The breeding ecology and behaviour of the augur buzzard *Buteo augur* in relation to different land-uses in the southern Lake Naivasha area, Kenya

A thesis submitted for the degree of Doctor of Philosophy at the University of Leicester (U.K.)

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Dedicated to Velia Carn and the memory of Leslie Brown, whose spirit still gracefully soars across the African plains

"..........*the augur buzzard is one of my favourite birds and I hope to make a fuller study of it in the future*"   Leslie Brown (1970)

Abstract

The breeding ecology and behaviour of the augur buzzard *Buteo augur* in relation to different land-uses in the southern Lake Naivasha area, Kenya

Munir Z. Virani

A comparative study of the breeding ecology and behaviour of the augur buzzard *Buteo augur* was made between 1995 and 1998 in the southern Lake Naivasha area, Kenya. Populations in Hell's Gate National Park (Hell's Gate) a protected area, and two other locations (both modified by humans) within the Lake Naivasha environs - Mundui and Sulmac-Oserian were compared. The main aspects studied were nesting density, nest-site selection, breeding behaviour, diet, hunting success, prey availability, breeding seasonality and breeding performance. The methods used were nest searches, augur buzzard ringing, nest and foraging observations, pellet and prey remains collection and analyses, transect counts to determine prey availability, nest site habitat data collection and recording the outcome of active nests.

Mundui had the highest density of augur buzzards at 0.83 pairs per km^2 compared to Hell's Gate (0.28 pairs per km^2) and Sulmac-Oserian (0.23 pairs per km^2). Augur buzzard pairs were more widely spaced in areas where human impacts had increased. Augur buzzards nested mainly in cliffs (in Hell's Gate) or trees (partly in Hell's Gate, exclusively elsewhere). In Mundui and Sulmac, augur buzzards selected mature, large canopied *Acacia xanthophloea* as nest trees while in Hell's Gate and Oserian, mature *Euphorbia magnicapsular* trees that grew on the steepest slopes were selected.

Augur buzzard pairs in the lake environs spent more time caring for chicks than their counterparts in Hell's Gate. This was shown by increased maternal care and paternal foraging which resulted in larger broods and more prey deliveries to nests respectively. The factors responsible for these were an abundant food supply coupled with reduced predation pressure and inter/intra-specific interactions. Augur buzzards in Hell's Gate exploited a broader range of prey, while those in the lake environs specialised on rodents, particularly mole-rats. Vegetation cover (mainly grasses) influenced mole-rat availability. In Hell's Gate, the availability of mole-rats also increased when temperatures were cooler. Augur buzzards in Hell's Gate made significantly more hunting attempts than those in the lake environs.

Augur buzzard breeding patterns at all sites were governed by rainfall, which in turn influenced vegetation cover, and consequently prey density and availability. Egg-laying occurred between April and September (with peaks between May and July) and appeared to be related to peaks in prey abundance. Augur buzzards in Mundui had the highest breeding success compared to Sulmac-Oserian and Hell's Gate (the lowest). High breeding success at Mundui was attributed to high mole-rat densities, availability of nest sites, reduced predation pressure and low human interference. Low breeding success in Hell's Gate was attributed to high predation pressure, a more limited food supply and overgrazed grasslands. Adult mortalities were highest in Sulmac-Oserian as a result of human persecution. The breeding success of augur buzzards was influenced by mortality of adults and the outcome of previous breeding attempts. The mean expectation of further life of augur buzzards in the southern Lake Naivasha area was estimated as 13 years, while juvenile survival was estimated to be 21.5%.

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CHAPTER ONE

INTRODUCTION

1.1 INTRODUCTION

Throughout the world, bird conservation problems are tied to pressing issues of human development (Fanshawe and Bennun, 1991), and habitat degradation emerges as the major threat (Brandl *et al.*, 1985; Schmutz, 1989; Thiollay, 1992; Sorley and Andersen, 1994). Raptors are a particularly vulnerable group because of their specific ecological requirements. Raptors are relatively bigger, have larger home ranges and occupy higher positions at the top of the food chain compared to most other avian groups. The numbers of raptors in Africa have declined dramatically and the ranges of others are now much reduced (Harrisson *et al.*, 1998). Eighteen birds of prey species are listed in the South African Red Data Book of Birds (Pickford and Tarboton, 1989). This is disproportionately high – whereas raptors comprise only 9% of the avifauna, they make up 17% of the threatened species (Pickford and Tarboton, 1989). Survival of most species depend on their abilities to adapt to and persist in highly modified environments, or on mankind's capacity to establish and maintain protected areas of sufficient size and quality to preserve self-sustaining populations (Burnham *et al.*, 1992). The conservation challenge therefore lies in identifying the threatened species, unravelling the causes of the problems facing them and implementing effective action before it is too late.

Habitat degradation has had impacts on raptor habitat use and hence abundance (Sorley and Andersen 1994). This may be through direct changes in habitat characteristics for example perch density and distribution (Enderson, 1964; Marion and Ryder, 1975; Stahlecker, 1978; Janes, 1984) or indirectly through impacts on prey abundance and availability (Baker and Brooks, 1981). Increased human density has increased the potential for direct persecution (Keran, 1981; Brown, 1991) with resulting changes in behaviour (Knight *et al.*, 1989) and species abundance and richness (Craighead and Mindell, 1981). Environmental contaminants associated with human settlements have also influenced raptor abundance and distribution (Newton, 1979; Richardson and Miller, 1997).

Kenya's problems include all these, yet the country possesses one of the richest and most diverse avifaunas in Africa. This reflects the country's varied habitats and the fact that it lies at the intersection of several biogeographic zones (Fanshawe and Bennun, 1991). Seventy-five diurnal raptors and 16 nocturnal owls have been recorded, making up roughly 20% of the world's raptor species (Britton, 1980; Brown *et al.*, 1982; Fry *et al.*, 1988; Virani and Watson, 1998). However, human population growth combined with increased urbanisation and industrialisation in the country have resulted in rapid alteration and degradation of habitats (Fanshawe and Bennun, 1991). Natural vegetation is often replaced by small and large scale agriculture, horticulture, grazing or shifting cultivation, all of which are not only a threat to the continued existence of Kenya's diverse ecosystems, but also to their biotic and genetic diversity, much of which is yet to be scientifically documented (Mwaura and Moore, 1991). Human-caused habitat alteration has had a profound impact on raptor abundance and richness. For example, a study in south-central Kenya showed that differences in land-use practices between undisturbed and man-altered habitats were directly responsible for significant changes in raptor community structure (species richness and density) (Sorley and Andersen, 1994). The population of African fish eagles *Haliaeetus vocifer* at Lake Naivasha has declined by over 50% since 1969 as a result of increasing human pressure (Virani and Harper, 1998). Riparian forests have been cleared for horticulture and livestock rearing, whilst depletion of fish stocks due to over-fishing has severely reduced fish eagle breeding success (Virani and Harper, 1998).

Sorley and Andersen (1994) had stressed the need for an urgent study to determine the contribution of various factors related to land-use practices that influence raptor distribution and abundance in East Africa; in particular factors contributing to the decline of previously common road-side raptors such as augur buzzards *Buteo augur*, black-shouldered kites *Elanus caeruleus* and long-crested eagles *Lophaetus occipitalis*. All three species occur in the Lake Naivasha region of Kenya where, over its northern catchment boundary with Lake Elementeita, natural vegetation losses as high as 60% have been attributed to rapidly changing land-use patterns combined with human population growth rates of 5.7% per annum (Mwaura and Moore, 1991). In the southern Lake Naivasha area, horticultural intensification and human settlement has replaced 35%

of the natural vegetation (Becht, in prep.). The remaining natural and semi-natural areas are under threat from further clearance by humans and from grazing by domestic livestock. These changes may have profound impacts on the behaviour and ecology of raptors in the area. One raptor in particular, the augur buzzard (Plate 1.1), was known to inhabit a wide variety of habitats ranging from savanna grasslands and *Acacia* woodlands to areas modified by intensive agriculture and pastoral grazing (Fry *et al.*, 1988). This study was conceived to compare and contrast the ecology of the augur buzzard in the southern Lake Naivasha area, in relation to different land-use practices.

Plate 1.1: Augur buzzard *Buteo augur*.

1.2 WILDLIFE AND LAND-USE PRACTICES IN KENYA

Kenya has one of the highest remaining concentrations of tropical savanna wildlife in the world. It has been recognised by the state and the international community as a "unique world heritage" which should be preserved for posterity (Akama *et al.*, 1996). Kenya also has the highest annual human population growth rate in the world (c. 4%). Nearly 88% of Kenya's human population is directly dependent on rain-fed agriculture (IUCN, 1992). Furthermore, small-scale subsistence agriculture and livestock grazing is the most prevalent land-use throughout much of Kenya (Sorley and Andersen, 1994). The high annual human population growth rate, combined with limited land availability in the

agriculturally productive highlands, has resulted in immigration to marginal areas. In some parts of Kenya, such as the Rift Valley (where Lake Naivasha is located), the population growth rates are 2 to 10 times the country's average resulting in the land exceeding its carrying capacity (Sutherland *et al.*, 1991). In Naivasha division, the human population almost trebled between the period 1979 to 1997 (Ministry of Planning and National Development, 1997) (Figure 1.1).

Land-use interests in Kenya, such as agriculture, tourism, ranching, wildlife management, forestry and water conservation - each of them valid and nationally productive usages of land - are in competition and often in conflict over large areas of the country. Not only are various arms of the Government in disagreement or confusion on these issues, but this is compounded by the demands of a burgeoning population, which
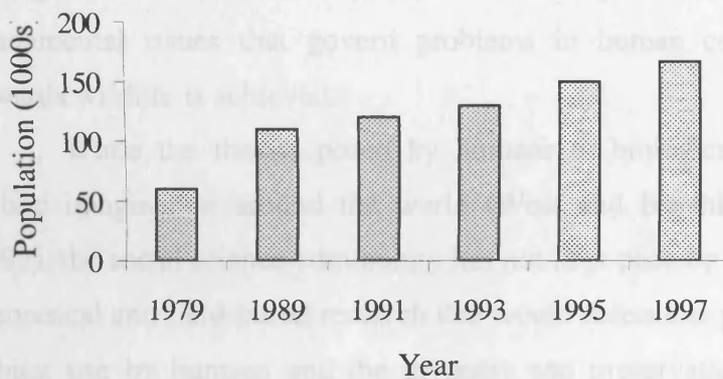
Figure 1.1: Human population growth trend in Naivasha division from 1979 to 1997 (source: Ministry of Planning and National Development, Nakuru, Kenya)

are haphazardly realised in the absence of clear land-use policies (Berry, 1993). This lack of land-use policy has clearly affected the country's wildlife resources. For example between the period from 1920 to 1970, this resource had, as a direct result of increasing human pressure, been seriously depleted by as much as 50% (KNR, 1972). Conflicts in land-use and threats to the wildlife resource and/or its habitat were attributed as the principal causes (KNR, 1972). Although only 8% of the land in Kenya has been designated in the form of protected national parks, the majority of wildlife was formerly found outside these areas. Since 1977, when hunting was made illegal, at least 40% of the range animals have disappeared from Kenya's savannas – a drop of at least 412,000

animals (McKinley, 1998). Wildlife outside designated game parks and reserves is dwindling and present estimates of these disappearances stand at between 2 and 3% per year (McKinley, 1998).

Wildlife conservation efforts of the Kenya government confront complex and often persistent social, political and ecological problems. These include land-use conflicts between the local people and wildlife, local peoples' suspicions and hostilities toward state policies of wildlife conservation, and accelerated destruction of wildlife habitats (Akama et al., 1996). By formulating a political-ecology framework in the analysis of the social factors of wildlife conservation in Kenya, Akama et al. (1996) postulated that the overriding issues impacting wildlife conservation were increasing levels of poverty, famine and malnutrition. The conservation of Kenya's wildlife depends on social and ecological solutions to these problems. This may be realized if an understanding of the fundamental issues that govern problems in human communities and their attitude towards wildlife is achieved.

While the threats posed by humans to biological diversity have captured the public imagination around the world (West and Brechin, 1991; Wells and Brandon, 1992), the social science community has not kept pace by providing the kind of in-depth, theoretical and field-based research that would determine plausible relationships between habitat use by humans and the diversity and preservation of the environment (Little, 1996). Understanding the ecological requirements of key indicator species that are sensitive to habitat change can bring about effective community-wildlife and land-use policies based on sound conservation principles.

1.3 RAPTORS AS CONSERVATION TOOLS

The concept of using organisms, especially plants, as indicators of environmental factors has been widely accepted by ecologists as scientific doctrine. However, Morrison (1986) has described the use of birds as direct indicators of specific environmental changes as tenuous at best. He concluded that although birds certainly respond to change, they seldom respond in distinctly different ways to specific changes. The problem with using

birds as indicators is separating the myriad of factors that can cause changes in bird populations. The use of birds as 'conservation tools" is thus a far more appropriate term than 'indicator'. This is because an understanding of the functional and ecological responses of birds to natural and/or anthropogenic effects can help in formulating management and conservation guidelines to maintain ecosystem health and conserve those under threat (especially in third world countries).

