# Factors influencing the breeding performance of the Augur Buzzard *Buteo augur* in southern Lake Naivasha, Rift Valley, Kenya

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The breeding performance of Augur Buzzards *Buteo augur* in 1995-1998 was compared between three different areas south of Lake Naivasha, Kenya. These were 1) a national park (Hell's Gate), 2) an undisturbed *Acacia* woodland-pasture (Mundui) and 3) an intensively farmed horticultural area (Sulmac-Oserian). Augur Buzzards in Mundui had the most optimal nesting habitat, produced the most fledglings (1.6 chicks per year), enjoyed an abundant food supply as their land was not heavily grazed, and suffered the least persecution. In contrast, Augur Buzzards in Hell's Gate produced the fewest fledglings (0.5 chicks per year). Their food supply was not abundant and their nests were confined to cliffs and short shrubs making them vulnerable to predation. Augur Buzzards in Sulmac-Oserian performed intermediately. They produced 0.8 chicks per year and suffered the highest adult mortalities (12%) from human persecution.

Height of grass in fields within a pair's territory was the most important variable in predicting whether Augur Buzzards attempted to breed or not. Mean annual adult mortality was lowest at Mundui (4.8%) and highest at Sulmac-Oserian (12%). Adult mortality and the success of previous breeding attempts were the most important predictors in determining breeding performance.

**Introduction**

Breeding performance is one of two important ecological parameters by which the health and survival of a species is measured; the other being adult survival. Breeding performance is influenced by various extrinsic factors that may work in concert with one another. In the absence of anthropogenic factors, the availability of food and suitable nest sites rank as the most important ultimate factors, although rainfall can act as a proximate one (Newton 1994).

Prey abundance/availability, prey diversity, nesting substrates, proximity to adjacent breeding pairs, perching sites and artificial structures can influence breeding performance in raptors (Kostrzewa 1996), Austin and Houston 1997, Potapov 1997, Zelenak and Rotella 1997). High adult mortality has a negative influence on breeding performance (Keran 1981). Intra-specific disturbance and competition, new nests, age of paired birds, predation and human impact on the habitat are equally important factors that influence the breeding performance of raptors (Newton 1979).

Augur Buzzards *Buteo augur* commonly occur in the central highlands and the Rift Valley of Kenya. They adapt well to cultivated land and dense human habitation (Brown *et al*. 1982, Muhweezi 1990). In Kenya's Lake Naivasha region, the species is highly adapted to nesting on both cliffs and trees (Virani 1999). Its diet consists mainly of rodents; the yellow-toothed mole-rat (henceforth mole-rat) *Tachyorectes splendens* which, because of its high densities in cultivated areas, has become the Augur Buzzard's principal food source (Virani 2006). In the southern parts of the Lake Naivasha area, there has been an increase in human and livestock population growth with resultant impacts on the ecosystem and its associated flora and fauna (Harper 2006). Overgrazing by livestock and conversion of *Acacia* woodland pastures and agricultural fields to intensive horticultural activities present ecological challenges to Augur Buzzards that can potentially influence their breeding performance and survival.

The aims of this paper are 1) to compare the breeding performance and mortality of Augur Buzzards in three different areas; and 2) to determine by use of logistic regression models which ecological variables contribute most to predicting the probability that a pair of Augur Buzzards breed and, if they do, whether they are successful or not.

**Study area 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 1890m (Figure 1). Three areas with different land-use patterns were selected as study sites. These were Hell's Gate National Park (henceforth Hell's Gate), Mundui ranch and the Sulmac-Oserian horticulture area (Figure 1). Hell's Gate lies 2km south of Lake Naivasha and is a protected area where Augur Buzzards nest both on cliffs and on trees. The land-use is conservation and tourism with moderate to extreme levels of wild herbivore grazing. Mundui ranch is located west of Lake Naivasha and comprises open *Acacia xanthophloea* woodland pastures. The land-use is private cattle ranching, high-paying tourism with minimal human disturbance. Sulmac-Oserian consists of two separate horticultural areas located between Hell's Gate and Mundui. The land-use is primarily intensive horticulture (mainly open and greenhouse - covered fields growing flowers [roses and carnations] for export), human settlements (primarily low-quality housing for workers of the horticulture industry), livestock grazing by pastoralists and vehicular traffic. At Mundui, Augur Buzzards nested on *A. xanthophloea* trees while at Sulmac-Oserian, they nested on either *A. xanthophloea, Euphorbia magnicapsular*, or *Eucalyptus* spp. A more detailed description of the study area can be found in Virani (2006).

The study was conducted over three years between January 1995 and January 1998. To identify a list of potential variables that influence breeding performance, data were collected on nests and nesting substrates, breeding performance and adult mortality. Between January and September 1997, additional variables such as soil softness, grass height and mole-rat availability were also collected and used in evaluating their influence on breeding performance (see Virani 2006). A human impact index (HII) was calculated and used to rank this effect in analyses.

