepherd, Sarah Kraak, Matt Johnson, Joah Madden and Arjun Amar for their assistance.

Table 1. Correlation analysis of various environmental factors with mole-rat availability in three different land-use areas in the southern Lake Naivasha area, 1997.

Parameter	**Hell's Gate**		**Mundui**		**Sulmac-Oserian**	
	R	r^2	r	r^2	r	r^2
monthly rainfall (97)	0.26	0.07	0.16	0.03	0.32	0.10
mean of monthly rainfall (95-97)	0.22	0.05	-0.09	0.01	0.26	0.07
temp range (97)	-0.84**	0.70**	-0.53	0.28	-0.48	0.23
mean temp range (95-97)	-0.72*	0.52*	-0.56	0.31	-0.43	0.18

* p < 0.05; ** p <0.01 (two-tailed).

Table 2. Inter-correlations of various factors in Hell's Gate.

Factot	**Rain (97)**	**xRain (95-97)**	**Tempr (97)**	**xTempr (95-97)**	**Soil softness**	**Grass height**
Rain (97)	1.00	0.84**	-0.50	-0.41	0.71*	[illegible]
xRain (95-97)		1.00	-0.50	-0.46	0.55	0.08
Tempr (97)			.00.	0.95**	-0.89**	-0.74*
xTempr (95-97)				1.00.	-0.82**	-0.73*
soil softness					1.00.	0.73*
Grass height						1.00.

* p < 0.05; ** p < 0.01

Table 3: Inter-correlations of various factors in Mundui.

Factor	Rain (97)	xRain (95-97)	Tempr (97)	xTempr (95-97)	Soil softness	Grass height
Rain (97)	1.00	0.84**	-0.50	-0.41	0.71*	0.16
xRain (95-97)		1.00	-0.50	-0.46	0.48	-0.14
Tempr (97)			1.00.	0.95**	-0.51	-0.36
xTempr (95-97)				1.00	-0.39	-0.28
soil softness					1.00	0.13
grass height						1.00

p < 0.05; ** p < 0.01

Table 4. Inter-correlations of various factors in Sulmac-Oserian.

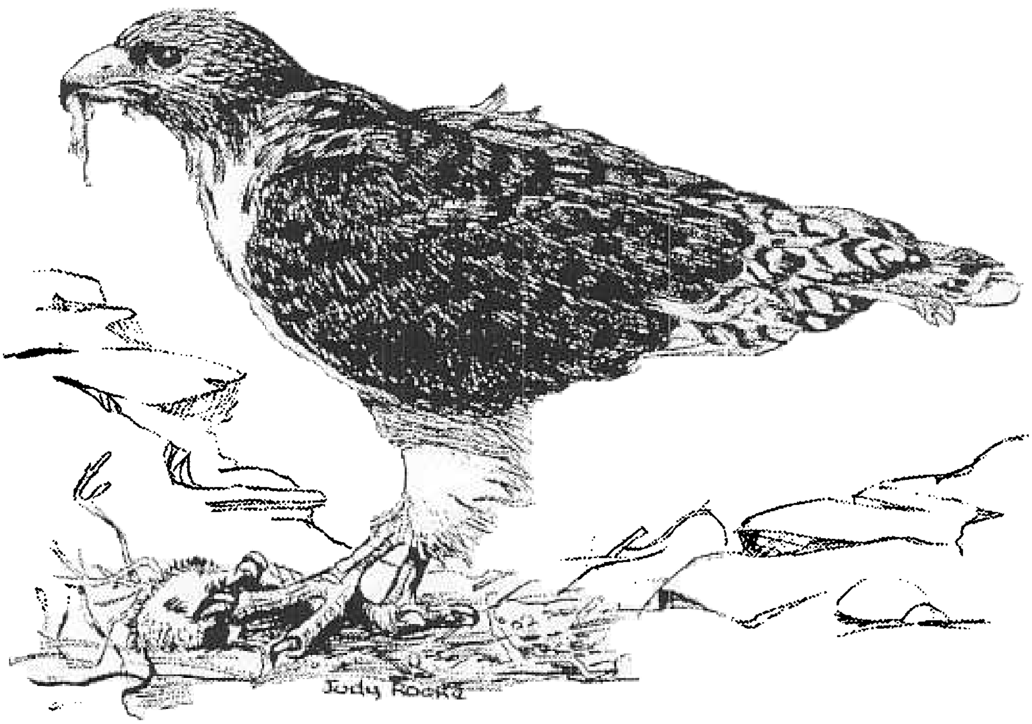
Factor	Rain (97)	xRain (95-97)	Tempr (97)	xTempr (95-97)	Soil softness	Grass height
Rain (97)	1.00	0.84**	-0.50	-0.41	0.82**	0.31
xRain (95-97)		1.00	-0.50	-0.46	0.68*	-0.07
Tempr (97)			1.00	0.95**	-0.79*	-0.32
xTempr (95-97)				1.00	-0.74	-0.25
soil softness					1.00	0.42
grass height						1.00

* p < 0.05; ** p < 0.01 df = 9; Rain (97) = mean monthly rainfall for 1997; xRain (95-97) = mean of mean monthly rainfall for 3 years (1995-97); xTempr (97) = mean monthly temperature range for 1997; xTempr (95-97) = mean of mean monthly temperature range for 3 years (1995-97).