Raptor studies have been used as effective tools for conservation in a number of projects around the world (e.g. peregrine falcon *Falco peregrinus* - USA; Mauritius kestrel *Falco punctatus* - Mauritius; Madagascar fish eagle *Haliaaetus vociferoides* - Madagascar) (Burnham *et al.*, 1992). Firstly, because raptors have large area requirements and low densities, they play the role of "umbrella species". This is based on the concept that any protected area encompassing viable raptor populations or complete communities, protects sufficient habitat and populations of most, if not all, other species in the food web below (Thiollay, 1992). Secondly, since raptors occupy top positions in terrestrial and aquatic food webs, they may be used as indicators to detect pesticides and other contaminants (Newton, 1979), and serve as a measure of man's impact on landscape patterns (Reichholf, 1974). Many studies have used organisms as information systems for underlying landscape to determine the influences of bio-geographical variables on the spatial and temporal distributions of species (Muller, 1981). Finally, raptors are popular, charismatic organisms representing our natural world, and several have become significant 'flagships' for conservation arousing public interest and supporting wider conservation programmes (Burnham *et al.*, 1992; Thiollay, 1992). The Philippine Eagle Project is an example of how a 'flagship' raptor can be used in a broader habitat conservation and land use management scheme (Thiollay, 1992). In Kenya, the Sokoke scops owl *Otus ireneae* has become a flagship species of the Arabuko-Sokoke forest, and its existence (alongside other Red Data Book birds) has provided the stimulus to conserve the forest (Fanshawe, 1993; Virani, 1995).

1.4 THE IMPORTANCE OF RAPTOR STUDIES IN KENYA

Virani and Watson (1998) reviewed four main factors that affect raptor density and diversity in the east African tropics, as a result of changes in habitat that accompany human-land use pressures:

- overgrazing by domestic livestock resulting in the alteration of original vegetation cover, potentially affecting prey abundance and distribution (Sorley and Andersen, 1994);

- impact of cultivation that completely replaces native vegetation and involves the use of pesticides and fertilizers potentially toxic to raptors and other vertebrates (Sorley and Andersen, 1994);

- human hunting pressure that diminishes prey populations (Sorley and Anderson, 1994); and

- direct human persecution (Keran, 1981) with resulting changes in behaviour (Knight *et al.*, 1989), species abundance and diversity (Craighead and Mindell, 1981), and indirect persecution through secondary poisoning (Thomsett pers. comm.).

The extent of negative impact resulting from habitat alteration varies according to different ecological requirements of different raptor species (Brown 1980).

Finding effective solutions to the threats posed to raptors requires a sound understanding of the factors that influence their ecology and behaviour. Prior to 1980, the late Leslie Brown published almost a quarter of all that is written about raptors in Africa (Virani & Watson 1998) and thus provided a solid framework to build on for the future. The majority of his fieldwork was conducted in Kenya, and his classical studies on the African fish eagle *Haliaeetus vocifer* at Lake Naivasha (Brown and Hopcraft, 1973; Brown, 1980; Brown and Britton, 1980) and the eagles of Embu Hill (Brown, 1952-53; Brown, 1955; Brown 1970) are still widely referred to. Sadly, after his death in 1980, interest in raptor biology in Kenya came to a virtual halt save for a handful of enthusiasts who continued watching and enjoying Kenya's raptors. Small-scale raptor studies were conducted intermittently by overseas researchers. Some examples were census studies on the African fish eagle (Cambridge University Expedition, 1979; Reading University

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Expedition, 1986; Smart, 1991), distribution and density surveys of the Sokoke scops owl *Otus ireneae* (Kelsey and Langton, 1984) and pesticide studies on raptors (Lincer *et al.*, 1981). These studies were short, spanning a few days, or were part of an overall expedition focussing more on other aspects such as vegetation analysis and species counts. There was still an urgent need for a focused, more co-ordinated study on individual raptor species threatened by anthropogenic impacts.

In the East African region, information obtained from ecologically-based raptor studies can be used to achieve conservation goals. For example, a study on the ecology of raptors in the Impenetrable Forest in Uganda provided vital information on seven raptor species, and in consequence, aided in the formulation of a management plan for the forest (Muhweezi, 1990). In order to achieve conservation using raptors as indicators of good ecological health, knowledge about their basic ecology is vital. However, there is a large gap in the knowledge of the basic ecology of most raptors in the East African region. In a survey on the state of ecological knowledge and conservation status of raptors in Africa, almost 61% of raptors were rated as poorly understood in aspects of distribution, population dynamics, breeding biology and feeding ecology (Virani and Watson, 1998). Almost 40% of all the breeding raptors that occur in the East African region (n = 79) have been listed as either Endangered (1), Vulnerable (14) or Near Threatened (15) (Bennun and Njoroge, 1996). Thus a lack of sufficient knowledge about the basic biology of East African raptors, coupled with their high local conservation importance, has fuelled the need to better understand the basic ecological requirements of key raptor species. Raptor studies are thus an ideal tool to focus on conservation strategies especially in areas prone to changes in habitat, both naturally and anthropogenic (Reichholf, 1974; Watson, 1991; Thiollay, 1992; Burnham *et al.*, 1992; Virani and Watson, 1998).

1.5 WHY AUGUR BUZZARDS?

There are usually two approaches to conservation studies. The first focuses on a threatened species because of intrinsic conservation concern – but because they are threatened, such studies may shed little light on underlying ecological processes

(especially in raptors). The second approach focuses on a more abundant species that show similar but less marked responses to land-use changes in order to understand the processes at work. This augur buzzard study falls into the latter category.

The main reason for selecting the augur buzzard is that it is widespread in the Naivasha area and has been considered adaptable to habitat changes (Fry *et al.*, 1988). This makes it an ideal study subject to detect the influence of land-use changes and consequently understand the reasons for any ecological responses observed. Other reasons for choosing the augur buzzard are:-

- Little is known about the behaviour and ecology of the Kenyan population.

- Few studies have been conducted on the augur buzzard. The first was in the Matopos Hills, in Zimbabwe, which focused on the bird's breeding biology, its interspecific relationships and population density (Lendrum, 1979). The second was a general ecological study of raptors in and around the Impenetrable Forest of Uganda (Muhweezi, 1990).

- Augur buzzard numbers are believed to be on the decline in areas of intensive land-use practices (Thomsett, 1988; Sorley and Andersen, 1994; Cunningham van Someren, pers. comm.).

- Individual birds can be easily distinguished as clear differences occur in plumage patterns and colour morphs (Steyn, 1982).

1.5.1 Distribution and status

Williams and Arlott (1980) considered the augur buzzard as one of East Africa's most frequently seen birds of prey. They found it common in the East African highlands where it inhabits open moorland country, mountains, forest glades, inland cliffs, and cultivation areas. Its distribution in Kenya ranges from the shores of Lake Victoria, across the eastern Rift Valley into the Tsavo plains before veering south into Tanzania, but it is rarely found at the coast (Lewis and Pomeroy, 1989).

Little information exists about the biology and ecology of the augur buzzard. The late Leslie Brown described the augur buzzard as one of his favourite birds and had hoped to make a fuller study of it. The bird was neglected perhaps because it seemed

abundant at the time (Brown, 1970). The augur buzzard is characterised as a common and locally abundant raptor (Fry *et al.*, 1988). It has also been portrayed as a species that is well adapted to cultivated land and dense human habitation (Fry *et al.*, 1988; Muhweezi, 1990). Whilst the augur buzzard is today relatively conspicuous and abundant, its numbers were higher in the past (Thomsett, 1988; Sorley and Andersen, 1994; Cunningham van Someren, pers. comm.). Between 1968 and 1972, road counts conducted along the Nairobi-Naivasha road yielded one augur buzzard every 5 km (Cunningham van Someren, pers. comm.), while road counts conducted along the same road between 1994 and 1997 have yielded one augur buzzard every 30 km (Thomsett, pers. comm; Virani, pers. obs.). Between 1965 and 1967, Brown (1970) found marked differences in the numbers of augur buzzards between areas of plains/thornbush (1 augur buzzard every 21 km) and areas of cultivated/inhabited lands (1 augur buzzard every 37 km). These differences, along with information on their general biology (diet and breeding success), need to be more accurately measured to determine the bird's present status in areas where changing land-use practices threaten its survival as well as that of other co-existing raptors. In the central highlands, augur buzzard numbers differed by a ratio of 24 to 1 between adjacent habitats of different land-use (Thomsett, 1988), while in Lukenya and Athi river, the difference was 3 to 1 (Sorley and Andersen, 1994). In Brown's study of the raptors of the Eagle Hill area in Embu, he noted a marked decline in the number of augur buzzards and attributed this to human population pressure (Brown, 1966).

1.6 AUGUR BUZZARD BIOLOGY

In mainland Africa, 8 species of buzzards (true *Buteo* spp) occur. Two of these, the Eurasian buzzard *Buteo buteo* and long-legged buzzard *B. rufinus*, are winter migrants, while the remaining 6 are African residents and intra-African migrants (Table 1.1).

Table 1.1: Summary of distribution and status of 8 *Buteo* sp. occurring in mainland Africa (from Del Hoyo *et al.*, 1994)

Buteo sp.	Distribution in mainland Africa	Status
Eurasian buzzard *Buteo buteo*	migratory; wintering along east and south-east Africa.	very common, not threatened
red-necked buzzard *B. auguralis*	intra-African migrant; west-Africa to Ethiopia and Guinea-Congo.	vulnerable to degradation of woodland
mountain buzzard *B. oreophilus*	resident in E. Africa; highlands of Ethiopia, S to Tanzania and Malawi.	vulnerable due to limited and patchy distribution of habitat
forest buzzard *B. trizonatus*	resident endemic to South Africa - Drakensberg to N. Transvaal.	range expanding as it adapts to alien plantations
long-legged buzzard *B. rufinus*	migratory; mainly north and north-east Africa.	little known
augur buzzard *B. augur*	resident; Ethiopia S to Zimbabwe W to S Angola and N and C Namibia.	vulnerable to changes in grasslands through overgrazing
Archer's buzzard *B. archeri*	endemic to the highlands of N Somalia.	status uncertain; vulnerable due to restricted range
jackal buzzard *B. rufofuscus*	southern Africa including S and C Namibia, S Botswana, and S Mozambique.	common, not threatened

The augur buzzard is considered to form a superspecies with Archer's buzzard *B. archeri* and the jackal buzzard *B. rufofuscus* (Brooke, 1975). Some authorities consider all three as conspecific (Del Hoyo *et al.*, 1994). In Africa, the augur buzzards' distribution ranges mainly from Ethiopia to southern Zimbabwe, while a disjunct

population exists in northern and central Namibia (Del Hoyo *et al.*, 1994) (Figure 1.2). The augur buzzard differs in calls and colouration, showing disjunct distribution and limited overlap with the range of the jackal buzzard in central Namibia where the two are believed to hybridize (R. Simmons, pers comm.). Within East Africa, 10 - 25% of the augur buzzard population comprise a melanistic morph especially in areas associated with higher rainfall (Lewis and Pomeroy, 1989). Females are similar but larger and typically have more extensive markings on their throats (Steyn, 1982).
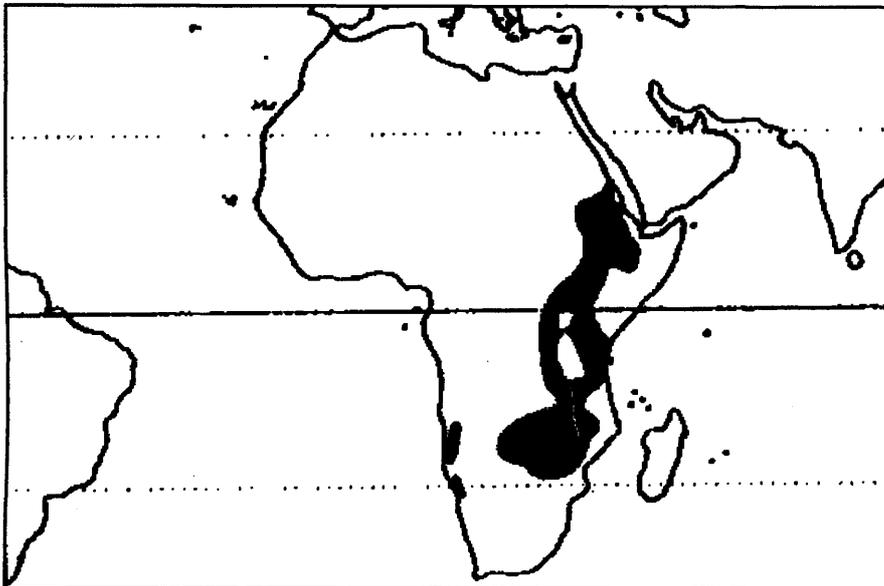
Figure 1.2: Distribution of augur buzzards in Africa (from Del Hoyo *et al.*, 1994).