**Nest searches**

Nest searches were conducted by observing Augur Buzzard pairs for evidence of breeding behaviour, such as carrying of nesting material or prey to the nest, courtship behaviour and territorial displays. Nests with evidence of eggs or chicks were considered active. Data on breeding performance were gathered from all active nests as follows: occupied nests (incubating adult present) were observed with a 20-60x spotting telescope from at least 200m to avoid disturbance. They were revisited at least once every two weeks to count the number of young and determine the eventual outcome of the nesting attempt. The possibility exists that a few unsuccessful breeding attempts may not have been detected. Laying and fledging dates were estimated from known hatching dates or ages of young determined from nestling growth (Steyn 1982). Juvenile Augur Buzzards were recorded as fledging successfully only if they were observed after leaving the nest. The locations of all known nests were recorded using a hand-held Garmin 12 XL GPS and the information entered into a GPS database using the software programme Mapinfo (1992) that calculated the mean nearest-neighbour distance between adjacent pairs. The most frequently used roost site was taken as the ‘centre of activity’ for non-breeding pairs to calculate nearest-neighbour distances. The nesting substrates of all nests were also recorded (e.g. cliff nests and species of tree nests).

**Breeding performance and mortality**

We measured three parameters to evaluate the breeding performance of 34 pairs of Augur Buzzards over the three-year period. This included nine pairs at Hell's Gate, seven at Mundui and 18 pairs at Sulmac-Oserian. The parameters were 1) Breeding rates – number of breeding attempts per pair per year (a breeding attempt was recorded when an Augur Buzzard was observed in incubation position regardless of the outcome of the attempt), 2) Breeding success - number of successful chicks fledged per breeding attempt per year, and 3) Productivity - number of successful chicks fledged per pair per site (including non-breeding pairs). In cases where nest failures were suspected, a thorough search was done below nests for evidence of predation such as egg-shells or feathers.

We ringed 57 individuals (83.8%) of the 68 birds (34 pairs) present in the study area. Adult mortality rates were calculated by counting the numbers of new Augur Buzzards that replaced dead or missing birds in known territories using data from ringed birds or recognition of individual facial and plumage characteristics of the unringed birds (11 individuals). Because ringed birds that were missing from known territories were not observed elsewhere in the study area, we assumed that they had died and were replaced. The annual mortality rate in the population was used to calculate a bird's mean further life expectancy using the following formula (Fry 1980):

$$s = \frac{2 - m}{2m}$$

Where s = mean adult further life expectancy (years),

m = mean annual mortality, estimated by the numbers of birds replacing dead or missing ones;

We assumed that the Augur Buzzard population was stable in order to use this formula. The expected lifespan of the Augur Buzzard in the Rift Valley at Lake Naivasha was also calculated using this formula, adding 1.6 years as the time period to reach adult plumage (from Steyn 1982). During the course of the study, bi-annual raptor surveys and Augur Buzzard trapping and ringing were conducted in areas adjacent to the study area as far as 20km away. This confirmed that no ringed or recognised birds were observed outside the study area. We used Generalized Linear Mixed Models to test breeding parameters between sites and years, and to avoid pseudo-replication (Lindstrom and Bates 1990, Engel and Keen 1994). Because each individual was known, we assigned pair identity and year as random factors, and site as a fixed factor.

**Mole-rat availability, grass height and soil softness**

We used data from Virani (2006) on mole-rat availability, grass-height and soil softness for each of the three sites. Grass-height was measured with a tape-measure and soil-softness calculated by inserting a calibrated metal rod in the ground (Virani 2006). Mole-rats are subterranean rodents that burrow just below the soil and come up to the surface regularly to clean their tunnels (see Jarvis 1969). Hence, we estimated mole-rat availability by counting the number of fresh mole-rat mounds per hectare per site. This was done on a monthly basis between January and September 1997 and was used to establish a monthly index of mole-rat availability to Augur Buzzards. Fresh mole-rats mounds were counted on twenty 25m x 4m transects covering a total area of $2000m^2$ per territory. Grass-height was used as an index of livestock/wild herbivore grazing pressure and amount of food available to mole-rats, while soil-softness was used as an index to represent moisture in the soil and mole-rat burrowing/tunneling effort (we assumed that the softer and wetter the soil, the easier it was for mole-rats to come up to the surface). We emphasise that grass-height measurements were meant to illustrate the impacts of livestock overgrazing and were thus a measure of the shortness of the grass rather than the tallness. For clarity, mole-rat index and mole-rat availability are used synonymously to emphasise mole-rat activity. Augur Buzzards hunt mole-rats as they come up to the surface to forage. While foraging, mole-rats create soft conical mounds on the surface and become vulnerable to predation. Because mole-rat availability in the south Lake Naivasha area is influenced by grass height (Virani 2006), we classified both these parameters plus soil softness into four categories in ascending order to represent the different magnitudes of each parameter per study site. The categories were split as follows: soil softness (< 9.9, 10.0 – 11.9, 12.0 – 13.9 and > 14cm), grass height (< 6.9, 7.0 – 8.9, 9.0 – 10.9 and > 11cm) and mole-rat availability (0.00 – 0.99, 1.00 – 1.99, 2.00 – 2.99, and > 3.00 mounds per $100m^2$). We justified this method because there were no significant differences in each of these parameters between adjacent Augur Buzzard territories. The only exception was mean grass height in the territory occupied by one pair in Sulmac-Oserian that was significantly taller than that growing in the territory occupied by an adjacent pair. Detailed descriptions of these methods can be found in Virani (2006).