Table 5. Best-fit multiple regression of two models to predict mole-rat availability in Hell's Gate, Mundui and Sulmac-Oserian in the southern Lake Naivasha area, 1997.

Model*	Site	Best-fit predictor	Beta coeff.	r^2	F	p
1	Hell's Gate	temp range	-0.841	0.71	16.91	**0.005**
1	Mundui	grass height	0.720	0.52	7.54	**0.029**
1	Sulmac-Oserian	NONE	-	-	-	-
2	Hell's Gate	grass height	0.785	0.62	11.27	**0.012**
2	Mundui	grass height	0.720	0.52	7.54	**0.029**
2	Sulmac-Oserian	grass height	0.626	0.39	4.51	0.071

*Model 1 predictors: rainfall (1997), temperature range (1997), soil softness and grass height; Model 2 predictors: Model 1 – temperature range (1997).



Augur Buzzard by Judy Rooke from *The Atlas of Southern African Birds*, 1997, Harrison, J.A. *et al.* (eds) published by BirdLife South Africa, Johannesburg.

References

Ambrose, A.S. 1984. "Holocene Environments and Human Adaptations in the Central Rift Valley, Kenya." Unpublished Ph.D. dissertation, University of California, Berkely.

Brown, L.H. & Britton, P.L. 1980. The breeding seasons of East African birds. Nairobi: East African Natural History Society.

Cave, A.J. 1968. The breeding of the kestrel, *Falco tinnunculus* L. in the reclaimed area Oostelijk Flevoland. Netherlands Journal of Zoology 18:313-407.

Delany, M.J. &. Roberts, C.J. 1978. Seasonal population changes in rodents in the Kenya Rift Valley. Bulletin Carnegie Museum of Natural History 6:97-108.

Hagen, Y. 1969. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent population fluctuations. Fauna 22:73-126.

Jarvis, J.U.M. 1969. The breeding season and litter size of African Mole-rats. J. Reprod. Fert., Suppl. 6:237-248.

Kingdon, J. 1974. East African Mammals. An atlas of evolution in Africa. Volume II Part B (Hares and Rodents). Academic Press.

Kinyamario, J.I. 1987. Primary productivity in relation to environmental variables of a semi-arid grassland ecosystem in Kenya. Unpublished PhD. thesis, University of Nairobi, Kenya.

Kiringe, J.W. 1990. A vegetation and large herbivore species survey in Hell's Gate National Park, Naivasha Kenya. Unpublished MSc. thesis, University of Nairobi, Kenya.

Litterick, M.R., Gaudet, J.J., Kalff, J. & Melack, J.M. 1979. The limnology of an African lake. Lake Naivasha, Kenya. Unpublished report produced for the SIL-UNEP workshop on African limnology (Inland waters: their ecology and utilisation), Nairobi, December 1979.

Newton, I. 1979. Population Ecology of Raptors. Berkhamstead: Poyser.

Newton, I. 1998. Population limitation in birds. Academic Press.

Pratt, D.J., Greenway, P.J. & Gwynne, M.D. 1966. A classification of East African rangeland with appendix on terminology. Journal of Applied Ecology 3:369-379.

Smart, A.C. & Taylor, C. 1990. An investigation of the diet of Verreaux's eagle owl *Bubo lacteus* and the barn owl *Tyto alba*, at Lake Naivasha, Kenya. African Journal of Ecology 28:153-156.

Smeenk, C. 1974. Comparative ecological studies of some East African birds of prey. Ardea 62.

Southern, H.N. 1970. The natural control of a population of tawny owls *Strix aluco*. Journal of Zoology London 162:197-285.

Strugnell, R.G. & Pigott, C.D. 1978. Biomass, shoot production and grazing of two grasslands in the Ruwenzori National Park, Uganda. Journal of Ecology 66:73-96.

Taylor, K.D. & Green, M.G. 1976. The influence of rainfall on diet and reproduction in four African rodent species. Journal of Zoology London 180:367-389.

Virani, M.Z. 1999. The breeding ecology and behaviour of the augur buzzard *Buteo augur* in relation to different land-uses in the southern Lake Naivasha area, Kenya. Ph.D. thesis, Department of Biology, University of Leicester (UK).

Widen, P. 1994. Habitat quality for raptors: a field experiment. Journal of Avian Biology 25:219-223.