The augur buzzard's habitat ranges from mountainous and hilly country covered in forest patches, open woodland savannas and grasslands, to over 5000 m around the peaks of Mount Kenya (Lewis and Pomeroy, 1989), including some isolated hills in otherwise flat terrain (Del Hoyo *et al.*, 1994). Augur buzzard pairs are intensely territorial, maintaining discrete territories regularly used by a long succession of different adults for up to 30 years or more (Fry *et al.*, 1988). Pairs remain year-round in their territory, defending it not only against other augur buzzards, but against other larger raptors such as Verreaux's eagles *Aquila verreauxii* (Fry *et al.*, 1988). In suitable habitat in the Impenetrable Forest, Muhweezi (1990) found nests of adjacent augur buzzard pairs

spaced approximately 1 km apart, while Lendrum (1979) estimated that each pair in the Matopos hills occupied an area of 17 km^2. The augur buzzard is considered a generalist feeder, its diet consisting of lizards, snakes, rodents and mole-rats *Tachyorectes splendens*, together with some small birds, insects and carrion (Del Hoyo *et al.*, 1994). It hunts mainly from a rock or tree perch, sometimes from soaring, hovering or gliding flight, rarely while walking about on the ground. It hunts both within forest or woodland, and over open habitats (Del Hoyo *et al.*, 1994).

Evidence obtained from nest-record cards suggested that the augur buzzard in East Africa breeds over all months but peak egg-laying occurs between June and September (Britton and Brown, 1980). Pairs have spectacular aerial flights and calling displays. Nests are built in a tree, or on a cliff ledge, or on a tree protruding from a cliff. Usually 2 (sometimes 3) eggs are laid (Lendrum, 1979). The incubation period is about 39-40 days while the nestling period is approximately between 48-55 days (Lendrum, 1979). Sibling rivalry is very common and there are no records of two young being reared together (Steyn, 1982). Breeding success in the Matopos hills between 1966 and 1977 was estimated at 0.62 chicks/pair/year (Lendrum, 1979).

In East Africa, the augur buzzard is considered vulnerable to extensive afforestation of grassland habitat, or to lowered carrying capacity through overgrazing (Muhweezi, 1990). However, it adapts well to human settlement and extends onto grasslands using small exotic plantations for nesting and roosting (Del Hoyo *et al.*, 1994). There is no evidence to suggest that pesticides have affected the species.

1.7 AIMS AND HYPOTHESES

1.7.1 Overall aim

The overall aim of the study was to determine how the ecology of the augur buzzard varied in three locations each with different land-uses within the southern Lake Naivasha area. The three different land-use areas were:

- Hell's Gate National Park (Hell's Gate) – a protected area consisting of a gorge with savanna grasslands and steep rocky cliffs, low human impact and moderate to extreme wildlife grazing;

- Mundui – a privately owned area consisting of open canopy *Acacia xanthophloea* woodland pastures, low human settlement and moderate wildlife/domestic grazing;

- Sulmac-Oserian – an area consisting of moderate to extreme levels of horticultural activity, human settlement and pastoral grazing.

The key ecological components compared in the different augur buzzard populations were their:

- nesting density and nest-site selection;
- breeding behaviour;
- diet and hunting behaviour;
- prey availability;
- breeding seasonality;
- breeding performance;

1.7.2 Null hypotheses

Based on the aims given above, the following null hypotheses were tested:

- there is no difference in the nesting density of augur buzzard pairs between populations in different land-use areas;

- nest-site selection is not influenced by habitat variables between augur buzzard populations in different land-use areas;

- there are no differences in the breeding behaviour of augur buzzards between populations in Hell's gate and the lake environs;

- there are no differences in the diet and hunting success of augur buzzards between populations in Hell's Gate and the lake environs;

- there is no difference in the amount of available prey to augur buzzards between populations in different land-use areas;

- the timing of egg-laying in augur buzzards is not correlated with environmental factors in different land-use areas;

- there is no difference in the breeding success between augur buzzard populations in different land-use areas;

- there is no relationship between breeding success and natural or anthropogenic factors in different land-use areas;

- there is no difference in mortality rates between augur buzzard populations in different land-use areas;

- there is no relationship between mortality rates and natural or anthropogenic factors in different land-use areas.

CHAPTER TWO

FACTORS INFLUENCING THE ECOLOGY OF RAPTORS

2.1 INTRODUCTION

This chapter reviews some of the factors that influence the ecology and behaviour of raptors with particular reference to buzzards (true *Buteo* spp). Comparatively little information exists about the ecology of tropical raptors as the majority of studies have been conducted on temperate species. Hence some factors such as day length and temperature may or may not bear any relevance to the ecology of the augur buzzard.

2.2 BREEDING DENSITY AND NEST-SITE SELECTION

As top predators, raptors may be sensitive indicators of the health of tropical ecosystems (Robinson and Wilcove, 1989). Rapidly changing land-use patterns in tropical countries have the potential to reduce the availability of suitable nesting sites for breeding raptors. One way to evaluate the impacts of limited nest sites in an area is to measure parameters such as breeding density and factors that influence nest-site selection (Berkelman, 1994). Studies in tropical countries such as French Guiana (Thiollay, 1989) and Guatemala (Whitacre and Thorstrom, 1992) have proposed using data on the nesting ecology of breeding raptors to design and manage protected areas. In the context of the augur buzzard study, knowledge about their nest-spacing and preference for particular nest-sites over others may provide information about their sensitivity to altered habitats and hence implications for habitat conservation.

2.2.1 Breeding density

The breeding densities of birds are limited by two main resources; food and nest-sites (Newton, 1994). Detailed studies of both these components are vital for understanding the ecological requirements of raptors in different habitats. However, the numbers of breeding raptors can also be limited to a lesser extent by natural enemies such as

predators (including man) and parasites (Newton, 1994). The evidence for a link between density and food in areas where nest-sites are not limiting is circumstantial (Newton, 1979). This is based on studies conducted on raptor body size, regional and annual variations in raptor breeding density, and long term changes in breeding density associated with changes in prey base (Newton, 1979). In many raptors, the more or less regular spacing of nests is well documented (Newton, 1979) and is generally taken as an indicator of territorial behaviour by which breeding populations are dispersed fairly evenly throughout suitable habitat (Dare and Barry, 1990). The degree of dispersion is usually quantified from nearest-neighbour distance between occupied nests. For example, in Scotland, the mean nearest-neighbour distances of common buzzard nests was 1.9 km. This distance was negatively correlated with abundance indices of their main prey, rabbits *Oryctolagus cuniculus* (Graham *et al.*, 1995). The modification of a raptor's natural habitat can influence its prey and nesting behaviour. In south-eastern Alberta, the abundance of ferruginous hawks *B. regalis* was limited by the availability of grassland habitat (Schmutz, 1984), while in California, population densities of Swainson's hawks *B. swainsoni* were limited by the availability of grasslands, riparian habitat and annual field crops (Smallwood, 1995).

Apart from studies on the African fish eagle, there have been no further documented studies on the distribution of terrestrial raptors in East Africa since Smeenk's (1974) work on the eagles in Tsavo East National Park (the distribution of African fish eagles at Lake Naivasha [Brown and Hopcraft, 1973; Brown, 1980, Virani and Harper, *in litt.*] and in the Kazinga Channel, Uganda [Sumba, 1988] have been well documented). Information about the distribution of augur buzzards in the southern Lake Naivasha area will provide a platform on which future studies can be based - for example to detect long-term changes in population density and territory shifts.

2.2.2 Nest-site selection

Raptors are among the few groups of birds whose numbers and nest success are in some regions clearly limited by the availability of suitable nesting places (Newton, 1979). The study of raptor habitat requirements, especially factors influencing nest-site selection,

have been useful in designing management and conservation plans for species at risk from rapidly changing land use patterns (Berkelman, 1994). Such studies are more valuable for species with specific habitat requirements; e.g. those dependent on forests or wetlands. There is often considerable intra-specific variability in the nest site characteristics of a given bird species. The choice of atypical nest sites may be reflected in the individuals' nesting success through such mechanisms as increased predation (Evans, 1978), ultimately influencing the evolution of nest placement within a species (Rich, 1980). The selection of nest-sites may involve a host of rather specific concerns ranging from local factors such as the thermal environment in the nests to broader factors including but not limited to the proximity of foraging areas (Cody, 1985). The range of nesting places that a species uses is influenced mainly by whether it can build a nest for itself, and the kinds of situations it can use; but within this range, choice is influenced by local availability, by on-the-spot competition with other species, by predation pressures, and by local traditions (Newton, 1979).

Despite their abundance in eastern Africa, little is known about many aspects of the biology of augur buzzards. In particular, very little has been published on augur buzzard nest-site selection. Compared to the majority of African raptors, augur buzzards are less specific in their habitats requirements and nest on many substrates, including cliffs (Lendrum, 1979; Gargett, 1979; Steyn, 1982) and trees (Muwheezi, 1990; Del Hoyo et al., 1994). A comparison of their nest-site selection in different land-use types may reveal their functional response and degree of adaptability to changing landscapes.

2.3 BREEDING BEHAVIOUR

Adult bird behaviour during the breeding cycle is geared towards achieving maximum reproductive success. Among raptors, biparental care is obligatory and there are no known cases of individuals successfully incubating or raising a brood entirely in the absence of a partner (Newton, 1979). Typically the male is involved in the reproductive attempt from courtship through to fledgling independence. In most species and among

most pairs, the male is the main or sole provisioner for the breeding attempt, at least until the nestlings are homeothermic.

Natural and anthropogenic factors influence adult breeding behaviour; for example females spend more time defending nests and males increase their hunting effort due to changes in vegetation cover or perch availability. An understanding of the ecological processes that influence changes in breeding behaviour gives a broader perspective when data on overall breeding performance are interpreted. In most raptors, nest attendance by adults occurs 90-100% of the day during the incubation stage and the first days after hatching (Rowe, 1947; Rettig, 1978; Stinson *et al.*, 1988). In some species, the female becomes reluctant to leave the nest shortly before hatching, even at the approach of the male with food (Newton, 1979). In those species in which males contribute to incubation, the female, usually dominant over the male (Carlier and Gallo, 1989; Hubert and Carlier, 1992), does not allow the male to perform incubation during the days immediately preceding and following hatching (Liversidge, 1962; Wiley and Wiley, 1981; Dewhurst *et al.*, 1988; Village, 1990).

Brooding behaviour seems to wane after the nestlings have attained their second down plumage, as suggested in the gyrfalcon *Falco rusticolus* (Jenkins, 1978), or after becoming able to control their own body temperature, as suggested in the Eurasian kestrel *Falco tinnunculus* (Village, 1990). Once the female stops brooding, she spends most of her time in the vicinity of the nest (Wiley and Wiley, 1981). Nest attendance progressively reduces to feeding bouts and finally to food deliveries to the young. In most raptors, the transition between these phases is gradual and can occur on different schedules from nest to nest within the same species (Newton, 1979). Although this nest attendance pattern has been quantitatively described in several species of buzzards (Hubert, 1990; Berkelman, 1994), data on the augur buzzard are mainly descriptive and qualitative (van Someren, 1956; Steyn, 1965; Weaving, 1972; Lendrum, 1979; Muhweezi, 1990).

Most studies of the parental behaviour in raptors implicitly assume that the adults behave in a way to satisfy the nestling's needs (Jenkins, 1978; Village, 1990). For example, adults assist the thermoregulation of their nestlings by brooding or shading when chicks are small (Newton, 1979), whereas the subsequent reduction in female nest

attendance is usually linked with the increasing nutritional requirements of the young. In many species studied, the females do not deliver prey to the nest once they begin to leave the young unbrooded (Matray, 1974; Jenkins, 1978; Wiley and Wiley, 1981). In the Eurasian kestrel, some females were never observed bringing prey to the nest during the nestling stage and attended the nest only during the first week following hatching (Village, 1990). The implication for this augur buzzard study is that different habitats may necessitate different parental behaviours resulting in differences in breeding performance and parental survival.

2.4 DIET AND FORAGING ECOLOGY

Food has long been recognized as a limiting factor in the ecology of birds (Lack, 1954). The amount of food that a raptor requires varies between species and between sexes. Comparison of a raptor's diet across a gradient of different habitats may reveal its sensitivity to the effects of habitat modification. This information can be used to determine the usefulness of raptor diet as a tool for monitoring the impact of changing land-use patterns in habitats surrounding protected areas. More importantly, studies on the diet of raptors describe their functional response to different land-use patterns and their effects on habitat and prey.

The quality and quantity of prey available to raptors plays an important role in influencing breeding performance. Generally, raptors that adapt to a specialist diet in one area are more successful (i.e. more chicks are produced per pair) than their counterparts in another area where a broader spectrum of prey is available. This is believed to be linked to hunting behaviour and has been shown in a study of two populations of golden eagles *Aquila chrysaetos*, one in the eastern and the other in the western highlands of Scotland (Watson, 1998). The ecological response of common buzzards to differences in prey base between different habitats is also well documented (Dare, 1989; Graham *et al.*, 1995; Austin and Houston, 1997). Breeding performance in generalist raptors is reduced because of the need to constantly modify their hunting behaviour in order to catch a diverse range of prey, which may result in reduced hunting efficiency (Watson, 1998).