**Human Impact Index (HII)**

An HII was calculated (modified from Brandl *et al*. 1985) as a qualitative measure of human activity and disturbance in 41 Augur Buzzard territories (Hell's Gate – 12, Mundui – 9, Sulmac-Oserian – 20) and its potential to affect breeding performance, by estimating the degree of land-use activity. Quantitative measurements of HII were not possible because the rate of increase of humans and horticultural units occurred rapidly over the three years and therefore the most practical way to correlate human activity was by obtaining a qualitative measure. The HII was developed based on four criteria:-

1) human settlement pressure – the proportion of area within a 1km radius from the nest of a pair that contains occupied human settlement structures;

2) grazing pressure (both domestic livestock and wildlife) – at every nest visit, an estimate of the numbers of domestic or wild herbivores seen grazing within a pair's territory (defined as the area within 1km radius of the nest) was recorded and an overall average taken over the study period to represent the level of grazing pressure. In addition, signs of heavily used grazing routes and the presence of *Felicia muricata* (a weed which grows in heavily grazed areas [J. Root, pers comm.]) were considered when assigning scores;

3) horticultural activity pressure – the proportion of area within a radius of 1km from the nest of a pair that is occupied by horticultural farming units;
4) direct human disturbance - the likelihood that the activity of Augur
Buzzards such as foraging and nesting would be disturbed by activities including mortality risk through persecution, electrocution or poisoning, based upon the number of dead Augur Buzzards collected over the three years of study. For example, 60% of all dead Augur Buzzards were collected in Sulmac-Oserian which justified a higher risk index.
Each category had a 5-point intensity of impact. Scores were assigned as follows: nil = 0, low = 1, moderate = 2, high = 3, extreme = 4. Scores from each category were added to obtain an overall HII that ranged from 0 to 16.

Scores for each category were ranked and median ranks for each variable were plotted on a bar chart to show how they varied for each site (Figure 2).

**Sources of variation in breeding success and productivity**

Nine ecological variables – nest type, nest age (old/new), previous brood, HII, nearest-neighbour distance (NND), mortality rate (MR), soil softness (SS), grass height (GH) and mole-rat availability (MRA) were evaluated for each territory to investigate sources of variation in breeding success and productivity. An iterative process was used that identified a short list of candidate models for a series of logistic regression models (Table 1). The results obtained from these models were used to suggest rather than to test hypotheses as the analyses were exploratory rather than confirmatory. The first step in the iterative process was a univariate analysis of these variables. Variables whose univariate results had an unadjusted significance of < 0.25 became candidates for multivariate logistic regression following Hosmer and Lemeshow (1989). Thus, variables that may have been important predictors of productivity only when considered together were not removed from consideration prematurely. Candidate variables were entered into multivariate logistic regression based on a significance level of 0.1 and those models that were < 0.1 were chosen. Separate logits were estimated for breeders vs. non-breeders and for successful vs. unsuccessful breeding attempts (Hosmer and Lemeshow 1989).

Two models each with two variants were developed to determine the best-fit variable that predicted the probability that: 1) Augur Buzzards did not breed; and 2) breeding attempts were unsuccessful.

Because logistic regression does not give rise to an $R^2_{adj}$ statistic, Darlington (1990) recommends the following statistic as a measure of goodness of fit:

$$LRFC_1 = \frac{\exp[(LL_{model}-LL_0)/N] - 1}{\exp(-LL_0/N) - 1}$$

where, exp refers to the exponential function (the inverse of the log function), N is sample size, and $LL_{model}$ and $LL_0$ are the log likelihoods of the data under the model and the null hypothesis respectively. This statistic is useful because it takes values between 0 and 1 which have much the same interpretation as values of $R^2_{adj}$ in a linear regression, and is more closely analogous to $R^2$. Therefore the $R^2$ values given in the results are pseudo-$R^2$ values.

## Results

### Mortality

Fifteen out of 57 marked and ringed adult Augur Buzzards were recovered or were missing from their territories over the three-year study period. Nine (60%) were in Sulmac-Oserian, four (26.7%) in Hell's Gate and two (13.3%) in Mundui. The mean annual mortality in the study area was estimated at 8.8%. Sulmac-

Oserian had the highest mean annual mortality (12%), followed by Hell's Gate (7.4%) and Mundui (4.8%). These differences were not significant perhaps due to the low sample size of birds recovered from each area (Chi-square; $\chi^2 = 2.410$, df = 2, $p > 0.05$). Mean annual mortality within Sulmac-Oserian varied from 3.3% at Oserian to 20.8% at Sulmac. The causes of death of the majority of adult Augur Buzzards were unknown. Human persecution, poisoning and electrocution on electricity pylons were the main known causes in Hell's Gate and Sulmac-Oserian, while in Mundui it was drowning in a cattle trough. Horticultural intensity and human disturbance was highest at Sulmac-Oserian and lowest at Mundui (Figure 2). Grazing pressure was lowest at Mundui compared to Hell's Gate and Sulmac-Oserian where it was higher (Figure 2). Human settlement was highest at Sulmac-Oserian and lowest at Mundui (Figure 2). Mean annual mortality rate was highly positively correlated with the Human Impact Index (HII) ($r = 0.64$, $n = 34$ pairs, $p < 0.001$) and negatively correlated with grass height ($r = -0.45$, $n = 25$ breeding pairs, $p < 0.05$).

**Breeding attempts and rates**

We observed 65 breeding attempts over the three-year study period. Sixteen were observed each at Hell's Gate and Mundui respectively while 33 breeding attempts were observed at Sulmac-Oserian. Breeding rates at each site did not significantly differ from year to year (Table 2, $p > 0.05$). Mundui ($1.13 \pm 0.09$ attempts per pair per year) and Sulmac-Oserian ($1.03 \pm 0.12$ attempts per pair per year) had the highest breeding rates, while Hell's Gate had the lowest ($0.69 \pm 0.15$ attempts per pair per year). These differences in breeding rates between the three land-use types over the three-years were significant ($p < 0.05$). Fifty-six breeding attempts in the overall study area were successful. All breeding attempts in Mundui were successful compared to 64.9% in Sulmac-Oserian (24, n = 37) and 63.6% in Hell's Gate (14, n = 22). There was a significant association between the type of land-use and the proportion of Augur Buzzards that bred successfully (Chi-square; $\chi^2 = 8.82$, df = 2, $p < 0.05$).

## Breeding success and productivity

Breeding success at each site did not significantly differ from year to year (Table 2). Overall breeding success in the study area was 0.95 $\pm$ 0.08 chicks per breeding attempt per year, while overall productivity was 0.81 $\pm$ 0.09 chicks per pair per year. This difference was not significant ($p > 0.05$). Breeding success per pair per year was significantly higher in Mundui (1.38 $\pm$ 0.12 than Sulmac-Oserian (0.85 $\pm$ 0.18) or Hell's Gate (0.72 $\pm$ 0.12) ($p < 0.01$). It was not significantly different between years in each land-use area (Table 2). Productivity was also significantly higher in Mundui (1.56 $\pm$ 0.18) than Sulmac-Oserian (0.78 $\pm$ 0.12) or Hell's Gate (0.47 $\pm$ 0.13) ($p < 0.001$). It was not different between years in each land-use area (Table 2).

## Factors affecting breeding performance

Six (75%) out of the eight breeding attempts that failed in Hell's Gate were due to predation. Four active nests were observed to be depredated by Olive Baboons *Papiocynocephalus anubis*, one to rock climbers climbing too close to a nest resulting in the eggs left unattended, and one for unknown reasons. The reasons for six (46.2%) out of the 13 breeding attempts that failed in Sulmac-Oserian were unknown, while the rest were due to nest-desertion, adult mortalities, human disturbance (nest-tree was felled), egg predation and heavy rainfall. The type of nest (cliff, tree), distance to its nearest neighbour, HII, or mortality rate did not have any influence on breeding performances in the study area.

## Previous breeding attempt

There was a highly significant relationship between the successful outcome of a previous breeding attempt and the proportion of successful breeding attempts that followed. Thirty-two breeding attempts that were successful out of a total of

49 (65%), had followed successful attempts, while eight that were unsuccessful, followed previously unsuccessful attempts (16%) (Chi-square; $\chi^2 = 10.55$, df = 1, n = 49, $p < 0.001$). Breeding Augur Buzzards that were unsuccessful also had a significantly higher mortality rate in their territories than successful breeders (Mann-Whitney; U = 218.5, z = -4.34, $p < 0.0001$).

**Mole-rat index, grass height and soil softness**

There was a significant positive linear trend between the grass height ($\chi^2 = 4.99$, p = 0.026) and Mole-rat index ($\chi^2 = 4.16$, p = 0.041) categories and the proportion of Augur Buzzards that bred in 1997. There was no significant association between the soil softness category and the proportion of breeding Augur Buzzards. Soil softness was positively correlated with grass height and the mole-rat index, but negatively correlated with nearest-neighbour distance (Tables 3 and 4). Grass height was positively correlated with soil softness and the Mole-rat index, which was negatively correlated with nearest-neighbour distance (Tables 3 and 4).

There was a significant positive association between the grass height category ($\chi^2 = 8.14$, p = 0.040) and the proportion of Augur Buzzards that bred successfully in 1997 (Chi-square test for trend; df = 1, n = 25 pairs [20 successful, 5 unsuccessful]). There was no significant association among the soil softness ($\chi^2 = 0.01$, p = 0.924) and mole-rat availability ($\chi^2 = 0.14$, p = 0.704) categories and the proportion of Augur Buzzards that bred successfully in 1997 (Chi-square test for trend; df = 1, n = 25 pairs [20 successful, 5 unsuccessful]).

**Logistic regression model**

Five out of the six variables that potentially influenced breeding were considered in the multivariate logistic regression Model 1, while four out the nine variables that potentially influenced successful breeding were considered for Model 2, based upon univariate test results (Table 5). Results of the multiple logistic regression showed that when considered together, only mortality rate (MR), outcome of previous brood (PB) and grass height (GH) were related to breeding attempts and breeding success (Table 6). The most parsimonious model for the multivariate regression of breeders versus non-breeders included only grass height (Model 1B in Table 6). Model 1A did not have any significant predictive variables (Table 6). The logistic model 1B predicting the probability of a pair breeding P(Br) was

$$1 - P(Br) = \frac{e^{-0.91 + 1.11\,(GH)}}{1 + e^{-0.91 + 1.11\,(GH)}}$$

……….(Model 1B)

It was slightly better than the null model (set at a significance level of 10%) ($p = 0.0495$) and had an $R^2$ value of 0.24. The model correctly predicted for 73.5% of the pairs that attempted to breed. The most parsimonious model for the multivariate regression of successful versus unsuccessful breeding attempts included mortality rate and the outcome of the previous brood (Models 2A [1995 – 1997] and 2B [1997 only] in Table 6). The logistic model 2A predicting the probability of a pair breeding successfully P(BrSux) was

$$1 - P(BrSux) = \frac{e^{3.63 - 17.18\,(MR) - 1.89\,(PB)}}{1 + e^{3.63 - 17.18\,(MR) - 1.89\,(PB)}}$$

……..(Model 2A)

while that of 2B was

$$1 - P(BrSux) = \frac{e^{4.32 - 18.66\,(MR) - 2.76\,(PB)}}{1 + e^{4.32 - 18.66\,(MR) - 2.76\,(PB)}}$$

……..(Model 2B)

Both models 2A and 2B contained coefficients different from zero (Wald $\chi^2$ test [Table 6]). They were both significantly better than the null model ($p < 0.05$ [Model 2A]; $p < 0.01$ [Model 2B] (Table 6) and had $R^2$ values of 0.50 and 0.56 respectively. The models correctly predicted for 81.6% (Model 2A) and 91.3% (Model 2B) of the pairs that bred successfully.