Another reason that probably contributes to reduce breeding performance is the comparative lack of sufficient prey in a specialist-turned-generalist raptors' optimum size range. This results in an over-dependence on large prey, and consequent inefficiencies when such items are carried to nests.

The foraging behaviour of raptors depends on factors such as size and availability of prey, and effective vantage points to conduct hunting forays (Hammond and Pearson, 1993). Other studies indicate that weather and plant cover also influence raptor foraging (Wakely, 1978; Bechard, 1982; Barnard, 1987; Preston, 1990; Hammond and Pearson, 1993). In cold weather, more food is needed to fuel the body, but less may be available. Wet weather can make hunting difficult, and during the breeding period, this puts pressure on males bringing in food for their mates (during courtship feeding and when females are incubating) and young.

The foraging behaviour of raptors is also influenced by vegetation condition, presence of conspecifics and other competitors, and the behaviour of the prey species (Newton, 1979; Giacchini and Pandolfi, 1992). Marti et al. (1993) found that dietary overlap in raptors with the same daytime activity was significantly greater than for asynchronously-active raptors. In generalist feeders, this can influence foraging behaviour (as well as breeding performance) in areas with greater raptor diversity and abundance. Prey activity influences the time of the day when raptors are most active. For example in Montagu's harriers Circus pygargus in central Italy, the greatest hunting activity occurred between 10h00 and 14h00 with a maximum between 12h00 and 13h00; these times coinciding with peak prey activity (Giacchini and Pandolfi, 1992). The diet and foraging behaviour of various buzzards (especially red-tailed hawks B. jamaicensis and common buzzards B. buteo) have been studied in detail (see Jedrzejewski et al., 1994; Berkelman, 1994; Marti and Kochert, 1995; Graham et al., 1995; Swann and Etheridge, 1995; Alivizatos and Goutner, 1997; Howell and Chapman, 1998). Most of these have studied the relationships between prey availability and its influences on other variables such as nest-spacing and breeding performance (reviewed in later sections). Without sound knowledge about the basic diet of a species, it is impossible to understand the factors that limit its distribution and abundance.

Little information exists about the diet of augur buzzards in Kenya. The few studies that were conducted were mainly done on single nests, and based on pellet analysis (Smeenk, 1974) and prey deliveries at nests (Van Someren, 1956). By analysing the diet of the augur buzzard in the southern Lake Naivasha area, this study aims to describe the functional response of the species in different land-use types and how it affects other ecological processes such as nest-spacing, breeding behaviour and performance.

2.5 PREY AVAILABILITY

The structure of any ecological community is determined by the balance between the availability of water and soil nutrients (Bell, 1982). Primary production is greatest where levels of light, temperature, water and mineral nutrients are all high (Ricklefs, 1979) and is dependent to some extent on soil type, particularly its water, mineral and nutrient retention. Rutherford (1978), in one review of African soil productivity, reported higher primary production on soils with a high clay content while sandy soils had a lower productivity. Differences in soil productivity result in differences in primary production which affects consumers living in various trophic levels of an ecosystem. Areas of high primary productivity positively influence the numbers of primary consumers and hence the performance of secondary consumers.

The importance of food abundance 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 factor influencing 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.

In any study of predators, a sound knowledge of the factors that influence their prey is vital in understanding the ecological dynamics of the predatory species. For example, in the Palava Biosphere Reserve (Czech Republic), the population dynamics of the common buzzard *Buteo buteo* is affected mainly by abundance of its most important prey, the common vole *Microtus arvalis* (Vorisek, 1997). In southern Scotland, the population dynamics of the common buzzard is affected by its primary prey, rabbits. Buzzards as a group have a more generalised diet than all other Falconiformes except for kites *Milvus* sp. (Jaksic and Carothers, 1985) but may adapt to a more specialised diet depending on the availability and abundance of the dominant prey at the time. The dynamics of many raptor-prey relations are still relatively scarce in literature and most of them are rather anecdotal.

In East Africa, rodents such as the yellow-toothed mole-rat *Tachyorectes splendens*, and the grass rats *Arvicanthis niloticus* and *Mastomys* sp. are important foods of some raptors such as black-shouldered kites, augur buzzards, tawny eagles, some falcons *Falco* sp. and several large owls (Brown and Britton, 1980). Cycles of rodent abundance have been mainly 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 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).

2.6 BREEDING SEASONALITY

It is generally agreed that the breeding seasons of birds are regulated by proximate factors that initiate breeding; and ultimate factors that control success through survival of the young (Brown and Britton, 1980). Subsidiary or modifying factors, such as nesting

condition, predation or persecution pressure, can halt the breeding cycle after it has started. Proximate factors must obviously come first, but ultimate factors may be more important for survival once the cycle has started (Baker, 1938; Lack, 1954; Immelmann, 1971). The breeding seasons of birds in the East African tropics have been summarised by Moreau (1950), Archer and Godman (1961), Benson *et al.* (1971), and Urban and Brown (1971). Most of these studies discussed breeding seasons in relation to climate and food supply. The most recent synthesis of the breeding seasons of East African birds is that of Brown and Britton (1980), who stated that "In East Africa, and other parts of Africa, the alternation between dry and wet seasons is the most important environmental factor affecting breeding seasons". There is however, great diversity among species in the occurrence, timing, and duration of breeding activities. In the tropics, breeding seasons of raptors are believed to be governed by rainfall patterns (Newton 1979), although little information exists (review in Brown and Britton, 1980). Newton (1979) suggested that raptors bred only during part of the year, when food was most readily available, while Hammond and Pearson (1993) postulated that raptors timed their breeding cycles to ensure that food was readily available to feed nestlings. My study refers to the pragmatic definition of the term 'breeding attempt' by Brown and Britton (1980) who considered that a definite attempt to breed was only made after an egg had been laid.

The majority of records on breeding seasonality of birds in the east African tropics are on passerines and hence may not fully reflect the breeding seasonality patterns of African raptors. A review of the breeding seasonality of some raptors, particularly of the African fish eagle *Haliaeetus vocifer,* is given by Brown (1980) and Brown and Britton (1980). These reviews are based on nest-record cards and may be subjected to various sources of bias. For example, the long breeding periods in raptors makes it difficult to 'slot' various breeding stages (incubation, early nestling, late nestling, fledgling) into definite seasonal time frames. Another source of bias is that raptors make large conspicuous nests that can result in multiple nest-record card returns, thus inflating sample size. Understanding the breeding phenology of tropical raptors requires long observation hours, patience and interest, all of which are lacking in Kenya. It follows that factors initiating egg-laying in tropical raptors are still poorly understood. In these areas (particularly equatorial regions), changes in photoperiod are not sufficiently large to be

used as proximate factors and thus many birds have evolved to respond in their breeding cycles to other environmental cues such as rainfall, temperature, conditions of the vegetation and food (Voous,1950; Moreau, 1950). With regard to ultimate factors, Brown (1970) emphasized the need for more detailed quantitative behaviour and population studies of favoured types of prey before ascertaining that the availability or abundance of prey animals is the ultimate controlling factor in the evolution of laying seasons of raptors in the tropics.

Based on the data of the East African nest record scheme, egg-laying in augur buzzards is spread over all months with peaks from June to September (Brown and Britton, 1980). In Zimbabwe, Harrison *et al.* (1998) suggested the possibility of a bimodal egg-laying season, although this is probably an artefact of a small sample size. The implications of studying the egg-laying seasons of augur buzzards is relevant in the context of understanding the factors that trigger breeding (rainfall, vegetation cover and prey availability). In terms of management, seasonal data about cliff-nesting augur buzzards in Hell's Gate National Park will provide information to park authorities in identifying periods when rock-climbing is least detrimental to nesting raptors.

2.7 BREEDING PERFORMANCE

Breeding performance is the yardstick by which the health and survival of any species is measured. In raptors, three components are usually ascertained:

- breeding attempt rate – this is the number of breeding attempts that a pair makes per year in order to raise young. Breeding attempts can either be successful (chicks reared to fledglings) or unsuccessful (no fledglings produced). A high breeding attempt rate does not necessarily reflect good breeding performance as a string of successive breeding failures followed by a successful breeding attempt also results in a high breeding attempt rate. A better measure of breeding performance is the breeding attempt rate to breeding success (see definition below) ratio – low ratios reflect good breeding performance while high ratios mean poor breeding performance;

- breeding success – this is a measure of the number of successfully raised chicks per breeding pair per year. While some pairs are usually more successful than others within an area as a result of territory quality, it is also useful to present information about the numbers of successfully raised chicks per *successful* pair per year.

- productivity – this is a measure of the number of successfully raised chicks per pair per year. This measure takes into account all pairs in an area regardless of whether breeding took place or not.

All three components of breeding performance are influenced by various factors, many of which work in concert with one another. In the absence of human factors, the availability of food and suitable nest sites rank as the most important, although climatic factors such as rainfall acts as a proximate factor (Newton, 1994). For example, in Zimbabwe's Hwange National Park, significantly greater breeding success was recorded in the African hawk-eagle *Hieraaetus spilogaster* in periods of greater rainfall which may have in turn increased food supply by increasing vegetation cover (Hustler and Howells, 1988). Breeding performance of common buzzards in Argyll, Scotland was strongly correlated with abundance of rabbits (Austin and Houston, 1997), while in the rough-legged buzzard *Buteo lagopus*, in the Siberian tundra, the rate of change of small mammal species diversity was the most important factor that influenced productivity (Potapov, 1997). The importance of nesting habitat features as an influencing factor in breeding performance has been shown in the common buzzard, where often-used territories showed the greatest breeding success (Kostrzewa, 1996). Nesting substrates also play an important part in determining breeding success. For example, nests built on cliff ledges and rocky outcrops are more vulnerable to predation than those on tall trees (Lendrum, 1979). Nesting location and proximity to adjacent breeding pairs also influences breeding success as seen in the ferruginous hawk *Buteo regalis* of northern Montana. Pairs that nested closer to cropfields and roads and farther from other breeding raptors produced more young than other nests (Zelenak and Rotella, 1997). In Zimbabwe's Matopos hills, rainfall and the previous year's breeding result were the two major factors that influenced breeding performance in the black eagle population (Gargett, 1990).

Periods of good breeding performance depend on the survival of adult birds. Areas with high adult mortality rates due to natural or human-induced factors have a negative influence on productivity (Keran, 1981). Other factors such as intraspecific disturbance and competition, new nests, age of paired birds, predation and man's impact on the habitat are equally important factors that have an influence on the breeding performance of raptors (Newton, 1979).

CHAPTER THREE
STUDY AREA – SOUTH LAKE NAIVASHA

3.1 THE STUDY AREA

The southern Lake Naivasha area (Plate 3.1 and Figure 3.1) was an ideal site for the study because augur buzzards are relatively common and also because sharp contrasting environmental features occur between areas of relatively disturbed (parts of the lake environs) and undisturbed habitats (Hell's Gate National Park). The southern Lake Naivasha area has experienced major agricultural development since the early 1970s, reaching exponential levels in the 1990s. Consequently, different land-use patterns have emerged (Plate 3.1).
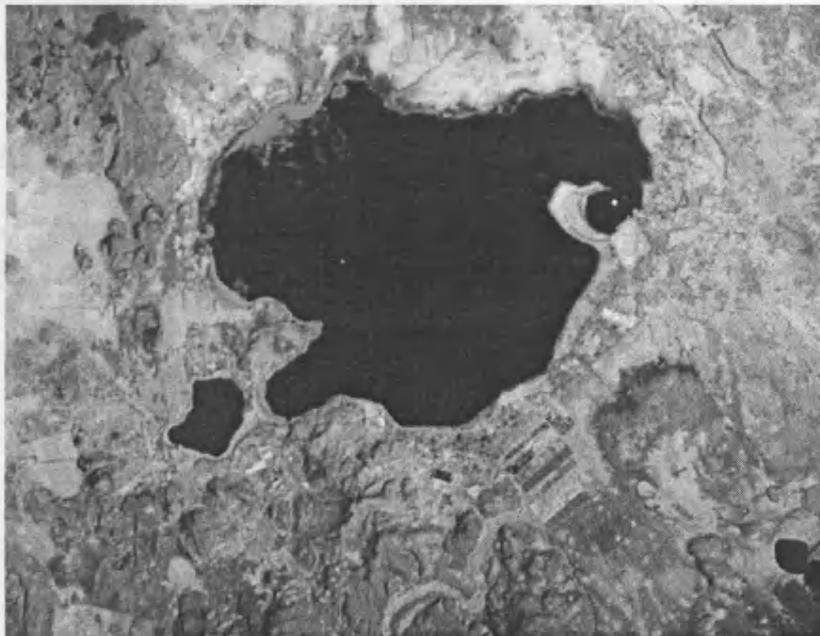
Plate 3.1: Satellite image of the Lake Naivasha basin taken in early 1995 (Courtesy ITE Netherlands). Brightly coloured areas south of the lake indicate agricultural/horticultural fields.