The most parsimonious regression models of P(Br) and P(BrSux) were significant, but their $R^2$ values were small (particularly for Model 1B). Thus while the models were significantly better than the null models, much variation in the data remains unexplained. The models predicting P(BrSux) had a higher $R^2$ value and better predictive ability than the model predicting P(Br).

Assuming the adult population is stable and that recruitment from the immature population equals the annual mortality (8.8% in the southern Lake Naivasha), then the mean life expectancy of an Augur Buzzard in the southern Lake Naivasha area was estimated at 12.5 years.

## Discussion

### Breeding performance

There was insignificant year-to-year variation in breeding rates, breeding success and productivity at each site suggesting that each area had consistent environmental influences on the outcomes of these parameters. In contrast, the significant differences in these parameters between sites further confirms that the land-use patterns at each site probably affected breeding performance. The higher breeding rate in areas of human land uses was attributed to higher mole-rat densities and greater nest-site availability. Mundui had a zero failure rate, while both Hell's Gate and Sulmac-Oserian had similarly high nesting failure rates. Thus high food availability as a result of suitable grass height in Sulmac-Oserian may have led to high breeding rates but high adult mortality and potential lack of breeding experience by new territory holders led to increased failures, because surviving parents had to abandon their eggs or nestlings and attract new mates that are usually inexperienced (Newton 1979).

Natural predation mainly by baboons, and a more limited food supply were most likely the causes of breeding failure in Hell's Gate. In Lendrum's (1979) study of Augur Buzzards in the Matopos hills Zimbabwe, eggs were depredated by Chacma Baboons *Papio ursinus*, White-necked Ravens *Corvus albicollis*, and pythons *Python sebae*.

Overall breeding performance in the study area was similar to that of the Matopos hills (Lendrum 1979), but higher than that of the Impenetrable Forest in Uganda, where breeding success was considered 'poor' (Muhweezi 1990, but no figures available). Our study was too short to detect any long-term fluctuations in breeding performance (usually associated with food supply, Newton 1979) within sites, as these can probably only be detected in studies of ten years or longer (Gargett 1990).

**Adult mortality**

The adult mortality rate was the most important predictor in the logistic regression model that determined whether breeding attempts were successful or not. The highest mean annual adult mortality rate occurred in Sulmac-Oserian where it ranged from 3.3% in Oserian to 20.8% in Sulmac. Mundui and Hell's Gate had relatively lower annual mortality rates. The low sample size of recovered adult birds perhaps precluded a significant result in annual mortality rates between sites. Sulmac-Oserian also had the highest number of adult mortalities of which all known causes were human related. The high adult mortality rate in Sulmac-Oserian was the main cause of unsuccessful breeding attempts. Eggs or chicks were usually deserted after a parent was killed. Observations indicated that dead Augur Buzzards were usually replaced within one or two days. Brown and Amadon (1968) have also documented this, while Newton (1979) cites a number of examples in other raptors.

The negative correlation with grass height suggests that areas that were extensively grazed experienced highest adult mortalities. Del Hoyo *et al*. (1994) stated that Augur Buzzards were vulnerable to extensive afforestation of grassland habitat, or through lowered carrying capacity through overgrazing. Cattle and goat herders were often seen throwing rocks at perched Augur Buzzards and they had regular contact with perching sites in areas where they grazed their livestock. Muwheezi (1990) reported that the most common cause of raptor mortality in the Impenetrable Forest was human disturbance. He observed that non-forest raptors were the most affected because the local people knew where the birds nested. Mundui, which was moderately grazed compared to the heavily grazed grasslands of Sulmac-Oserian, had a lower adult mortality rate.

The Augur Buzzard adult annual mortality rate of 8.8% in the study area is much lower than that recorded for adult Common Buzzards *Buteo buteo* (19 – 20%; Olsson 1958, Mebs 1964) and Red-tailed Hawks *B. jamaicensis* (21 – 24%; Henny and Wight 1972), although these high mortality rates were based on national ringing recoveries and can be biased (Newton 1979). Walls and Kenward (2001) showed that adult mortality rates of Common Buzzards in the United Kingdom are as low as 9% while those of first-year birds are about 35%. This is similar to the adult mortality estimates in this study although data are still lacking for estimates on juvenile Augur Buzzards.

The lifespan estimate was similar to that suggested by Brown *et al*. (1982) which was 13 years per bird. They estimated a juvenile 75% mortality rate before sexual maturity at three years and hypothesized that adults would require a breeding life of ten years; but their observations suggested that this was longer than normal.