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Figure 3.1: The core study area in the southern Lake Naivasha area.

3.2 LAKE NAIVASHA

3.2.1 Location, climate, geology and vegetation

Lake Naivasha (0° 45'S and 36° 20'E) is located in the eastern Rift Valley of Kenya at an altitude of 1890 m (Figure 3.1). It is a rather shallow lake with a mean depth of 5 m and an area of 120 km^2. It is a closed basin lake that exhibits large fluctuations in water level (Gaudet, 1979; Gaudet and Melack, 1981; Ojiambo, 1992). Lake Naivasha is the largest fresh water lake in Kenya's Rift Valley. It receives drainage from higher parts of the valley floor in the Kinangop Plateau and also from the montane regions of the Nyandarua Mountains and the valley floor east of the lake (Maitima, 1991). To the south, Mt. Longonot, Mt. Suswa, and other small volcanoes form a barrier which is broken by Njorowa Gorge (Maitima, 1991). Lake Naivasha lies within the range of the Intertropical Convergence Zone and prevailing winds are from the east and north-east. The climate of the area is warm and semi-arid (East African Meteorological Department, 1964). Air temperatures are moderate with monthly means varying little from 15.9 to 18.5°C. Mt. Kenya and the Nyandarua range capture most of their rainfall from the monsoons and cast a significant rainshadow over the central rift, particularly over the Naivasha basin, the central part of which receives less than 500 mm of rain per year (Ambrose, 1984). The combination of moderate temperature, low relative humidity and low rainfall make January and February the months with the highest evaporation (Litterick et al.,1979).

Volcanic rocks in the area consist of tephrites, basalts, trachytes, phonolites, ashes, tuffs, agglomerates and acid lavas such as rhyolites (Thompson and Dodson, 1963; Noble and Ojiambo, 1975) Hot springs and fumaroles are also observed within the lake catchment (Bonzongo et al., 1996).

The vegetation of the Naivasha basin falls in Ecological Zone IV of Pratt et al. (1966), a zone in which upland Acacia woodland is common. The slopes of the Rift Valley above Naivasha are covered by tropical Setaria spp. grassland which grades into the Tarchonanthus camphoratus bushland, typical of the Rift Valley floor (Litterick et al., 1979). Much of the lake shore is fringed by papyrus Cyperus papyrus while the area immediately behind the shoreline has a thin band of closed canopy Acacia xanthophloea

woodland with trees up to 35 m tall (Litterick *et al.*, 1979). This woodland tends to open up further inland into human-modified open canopy *Acacia* woodland pastures. Early settlers in the Naivasha area modified these *Acacia* woodlands by clearing bushes and trees and created pastures for grazing their cattle. The lake-side flora is quite diverse with 108 species of plants described (Gaudet, 1977).

3.2.2 Economic importance

The Lake Naivasha area has always been an important ecological site to Kenya (Harper *et al.*, 1990). Its diversity of flora and fauna in the range of vegetation-zones associated with the lake and its hinterland is greater than that of other Rift Valley lakes (Lincer *et al.*, 1981). In 1995, the lake was designated as a Ramsar site.

The Lake Naivasha area has a high economic value; it accounts for 75% of Kenya's horticultural exports. Cut flowers are grown for export on large farms along the southern and northern shores, and lucerne is grown under sprinkler irrigation to support an important dairy industry (Litterick *et al.*, 1979; Harper *et al.*, 1990). This intensive agricultural production is made possible by the readily available irrigation water, good quality volcanic soil and tropical climate. The lake area is also a focus for tourism (particularly bird watching) and recreation (boating and sport-fishing) which earn the country foreign exchange. In addition, a commercial fishery has also been built up over the past 30 years on the basis of introduced species, the products being exported to Nairobi and Nakuru in addition to local consumption (Harper *et al.*, 1990). The area has also become industrially significant as a consequence of the development of Olkaria, just to the south of the lake, as a site for geothermal energy generation, producing up to 43 megawatts which is 15% of Kenya's total energy-consumption (Harper *et al.*, 1990).

3.2.3 Threats

Over the years, in addition to fluctuations in water level, the lake has experienced changes in nutrient composition, plant structure and animal populations (Harper *et al.*, 1990). The increasing human population around the lake has resulted in some clearing of

riparian forests along the lake shores for agriculture and settlement. This has contributed to the decline of African fish eagles numbers by 50% since 1969 (Virani and Harper, 1998). The intensification of flower farming at Lake Naivasha has resulted in a subsequent influx of farm workers from all parts of Kenya (Ministry of Planning and National Development, 1997). The local Masai pastoralists have limited grazing areas for their cattle as more land is developed for horticulture (pers. obs.). Hence competition with wildlife grazers is high resulting in many parts of the region being overgrazed (J. Root, pers comm.). This has increased the pressure on the land as more areas are cleared to cater for the needs of an increasing human population. Since 1990, this trend has accelerated resulting in negative impacts on the flora and fauna of the lake and the environs (Virani and Harper, 1998; Harper *et al.*, in litt.). In addition to human-induced habitat alteration, the growth of the horticultural industry has raised concern amongst local inhabitants over the excessive extraction of water from the wetland systems and the use of agrochemicals (S. Higgins, pers comm.). Increasing human growth has also put a strain on the ecosystem with over-fishing and overuse of wetland plants (which would otherwise act as a buffer and filter for the water entering the lake).

Between 1995 and 1997, a total of 18 dead raptors were found in various locations in the southern Lake Naivasha area (S. Thomsett, G. Irvine, A. Amar, B. Mburu, pers. comm. and pers. obs.). These included four African fish eagles, three augur buzzards, two Ruppell's vulture *Gyps ruppellii*, two Egyptian vultures *Neophron percnopterus*, one tawny eagle *Aquila rapax*, one long-crested eagle *Lophaetus occipitalis*, one Steppe buzzard *Buteo buteo*, one Eleonora's falcon *Falco eleonorae* and three Eurasian hobbies *Falco subbuteo*. More than half of these were suspected of being poisoned while the causes of death of the rest were unknown but believed to be human-induced (e.g. electrocution, persecution, drowning). At least 5 poultry farmers around the Naivasha area have admitted to poisoning augur buzzards suspected of killing domestic fowl (Njuguna, unpublished). In a pesticide study conducted nearly 25 years ago, organochlorine residues detected in raptors were not found to significantly affect their breeding at Lake Naivasha, (Frank *et al.*, 1977), while in a subsequent study in 1994, residues found in fish eagles were also not considered significantly harmful (Thomsett, unpublished).

3.3 HELL'S GATE NATIONAL PARK

Hell's Gate National Park (Hell's Gate) (0° 30' and 1° 00'S, about 36° 30' E) is located in the southern part of the Lake Naivasha region and covers an area of 6825 ha (Figure 3.1). It was established as a national park in 1984 and as a result of its location was expected to relieve much of the tourist pressure on the Nairobi National Park (Wildlife Planning Unit, 1985). The mean annual rainfall is about 650 mm, irregularly distributed throughout the year, but with a peak in April/May (Lovari and Lucherini, 1992). The central feature of this area is an erosion channel formed by a southward overflow from Lake Naivasha when the water level was about 100 m higher than at present (Harper *et al.*, 1990). The northern half of this channel, known as Hell's Gate (Anon, 1990), is a sinuous, flat-floored feature, bordered by high volcanic cliffs on the western side and by hills and plateaux, that rise in step like fashion, on the eastern side. The soils, of volcanic or lacustrine origin, are porous resulting in quick drainage of rainwater (Lovari and Lucherini, 1992). The park's vegetation is mainly dominated by *Tarchonanthus camphoratus – Acacia drepanolobium* scrubland which rarely exceeds 4 metres in height and is varyingly dense or open. The floor of the gorge consists of open grasslands dominated by *Digitaria milanjiana* and *Cynodon dactylon*. The common low shrubs of this community are *Felicia muricata*, *Solanum incana* and *Sida cuneifolia*. The upland grasslands that occur on the cliff scree slopes and on cliff tops are dominated by tussock-forming grasses. In areas where steep slopes occur and along secondary gorges, characteristic trees include *Cussonia spicata*, *Schefflera abyssinica* and *Euphorbia magnicapsular*.

The main feature of the park is its impressive cliffs which serve as important nesting sites for raptors. These are characterised in places by well developed columnar jointing. The lower hills to the east are dissected by a variety of small gorges. Volcanic plugs, exposed by the erosion of surrounding pyroclastic rocks mark the northern and southern boundaries of Hell's Gate – Fischer's Tower to the north and Central Tower 6 km to the south. Towards the south western part of the park is the Ol-karia geothermal

power station and an area of higher ground with numerous steam vents (Figure 3.2). Raptors that nest on the cliffs include the augur buzzard, Verreaux's eagle *Aquila verreauxii*, lanner falcon *Falco biarmicus*, Egyptian vulture, Ruppell's vulture and spotted eagle owl *Bubo africanus*. Among these, the augur buzzard is one of the most common raptor with at least 10 resident pairs known (Lester, 1991; Thomsett pers comm.; pers obs.).

3.4 STUDY SITES

The study area was divided into three main study sites (Figure 3.2):
- Hell's Gate National Park (Hell's Gate);
- Mundui;
- Sulmac-Oserian.

Mundui and Sulmac-Oserian were not separated in the first year of study and are collectively referred to as 'lake environs'.