**Correlates of breeding performance – implications of the logistic regression model**

The logistic regression model showed that the height of the grass in a pair's territory was the most important variable in predicting whether Augur Buzzards attempted to breed or not. Grass height was positively correlated with mole-rat availability (Virani 2006), which was in turn negatively correlated with nearest-neighbour distance. Hence the probability that a pair would not breed was high if the foraging areas were overgrazed. Overgrazed grasslands implied less food for Mole-rats and other rodents which would reduce their breeding potential (and probably activity). This would result in less food for Augur Buzzards, affecting their capability to breed. Obviously rainfall would play an important role in the growth of grass. A pair's nesting substrate did not influence the success of a breeding attempt. Cliff nests were most vulnerable to depredation mainly because baboons were common in Hell's Gate and are skilled at climbing cliffs. All *Acacia xanthophloea* nests in Mundui were successful, constructed on tall and mature trees, and have thorns that offered protection against predators, and also experienced minimal human disturbance (Virani 1999). This magnitude of breeding success has been observed in other African raptors such as Wahlberg's eagles *Aquila wahlbergi* nesting on thorn trees (Simmons 1993). In Sulmac-Oserian, local people knew of some Augur Buzzard nest trees and affected their breeding success by either killing adults or cutting down nest-trees. *Euphorbia magnicapsular* trees had the most successful breeding success rates. These grow on steep slopes, usually at a distance from human influences, have fragile fronds that carry a poisonous milky sap, and are inaccessible to terrestrial predators.

Despite constraints from human disturbances and close distances to neighbouring pairs, Augur Buzzards established territories and attempted to breed even in areas with high human impact indices.

Success or failure in one year was correlated with breeding performance in the next, but other factors were also involved. Territorial occupancy, boundary changes and/or inter-specific contacts also affect the likelihood that a breeding attempt will be made (see also Gargett 1990). Pairs that were successful at breeding in their previous attempt were experienced, knew their foraging areas well, had adequate food supplies and their nests were well protected against predators. This was also found in the Hawaiian hawk *Buteo solitarius*, where almost 62% of the pairs that bred successfully attempted to breed the following year (Griffin *et al*. 1998). Brown (1970) suggested that in many African raptors, pairs bred in only two out of three years because there was a tendency for pairs that bred successfully to not nest the next year. This is true for some raptors such as some large eagles with longer breeding periods (including periods of long post-fledgling dependency). In the Verreaux's Eagle *Aquila verreauxii*, Gargett (1990) found that a successful breeding attempt in one year was almost invariably followed by non-breeding in the following year. While success of previous breeding attempts maybe an important predictor of success in Augur Buzzards and possibly a wide range of raptors, it is unlikely to be an ultimate factor in determining breeding success. This parameter cannot be measured in new pairs and therefore the usefulness of this model is restricted to birds that have bred before.

The Augur Buzzard population in the southern Lake Naivasha area appears to be stable. However, a move away from traditional livestock practices to more intensive horticulture is likely to pose a serious threat to the future survival of this species in the area.

*Acknowledgements* - This study was generously supported by grants from The Peregrine Fund (USA), The Aga Khan Foundation and The Earthwatch Institute. Rick Watson, David Harper, Simon Thomsett and Leon Bennun supervised MZV, for his PhD at the University of Leicester (UK). Thanks are also due to the staff of Elsamere Conservation Centre, particularly Mrs Velia Carn, University of Leicester Biology Department and the National Museums of Kenya. Permission to conduct this research was kindly granted by the Office of the President in Kenya and the Kenya Wildlife Services. Members of the Lake Naivasha Riparian Association granted permission to access their land. Alan Kemp, Rob Davies and Russell Thorstrom helped with providing useful suggestions on methodology while Jim Berkelman and Steve Redpath helped with suggestions on earlier drafts. Numerous Earthwatch Institute volunteers assisted during the study. We are also thankful to Maureen Harper, Kathy Parsons, Pradeep Ratnam, Arunav Gogoi, Barry Shepherd, Sarah Kraak, Matt Johnson, Joah Madden and Arjun Amar for their assistance. Todd Katzner, Rob Simmons, Ruth Tingay and Anthony Van Zyl helped to significantly improve earlier drafts. This paper is dedicated to the memory of Joan Root

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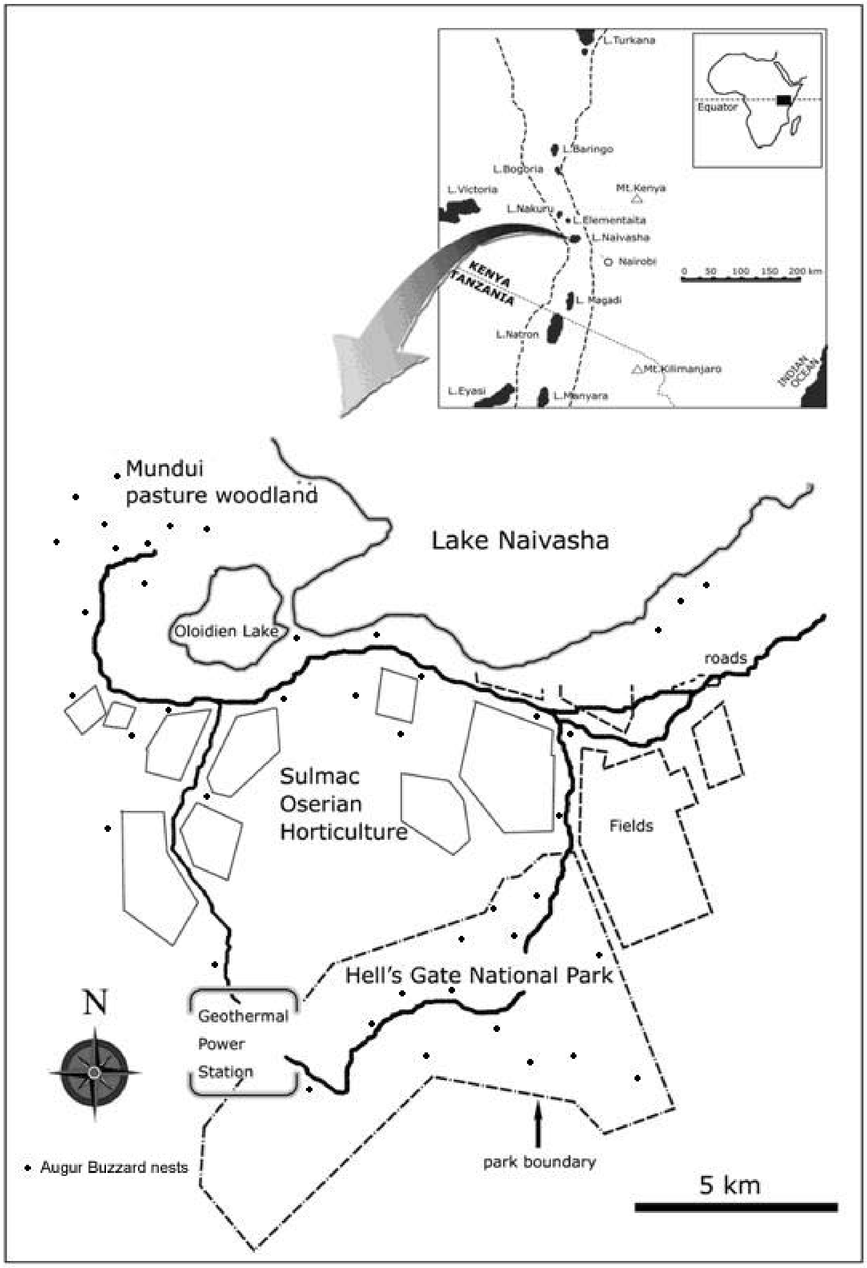
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Equator
L.Baringo
L.Bogoria
L.Victoria
Mt.Kenya
L.Nakuru
L.Elementaita
L.Naivasha
Nairobi
0 50 100 150 200 km
KENYA
TANZANIA
L. Magadi
L.Natron
Mt.Kilimanjaro
INDIAN OCEAN
L.Eyasi
L.Manyara
Mundui pasture woodland
Lake Naivasha
Oloidien Lake
roads
Sulmac Oserian Horticulture
Fields
Hell's Gate National Park
N
Geothermal Power Station
Augur Buzzard nests
park boundary
5 km

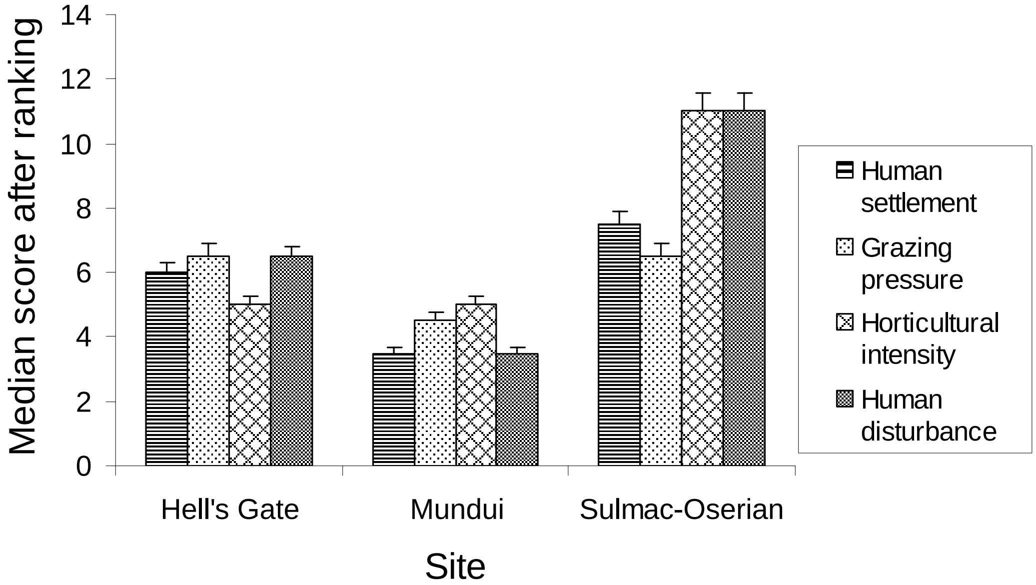
Median score after ranking
0
2
4
6
8
10
12
14
Hell's Gate
Mundui
Sulmac-Oserian
Site
Human settlement
Grazing pressure
Horticultural intensity
Human disturbance

**Table 1:** Variables used (shown by the '+' sign) in univariate analysis to create a shortlist of candidate variables for each logistic regression model

| Variable | breeders vs. non-breeders | | successful vs. unsuccessful breeding attempts | |
|---|---|---|---|---|
| | Model 1A | Model 1B | Model 2A | Model 2B |
| Nest type | | | + | + |
| Old/new nest | + | + | + | + |
| Nearest-neighbour distance | + | + | + | + |
| Outcome of previous brood | | | + | + |
| IHI index | + | + | + | + |
| Mortality rate | + | + | + | + |
| Soil softness | | + | | + |
| Grass height | | + | | + |
| Mole-rat index | | + | | + |