Mundui

Lake Naivasha

Oserian

Sulmac

HGNP

N
↑

park boundary

```
(  )   lake shore
 ~     road/track
H—H    1 km
:.::.  Acacia woodlands
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horticultural fields

geothermal activity
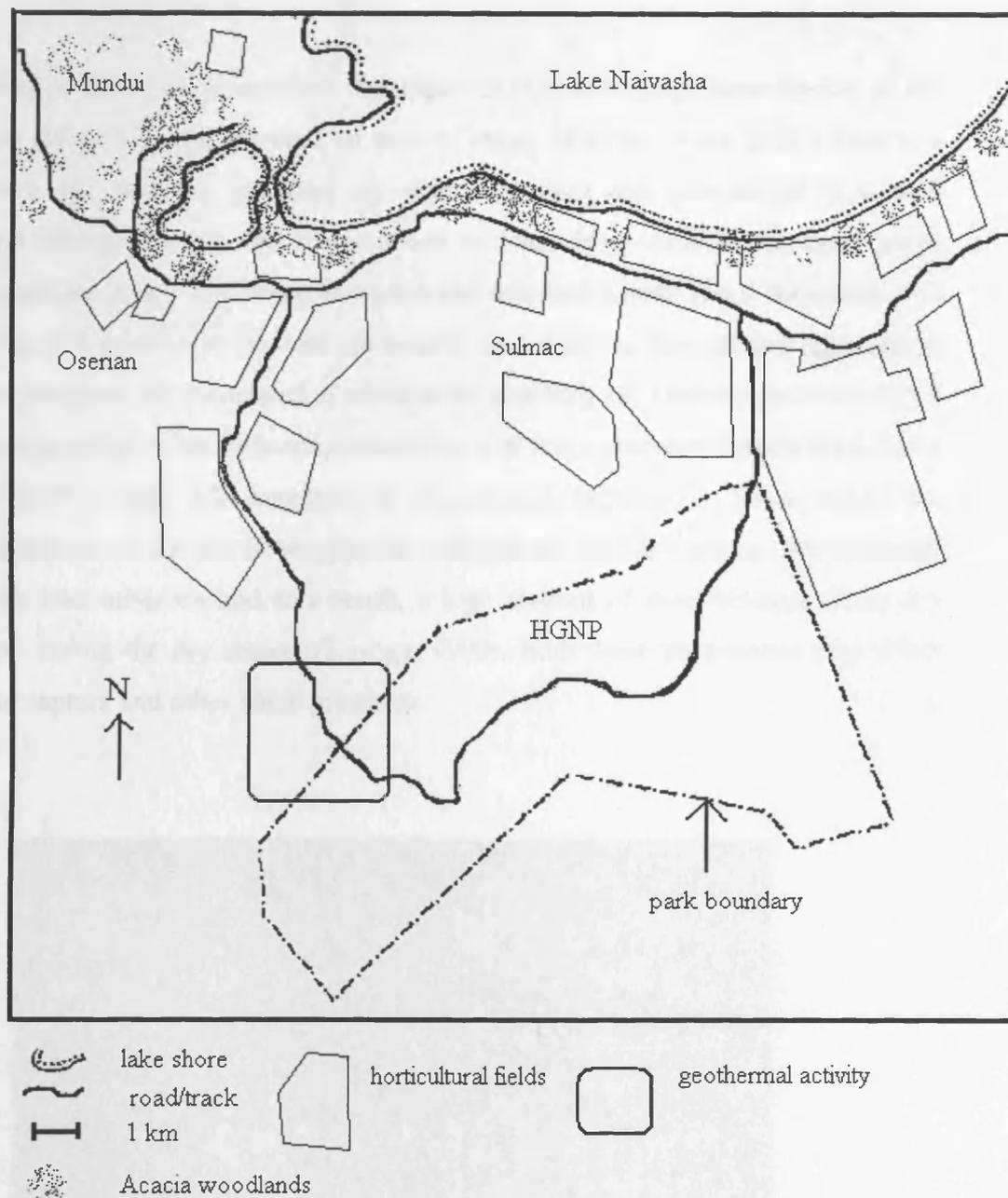
Figure 3.2: Land-use types in the southern Lake Naivasha area.

3.4.1 Hell's Gate

The study site in Hell's Gate included the upper Ol-Njorowa gorge (also known as the upper gorge) (Plate 3.2) and covered an area of about 2920 ha. Since Hell's Gate is a protected area, the land-use activities are mainly tourism and recreational (e.g. rock climbing and hiking). Tourist and maintenance vehicles drive through the upper gorge but their impact on animal behaviour is considered minimal. Local Masai tribesmen who live along the park's southern borders are usually seen walking through the upper gorge and have, on occasion, been accused of small-scale poaching (R. Obanda pers comm.). A series of water troughs in the park coupled with lack of large predators has enabled Hell's Gate to support a high concentration of mammalian herbivores. As a result, the grasslands adjacent to the water troughs are overgrazed. Hell's Gate is comparatively drier than the lake environs and as a result, a high amount of dead biomass (from dry grass) occurs during the dry season (Kiringe, 1990). Both these phenomena may affect prey base for raptors and other small predators.
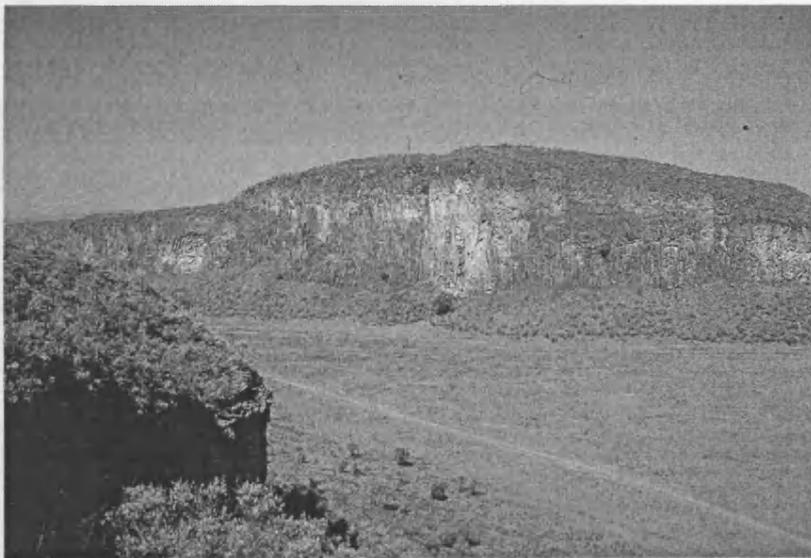
Plate 3.2: The upper gorge in Hell's Gate showing the main cliff face.

Hell's Gate is surrounded by human activities. Intensive horticulture is practiced adjacent to the park's northern and north-eastern boundary while human encroachment from pastoralists and farm workers in its southern and western boundaries is increasing (S. Thomsett, R. Obanda, pers. comm.; pers. obs.).

3.4.2 Mundui

The Mundui study site was located in the area west of Lake Naivasha and covered an area of approximately 1460 ha (Figure 3.2 and Plate 3.3). 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 *Acacia xanthophloea* trees 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.

Plate 3.3: *Acacia* **woodland pastures in Mundui.**

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3.4.3 Sulmac-Oserian

This study site was located along the Moi South Lake road running close to the lake's southern shoreline (Figure 3.2).

Sulmac

The areas of greatest horticultural activity were in the Sulmac area (5230 ha) just north and northeast of Hell's Gate (Figure 3.2 and Plate 3.4). 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 cater for 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.

Plate 3.4: Sulmac study site close to the lake shore. Note fringe of *Acacia* woodland between horticultural units and lake's shoreline.

Oserian

Between Hell's Gate and Mundui is the Oserian area (Figure 3.2 and Plate 3.5). 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) consisted 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.

Plate 3.5: Oserian study site close to Hell's Gate. Note presence of *Euphorbia magnicapsular* trees.

Because both Sulmac and Oserian have the same land-use practice, they were considered as one unit.

3.5 STUDY AREA TERMINOLOGY

In the context of this study, the term 'study area' refers to the southern Lake Naivasha area, incorporating all three study sites i.e. Hell's Gate, Mundui and Sulmac-Oserian.

CHAPTER FOUR
METHODS

4.1 INTRODUCTION

The study was conducted between January 1995 and January 1998. The following methods were used:- nest searches, augur buzzard trapping and ringing, nest and foraging observations, pellet and prey remains collection and analyses, transect counts to determine mole-rat availability, nest site habitat data collection and recording the outcome of active nests.

4.1.1 Timetable

The duration of the study was divided into three distinct periods covering three field seasons:

- 1995 – nest searches were conducted; birds were trapped and ringed; nests were monitored for breeding success; data were collected on breeding behaviour, prey items, prey delivery rates, interaction rates and brood sizes. Hell's Gate was compared with the lake environs.
- 1996 – more nest searches were conducted; data were collected on foraging behaviour, hunting success and strike rates; breeding success was recorded and more birds were ringed. Hell's Gate was compared with the lake environs.
- 1997 – data were collected on mole-rat availability, grass height, soil softness and nest site variables; breeding success was monitored and more birds were ringed. Hell's Gate was compared with Mundui and with Sulmac-Oserian.

4.2 NEST SEARCHES

Searches were conducted by intensively watching augur buzzard pairs for evidence of breeding behaviour such as carrying of nesting material or prey to nest, courtship

behaviour and territorial displays. Five nests were already known and local residents also helped to locate new nests during the course of the study. New nesting territories were systematically located by driving and careful observation along the upper gorge in Hell's Gate, in Mundui, and around Sulmac-Oserian. The vehicle was stopped at 1-km intervals during the road surveys and an attempt was made to attract territorial augur buzzards by imitating their call for 5 to 10 minutes. Nests with evidence of eggs or young were considered active. Productivity data were gathered from all active nests. Occupied nests (incubating adult present) were observed from at least 200 m with a 20-60x spotting scope to avoid disturbance. All occupied nests were revisited at least once every two weeks to count the number of young and determine the eventual outcome. Some nests were visited more frequently than others, since the latter were further away from the base camp and more inaccessible. Taking these circumstances into account, there is a remote possibility that a few breeding attempts (mainly unsuccessful ones) may have occurred unobserved hence over-estimating breeding success. Laying and fledging dates were estimated from known hatching dates or ages of young determined from nestling growth (Steyn, 1963). Unless field evidence indicated otherwise, juvenile augur buzzards were recorded as fledging successfully only if they were observed after leaving the nest. The proportion of normal and melanistic-morphed birds was recorded for all known pairs. A Chi-squared test was used to test if there was a relationship between sex and colour morph.

The locations of all known nests were recorded using a hand-held Garmin 12 XL GPS system (Garmin, 1997), and the information entered into a GPS database using the software program MAPINFO (1992) which calculated the 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. Analysis of variance (ANOVA) was used to test for differences in the mean nearest-neighbour distances in each of the three study sites. The total area occupied by all known pairs in a particular site was determined by linking the nests on the outside of the study site to produce a convex polygon. The area was then extended to include the territories of the outermost pairs by adding a boundary of half the mean minimum inter-nest distance

(Watson, 1989). The area enclosed by this polygon and hence the density of augur buzzard pairs was calculated using MAPINFO (1992)

4.2.1 Increasing human impact index (IHI)

The IHI index (modified from Brandl *et al.*, 1985) was based on an estimation of the degree of land-use activity, as a measure of increasing human impact on augur buzzard territories and its potential to influence breeding performance. The IHI index was divided into four categories and each was assigned a score from 0 to 4 based on its degree and intensity. Scores were assigned as follows: nil = 0, low = 1, moderate = 2, high = 3, extreme = 4. The IHI index thus ranged from 0 to 16 (Table 4.1). The four categories were:

- human settlement pressure – the proportion of area within a 1 km radius from the nest of a pair that is occupied by houses and other human settlement structures;

- 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 pairs' territory 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;

- horticultural activity pressure – the proportion of area within a radius of 1 km from the nest of a pair that is occupied by horticultural farming units;

- direct human disturbance - this index was based on the likelihood that the activity of augur buzzards such as foraging and nesting would be negatively influenced by man (this category also included the potential likelihood that an augur buzzard would die as a result of human persecution, electrocution or poisoning). Mortality rates in different land-use areas were also considered.

To determine whether land-use activity influenced nest-spacing in augur buzzards, the IHI index was correlated with the square of the mean nearest-neighbour distance. The mean nearest-neighbour distance was the mean of the distance from one nest to its two closest neighbouring nests. The mean nearest neighbour distance was squared to obtain a

Table 4.1: Human impact index at different nest sites in the southern Lake Naivasha area.

SITE	Nest	human settlement	grazing pressure	horticulture intensity	human disturbance	Total score
Hell's Gate	H1	0	4	1	1	6
	H2A	1	4	2	1	8
	H2B	0	4	1	1	6
	H3A	0	4	0	1	5
	H3B	0	4	0	1	5
	H4A	0	4	0	1	5
	H4B	0	4	0	1	5
	H5A	0	4	0	1	5
	H5B	0	4	0	1	5
	H6	0	4	0	1	5
	H7	0	4	0	1	5
	H8	0	4	0	1	5
Sulmac-Oserian	R1	2	3	2	2	9
	R2	2	3	3	3	11
	R3	2	3	4	3	12
	R4	2	3	4	3	12
	S1	4	3	4	4	15
	S2	4	3	4	4	15
	S3	3	4	3	3	13
	S4	3	4	2	3	12
	S5	3	4	3	3	13
	S6	3	3	2	3	11
	S7	2	3	3	2	10
	S8	2	3	3	3	11
	O1A	2	4	2	3	11
	O1B	2	3	3	3	11
	O2	1	3	2	3	9
	O3	2	3	3	3	11
	O4A	2	4	4	3	13
	O4B	2	4	4	3	13
	O5	2	4	2	1	9
	O6	4	4	1	3	12
Mundui	K1	2	2	0	2	6
	K2	2	2	0	2	6
	K3	2	3	0	2	7
	K4	1	2	0	1	4
	K6	1	2	0	1	4
	K7	1	2	0	1	4
	K8	1	2	0	1	4
	K9	1	2	0	1	4
	K0	1	2	0	1	4

measure of density. A Chi-squared test was used to examine if there was a relationship between nest-closeness and visibility of nests by neighbours. Nests less than 1.2 km from neighbours were considered close, while those greater than 1.2 km were considered far. Visibility of nests from neighbours was assessed by climbing as close to a nest as possible and determining whether a neighbour's nest could be seen using a telescope. All pairs studied were resident all year round, while a few vagrant augur buzzards were seen from time to time.

4.3 AUGUR BUZZARD TRAPPING AND RINGING

Augur buzzards were periodically trapped for ringing and to obtain information on biometrics and weight. Birds were trapped using a standard *Bal-Chatri* baited with live white mice (Berger and Mueller, 1959). Standard D size aluminium rings (National Museums of Kenya) and individually distinctive coloured rings were attached to the birds' tarsi.

4.4 NEST-SITE CHARACTERISTICS AND SELECTION

Data on nest-site charactersitics were just collected for tree nests (n = 38; Hell's Gate = 7, Mundui = 12, Sulmac = 8, Oserian = 11) as cliff nests occurred only in Hell's Gate. The term 'nest-site' is used to refer to the nest tree and an area of radius 50 m around it. Characteristics of nest-sites were quantified using several variables. These were:

- tree species;
- slope of land where tree was located;
- aspect (direction of the slope);
- diameter of tree at breast height (dbh);
- tree height;
- nest height;

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- canopy size (the mean distance from the base of the tree to the outer edge of the tree canopy in the four cardinal directions) ; and

- the distance to the nearest tree (mean inter-tree distance from nest tree) within 50 m of each of the four quadrants of the nest or reference tree.

These measurements were compared with similar measurements at randomly selected sites (reference trees) to test for selection. Kruskal-Wallis analysis was used to test if there were any differences in the nest site variables between the different study sites. The procedure followed was that already established in a number of raptor habitat selection studies (Titus and Mosher, 1981; Warkentin and James, 1988; Bechard *et al.*, 1990; Berkelman, 1994).

4.4.1 Reference trees

Reference trees were selected by dividing each land-use area into a grid and then selecting 69 grid squares (10 in Hell's Gate, 29 in Mundui and 30 in Sulmac-Oserian) using a random number table. From the centre of each selected grid square, a 6-inch nail was tossed in the air and I walked 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). At the end of the walking time the closest tree greater than 4 m in height was selected as a reference tree. Mann-Whitney analysis was used to test if nest trees and reference tree variables differed significantly. It was necessary in the analysis to treat Sulmac-Oserian as two separate sites (Sulmac and Oserian) because of obvious differences in dominant tree species and slope of the land of nest trees. Kruskal-Wallis was also used to test if there was a difference in the distance to 'potential nest trees' from reference trees as well as for differences in the number of alternative nests used per pair.

4.5 BREEDING BEHAVIOUR

Breeding behaviour data were collected between April and October 1995. The breeding cycle was divided into periods distinguished by specific breeding stages, namely incubation, early nestling (downy nestling <c. 25 days old) and late nestling period (brown feathered nestling, >c 25 days old). Four-hour watches of visually accessible nests were conducted for a total of 8 nesting attempts (4 in Hell's Gate and 4 in the lake environs) from 8 pairs of augur buzzards. Nest observations were made on a systematic basis but also influenced by availability (as well as visual accessibility) of active nests. These were observed on a rotational basis at different times of the day. A 'day' was divided into three time sessions: from 06h30-10h30, from 10h30-14h30 and from 14h30-18h30. A 20-60x spotting scope, plus a 10x50 pair of binoculars were used to observe breeding activity while the 10-minute interval sampling method (Altmann, 1974) was used to record augur buzzard activity and location with respect to the nest. I sat in a chair placed usually under a tree not less than 200 m from a nest. From my experience, my presence during observation sessions did not appear to have any interference on parental breeding behaviour. The only possible source of interference during the observation sessions would have been that the tree under which I was seated, was not used as a perch. Each session comprised the following:

- I usually arrived at the nest site at least 15 minutes prior to the start of the session where a thorough attempt was made to search for the location and activity of each of the adults;

- at the start of a session and every 10 minutes thereafter, the location (with respect to the nest) and activity of both adults were recorded (Altmann, 1974) (Table 4.2)

- all events such as territorial displays, interactions with other species, hunting attempts and prey-deliveries that occurred between each 10-minute data points were also recorded (Table 4.2).

The proportion of time spent conducting various activities by each adult augur buzzard in relation to the distance from the nest was calculated and Mann-Whitney analysis was used to test for differences in time budget. Breeding data were categorised

into site (Hell's Gate and lake environs), sex (male and female) and breeding stage (incubation, early nestling and late nestling). Further subdivision of the data into daily activity patterns based on two-hourly intervals would have drastically reduced the sample size and hence these were not statistically analysed. Inferences were mainly drawn on activities such as incubation, nest attendance, brooding, feeding of young and eating. Standard ANOVA was used to test for differences in prey delivery rates, and aggressive interactions in relation to time of the day, breeding stage and brood size, while a t-test was used to test for differences in feeding rates to chicks.

Table 4.2: Codes used for recording the breeding behaviour of augur buzzards

LOCATION CODES

The following location data were recorded for each adult augur buzzard with respect to its nest after every 10 minutes:

1 = in or at nest
2 = < 100 m from nest
3 = 100 m to 200 m from nest
4 = > 200 m from nest
5 = oos = out of sight (hence location unknown)

ACTIVITY CODES

Recorded for each adult after every 10 minutes

inc = incubating
bro = brooding
att = attending chick at nest
fed = feeding chick
eat = eating
f/s = flying or soaring
pch = perched
oos = out of sight

EVENT CODES

Recorded for each adult as and when they occurred during the entire observation period

lprey = lands on nest with prey
sp.interact = interacts with another species
pbd = pair bonding display
ha+ = successful hunting attempt
ha- = unsuccessful hunting attempt

4.6 DIET, HUNTING AND PREY AVAILABILITY

Data were collected in the following ways to give three partly-independent measures of diet:

- recording of prey items delivered at nests;
- analysis of prey remains and pellets collected beneath nests and common perching posts;
- direct observations of birds making kills;

In addition, a survey was conducted between January and September 1997, to investigate the seasonal availability of the yellow-toothed mole-rat *Tachyoryctes splendens* (Ruppell) (Plate 4.1). The yellow-toothed mole-rat is the principal food source of the augur buzzard in the Naivasha area (Smeenk, 1974; S. Thomsett, pers comm; this study). The yellow-toothed mole-rat is hereafter referred to as mole-rat. In the context of this study, the terms prey availability and mole-rat availability are synonymously used.

Plate 4.1 Yellow-toothed mole-rat *Tachyoryctes splendens*.

4.6.1 Observations of prey deliveries at nests

Detailed observations of prey delivery were conducted for 346 hours between 27 April and 4 October 1995 on 8 nests – 4 in Hell's Gate and 4 in the lake environs). These observations began during the incubation stage and continued until chicks fledged. They were evenly spaced over the daylight period and 87 deliveries to nests were observed and delivery time recorded. Prey items delivered to nests were identified either as non-rodent mammals, rodents, birds, reptiles or arthropods. Biomass of each prey item delivered was estimated (Kingdon, 1974). Fisher's exact test was used to test for differences in the proportion of prey items delivered by males and females between Hell's Gate and the lake environs. A Chi-squared test was used to test if there was a relationship between type of rodent delivered and time of the day, while Fisher's exact test was used to test for differences in the proportion of rodent and non-rodent prey between the two sites.

4.6.2 Prey remains and pellets

Prey remains and pellets were collected from under 13 nests (5 in Hell's Gate and 8 in the lake environs) and hunting perches monthly between April and September 1995. Remains were sorted in the laboratory to identify individuals. Pellets were dried in an oven at 60°C for 48 hrs and then weighed. They were then dissected and prey items were identified either as non-rodent mammals, rodents, birds, reptiles or arthropods. Dietary composition was estimated as the percentage of pellets that contained named prey items. Soft-bodied invertebrates such as earthworms and slugs could have been missed, although there was no evidence that augur buzzards were eating these. Other sources of bias were that certain prey remains such as mole-rat skulls were more easily collected, as they were larger and more conspicuous than other smaller prey remains. It was also not possible to establish whether every single pellet collected was regurgitated by augur buzzards (as other raptors may have also regurgitated them). Freshly regurgitated pellets were also eaten by arthropods and decomposed easily. Fisher's exact test was used to test for differences in the proportion of rodent and non-rodent prey in remains and pellets between Hell's Gate and the lake environs.

4.6.3 Direct observations of kills

In most raptors that exhibit reversed sexual dimorphism, males normally provide the majority of food to nestlings (Newton, 1979). The hunting behaviour of 18 augur buzzard males (7 in Hell's Gate and 11 in the lake environs) was studied for 100 hours between January and September 1996. Observations were made between 09h00 and 14h00 as this was the period when most prey items were delivered at nests. Prey caught was identified where possible from direct observations of kills. Biomass of each prey item killed was also estimated. Hunting attempts, from a perch or from a hover, were classified as either successful (i.e. when augur buzzards were observed consuming or carrying prey immediately after an attempted hunt) or unsuccessful (i.e. when augur buzzards were observed not consuming or carrying prey). Data on hunting success rates were log transformed to obtain a normal distribution. A student's t-test was used to test for differences in hunting attempt and success rates. Hunting success rates were correlated with monthly and mean monthly rainfall and temperature ranges. Standard ANOVA was used to test if hunting success rates differed quarterly (January-March, April-June, July-September) and during different weather conditions (sunny/overcast). A student's t-test was used to test if hunting success rates differed during breeding and non-breeding periods.

4.6.4 Mole-rat availability

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) (Figure 4.1). Mole-rats make conspicuous conical mounds on the ground as a result of their burrowing behaviour (Kingdon, 1974) (Plate 4.2). 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.

Plate 4.2: Fresh mole-rat mounds used as indices of mole-rat availability.
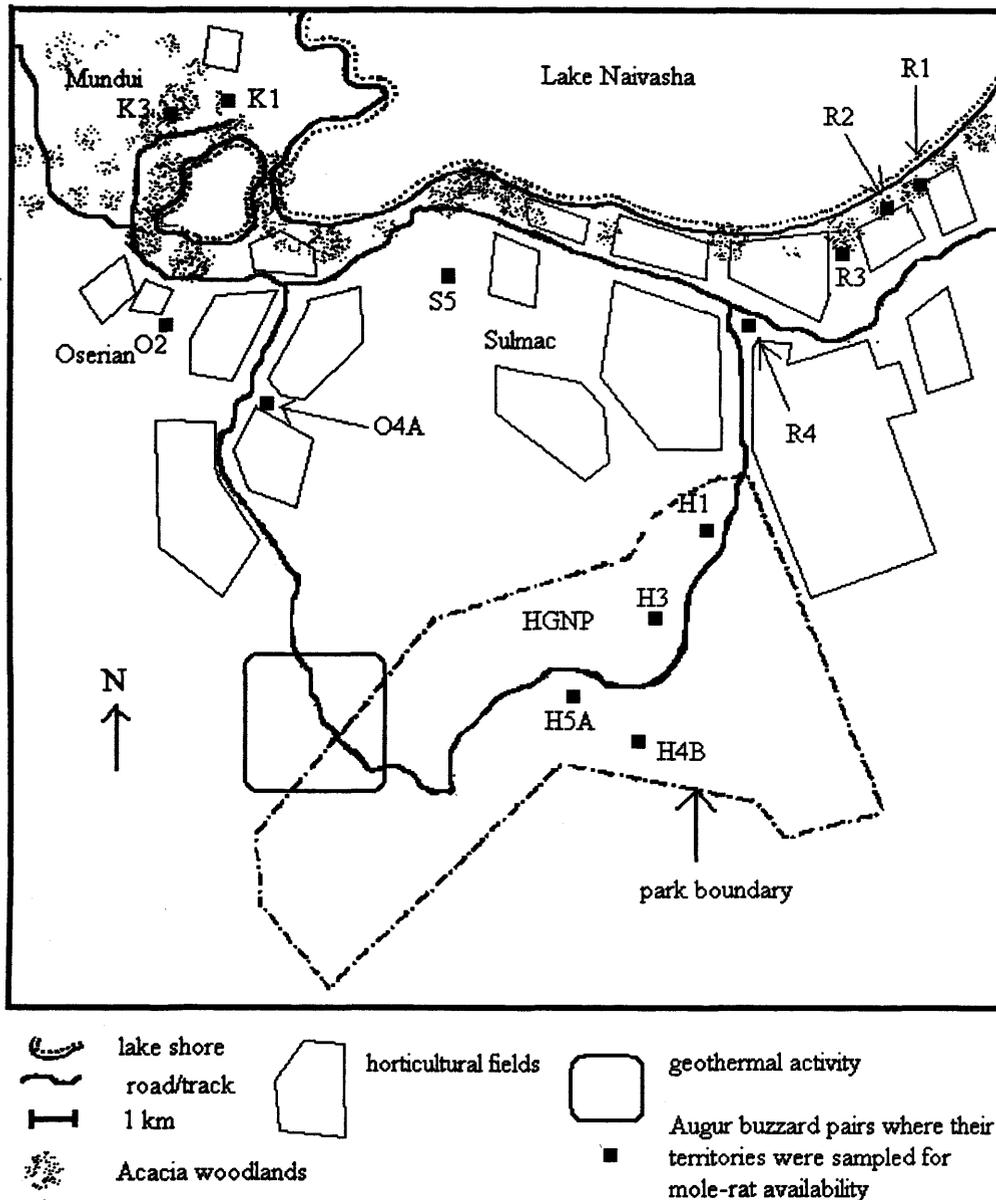
Figure 4.1: Location of pairs where territories were sampled for mole-rat availability

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 (Figure 4.1). 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 had an equal opportunity to sample mole-rats. Starting points for each transects were selected using the method described for selecting reference trees (section 4.4.1). 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 penetration (hereafter referred to as soil softness) was recorded as the softness 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.