**Table 2:** Breeding rates, breeding success and productivity of Augur Buzzards at southern Lake Naivasha over the study period

| Site | Breeding rate[1] (se) | | | Mean (se) | p value* |
|---|---|---|---|---|---|
| | 1995 | 1996 | 1997 | | |
| Hell's Gate | 0.80 (0.25) | 0.73 (0.30) | 0.55 (0.21) | 0.69 (0.15) | > 0.05 |
| Mundui | 1.00 (0.00) | 1.40 (0.25) | 1.00 (0.00) | 1.13 (0.09) | > 0.05 |
| Sulmac-Oserian | 1.11 (0.20) | 1.15 (0.22) | 0.86 (0.18) | 1.03 (0.12) | > 0.05 |
| | Breeding success[2] (se) | | | | |
| Hell's Gate | 0.67 (0.17) | 0.70 (0.30) | 0.80 (0.20) | 0.72 (0.12) | > 0.05 |
| Mundui | 1.25 (0.25) | 1.40 (0.19) | 1.43 (0.20) | 1.38 (0.12) | > 0.05 |
| Sulmac-Oserian | 0.88 (0.21) | 0.96 (0.24) | 0.70 (0.15) | 0.85 (0.18) | > 0.05 |
| | Productivity[3] (se) | | | | |
| Hell's Gate | 0.50 (0.17) | 0.46 (0.28) | 0.46(0.21) | 0.47 (0.13) | > 0.05 |
| Mundui | 1.25 (0.25) | 2.00 (0.45) | 1.43 (0.20) | 1.56 (0.18) | > 0.05 |
| Sulmac-Oserian | 0.89 (0.20) | 0.92 (0.24) | 0.57 (0.17) | 0.78 (0.12) | > 0.05 |

*p value refers to a test of differences amongst years
[1]number of breeding attempts per pair per year
[2]number of successful chicks fledged per breeding attempt per year
[3]number of successful chicks fledged per pair per site

**Table 3:** Correlation coefficients for habitat and competition variables measured at 34 augur buzzard territories in the southern Lake Naivasha area, 1997

| | HII | NND | MR | SS | GH | MRA |
|---|---|---|---|---|---|---|
| IHI | 1.00 | 0.32 | 0.59** | -0.05 | -0.27 | -0.06 |
| NND | | 1.00 | -0.13 | -0.46** | -0.33 | -0.60** |
| MR | | | 1.00 | 0.10 | -0.39** | -0.10 |
| SS | | | | 1.00 | 0.35* | 0.82** |
| GH | | | | | 1.00 | 0.53** |
| MRA | | | | | | 1.00 |

**Note:** Variables measured were HII index, nearest-neighbour distance (NND), mortality rate (MR), soil softness (SS), grass height (GH) and mole-rat availability (MRA). Significant correlations are indicated as follows *, $p < 0.05$, **, $p < 0.01$, $n = 34$ territories (25 breeding and 9 non-breeding pairs).

**Table 4:** Correlation coefficients for habitat and competition variables measured at 25 augur buzzard nests in the southern Lake Naivasha area, 1997

| | HII | NND | MR | SS | GH | MRA |
|---|---|---|---|---|---|---|
| IHI | 1.00 | 0.45* | 0.64** | -0.27 | -0.51** | -0.35 |
| NND | | 1.00 | -0.01 | -0.40* | -0.42* | -0.67** |
| MR | | | 1.00 | -0.20 | -0.45* | 0.02 |
| SS | | | | 1.00 | 0.29 | 0.82** |
| GH | | | | | 1.00 | 0.42* |
| MRA | | | | | | 1.00 |

**Note:** Variables measured were HII index, nearest-neighbour distance (NND), mortality rate (MR), soil softness (SS), grass height (GH) and mole-rat availability (MRA). Significant correlations are indicated as follows *, $p < 0.05$, **, $p < 0.01$, $n = 25$ nesting pairs (20 successful, 5 unsuccessful)

**Table 5:** Summary of univariate results of 9 explanatory variables and their relationship to 1) breeding vs. non-breeding pairs; and 2) successful vs. unsuccessful breeding attempts.

| Variable | breeders vs. non-breeders p value | successful vs. unsuccessful p value |
|---|---|---|
| Nest type | - | 0.339 |
| Old/new nest | - | 0.294 |
| Previous brood | - | **0.001** |
| IHI | **0.130** | 0.266 |
| NND | **0.234** | **0.186** |
| MR | 0.424 | **0.0001** |
| SS | **0.112** | 0.924 |
| GH | **0.026** | **0.040** |
| MRA | **0.041** | 0.704 |

**Table 6:** Multiple logistic regression models predicting the probabilities of an Augur Buzzard pair a) attempting to breed (models 1A and 1B) and b) breeding successfully (Models 2A and 2B)

| Model Type | Model Variable | B | se | Wald $\chi^2$ | p value |
|---|---|---|---|---|---|
| Breeders vs non-breeders | | | | | |
| 1A | none | - | - | - | - |
| 1B | grass height | 1.11 | 0.57 | 3.86 | **0.0495** |
| | constant | -0.91 | 0.93 | 0.96 | 0.3274 |
| Successful vs. unsuccessful | | | | | |
| 2A | mortality rate | 17.18 | 6.27 | 7.52 | **0.0061** |
| | previous brood | -1.89 | 0.88 | 4.64 | **0.0313** |
| | constant | 3.63 | 0.94 | 14.82 | **0.0001** |
| 2B | mortality rate | -18.66 | 10.67 | 3.06 | **0.0802** |
| | previous brood | -2.76 | 1.55 | 3.17 | **0.0749** |
| | constant | 4.32 | 1.78 | 5.93 | **0.0149** |

NB: Significance level set at 0.1