Monthly mole-rat indices were correlated with rainfall, grass height, soil softness. and the proportion of augur buzzard pairs that laid in each month. Standard ANOVA was used to evaluate whether mean monthly mole-rat indices differed during various breeding stages of which five were distinguished: courtship/display, incubation, nestling, fledgling and non-breeding.

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.

4.7 BREEDING CHRONOLOGY

The proportion of augur buzzard pairs laying per month in different land-use areas (Hell's Gate, Mundui and Sulmac-Oserian) was recorded over the 3-year study period. A student's t-test was used to test if more breeding attempts occurred in the 6-month period April to September, or October to March. These two periods were chosen because each 6-month block was characterised by initial heavy rainfall followed by a progressive period of drying. Correlation analysis was used to test for associations between percentage of breeding attempts and natural climatic factors such as mean monthly rainfall, mean of mean monthly rainfall (for the three years 1995-1997), mean monthly temperature range, and mean of mean monthly temperature range. Other factors likely to influence the timing of egg laying such as the influence of soil softness, grass height and prey availability on the timing of egg laying were also tested for correlation.

Two best-fit stepwise multiple regression models were developed to determine which of the climatic (rainfall, temperature) or natural (soil softness, grass height, mole-rat availability) variables best predicted the timing of egg-laying in augur buzzards. The variables for Model 1 included mean monthly rainfall and temperature range for the period January to September 1997, plus mean monthly data on soil softness, grass height and mole-rat availability. Model 2 included all the mentioned variables except soil softness.

4.8 BREEDING PERFORMANCE

The numbers of successful fledglings per pair per year were recorded from all known nests. In cases where nest failures were suspected, a thorough search was made below the nest for evidence of predation such as egg-shells or feathers. Annual mean breeding rates

were calculated for each pair by determining the number of breeding attempts made over the 3-year study period. Adult mortality rates were calculated by counting the numbers of new augur buzzards that replaced dead or missing birds in known territories using recognition of individual plumage characteristics or rings. Hence if 4 dead birds or replacements were found in Hell's Gate over the study period (out of a total of 18 individuals), then the mean annual mortality was approximately 7.4%. All missing birds that were replaced were assumed to be dead. The annual mortality rate in the population was used to calculate the 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;

It had to be assumed that the augur buzzard population was stable in order to use this formula.

4.8.1 Factors related to breeding success and productivity

Nest type

The breeding success rate of each nest type (e.g. cliff or tree species) was recorded. A Chi-squared test was used to examine relationships between the type of nest used and the proportion of successful breeding attempts, as well as between old and new nests and whether a breeding attempt was successful or not. ANOVA was used to test for differences between the number of chicks reared per nest among the types of nest used.

Soil softness, grass height and mole-rat availability

It was necessary to extrapolate data on soil softness, grass height and mole-rat availability to include the territories of all known pairs of augur buzzards, because data were only collected from 13 occupied territories. Data on soil softness, grass height and mole-rat availability were placed into 4 categories so that they were representative of a general area rather than a territory (Table 4.3). This categorisation assumed (but also tested) the null hypotheses that the mean soil softness, grass height and mole-rat availability did not significantly differ between adjacent territories that were sampled and adjacent territories that were not. For example, if the territories of hypothetical pairs X and Y were sampled for mole-rats in an area (A) consisting of 4 adjacent pairs W, X, Y and Z, then a non-significant difference in mean mole-rat index between territories X and Y would assume that territories W and Z (by virtue of them being adjacent to X and Y respectively) would have a similar mole-rat index.

Table 4.3: Data on soil softness, grass height and mole-rat availability classified into 4 categories in ascending order.

VARIABLE	CATEGORY 1	CATEGORY 2	CATEGORY 3	CATEGORY 4
soil softness	< 9.9 cm	10.0 – 11.9 cm	12.0 – 13.9 cm	> 14 cm
grass height	< 6.9 cm	7.0 – 8.9 cm	9.0 – 10.9 cm	> 11 cm
mole-rat availability*	0.00 – 0.99	1.00 – 1.99	2.00 – 2.99	> 3.00

* mole-rat availability figures expressed as mounds per are.

Other factors

The Mann-Whitney test was used to examine differences between successful and unsuccessful breeders as well as between breeders and non-breeders for the following variables:

• Increasing Human Impact (IHI) index;
• nearest-neighbour distance;
• mortality rate;
• previous breeding attempt.

4.8.2 Sources of variation in breeding success and productivity

Several properties of the data set were evaluated before investigating sources of variation in breeding success and productivity. Tests were conducted to determine whether or not pairs of productivity measures collected at the same nests in different years were correlated. This was because some nests were used in all three years. It was however assumed (and confirmed; see results) that the correlations were not significant and hence breeding success and productivity data collected at the same nests in different years were treated as independent. Correlation coefficients were also used to investigate relationships between pairs of explanatory variables measured at all nests.

All possible combinations of explanatory variables were evaluated to investigate sources of variation in breeding success and productivity (Table 4.4). An iterative process was used that identified a short list of candidate models for a series of logistic regression models. The results obtained from these models were aimed at suggesting rather than testing hypotheses as the analyses were exploratory rather than confirmatory.

The first step in the iterative process was a univariate analysis of the variables that were thought to be potentially related to breeding success and productivity (Table 4.4). Variables whose univariate results had an unadjusted significance of < 0.25, were candidates for multivariate logistic regression. Thus variables that may have been important predictors of productivity only when considered together were not removed from consideration prematurely (Hosmer and Lemeshow, 1989). Candidate variables were entered into multivariate logistic regression, and the best model was chosen. The significance level was set at 0.1.

Breeding augur buzzards were used as the reference group because there were three response categories; breeders, successful or unsuccessful breeders, and non-breeders. 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:

- augur buzzards did not breed – Model 1a (all years minus soil softness, grass height and mole-rat availability) and Model 1b (1997 only);

- breeding attempts were unsuccessful – Model 2a (all years minus soil softness, grass height and mole-rat availability) and Model 2b (1997 only).

Table 4.4: 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
land-use	+	+	+	+
nest type			+	+
nearest-neighbour distance	+	+	+	+
outcome of previous brood			+	+
IHI index	+	+	+	+
mortality rate	+	+	+	+
soil softness		+		+
grass height		+		+
mole-rat index		+		+

4.9 CLIMATE DATA

Climate data were kindly provided by Sulmac Ltd from their automatic weather station. The southern Lake Naivasha area experiences short-term differences in local weather patterns especially in rainfall, but differences in the area over longer time are negligible (J. Juma, J. Root pers. comm.). Four types of data were collected:

- mean monthly rainfall;
- mean monthly rainfall for the 3-year period 1995-1997;
- mean monthly temperature range (the difference between the mean monthly maximum and mean monthly minimum temperatures);
- mean monthly temperature range for the 3-year period 1995-1997;

Temperature range was used instead of temperature because it gave a more accurate measure of the monthly variation between maximum and minimum temperature.

4.10. STATISTICAL SOFTWARE

Mann-Whitney, Kruskal-Wallis, student's t-test and ANOVA were conducted using the software MINITAB (version 8.2). The ANOVA analyses automatically conducted post-hoc tests to determine which variable(s) significantly differed from others. Correlation and regression analysis, multiple logistic regression and multiple regression analysis were performed using the software SPSS for Windows (version 8).

CHAPTER FIVE

NESTING DENSITY AND NEST-SITE SELECTION

5.1 NESTING DENSITY

A total of 42 pairs (84 birds) were located in the overall study area (Figure 5.1). In Hell's Gate, there were 13, in Mundui, 9 and in Sulmac-Oserian, 20. Of these, 73 individuals (86.9%) were normal-morph augur buzzards while 11 (13.1%) were melanistic-morph (Table 5.1). There was no significant relationship between sex and colour morph (Chi-square; df = 1, χ^2 = 0.941, p > 0.05).

Table 5.1: Numbers (and percentages) of normal and melanistic-morphed augur buzzards in the southern Lake Naivasha area, Kenya.

	normal-morphed (%)	melanistic-morphed (%)
males	38 (45.2)	4 (4.8)
females	35 (41.7)	7 (8.3)

The overall density of augur buzzards in the study area was 0.45 pairs per km². Mundui had the highest concentration at 0.83 pairs per km² while Hell's Gate had 0.28 pairs per km² and Sulmac-Oserian, 0.23 pairs per km².

The mean nearest-neighbour distance between pairs in the study area was 1.35 km (n = 42 nests, se = 0.09, range 0.43 – 2.71). Pairs were more closely spaced in Mundui at 0.88 km (n = 9, se = 0.08, range = 0.43 – 1.14) while in Hell's Gate and Sulmac-Oserain, the mean nearest-neighbour distances were 1.29 km (n = 14, se = 0.09, range = 0.81 – 1.90), and 1.62 km (n = 19, se = 0.14, range 0.66 – 2.71) respectively. These distances were significantly different (ANOVA, df = 41, F = 7.43, p < 0.01). The square of the mean-nearest-neighbour distance was significantly positively correlated with the Increasing Human Impact index (IHI) (r = 0.46, p < 0.001) (Figure 5.2).
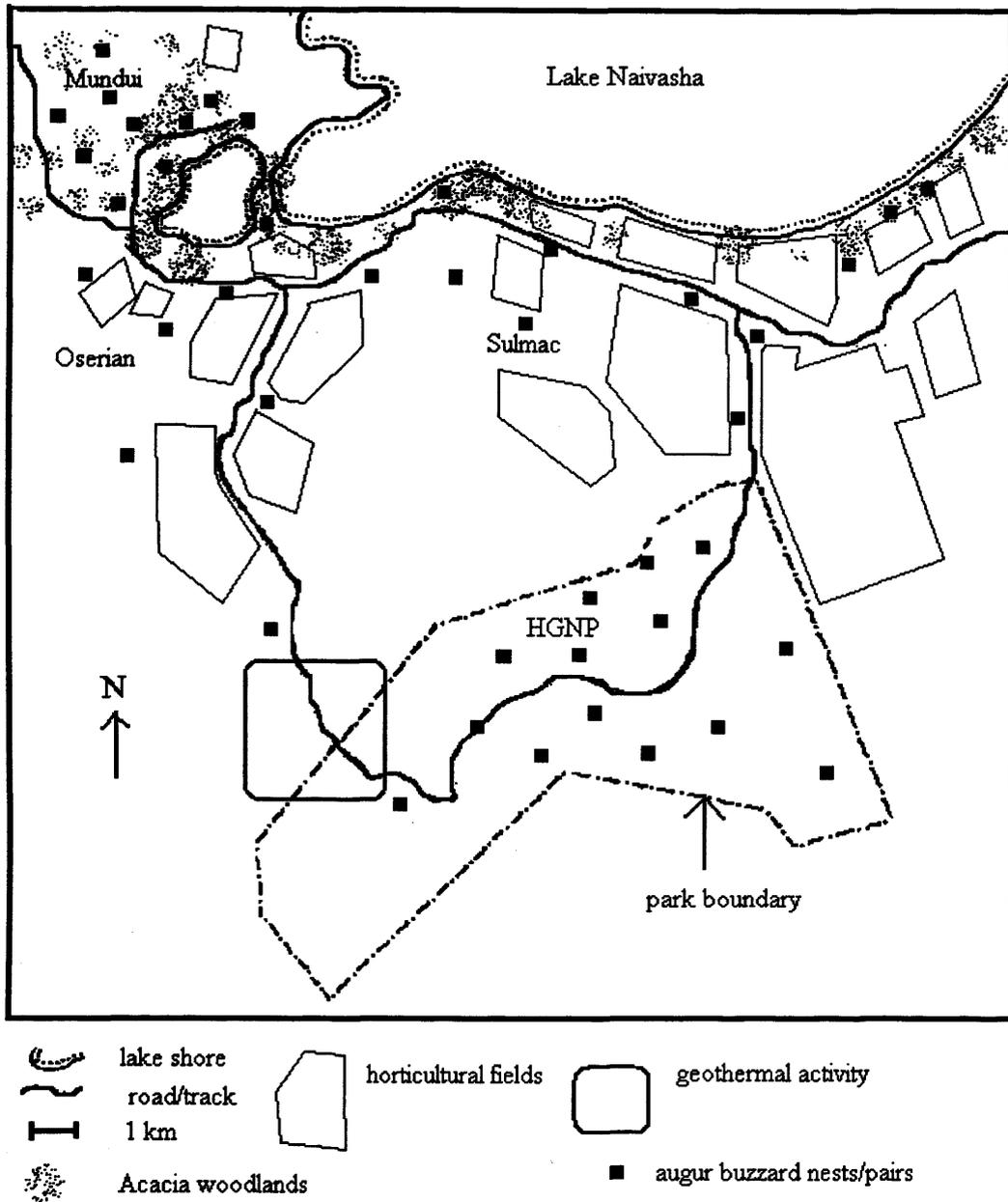
Figure 5.1: Distribution of augur buzzard nests/pairs in the southern Lake Naivasha area. (The open spaces immediately to the north-west and south of the boundaries of Hell's Gate were not sampled as these areas were inaccessible).
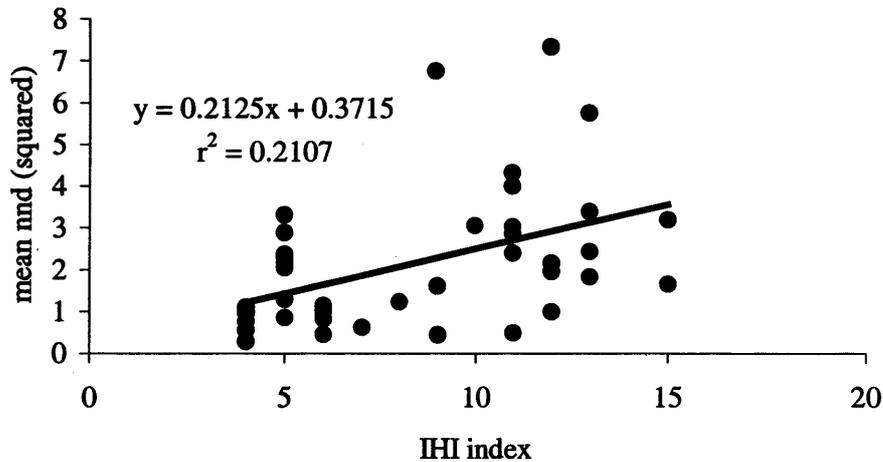
Figure 5.2: Linear regression of IHI index on the square of the mean nearest-neighbour distance (nnd) of 42 pairs in the southern Lake Naivasha area.

Six out of the 42 pairs had nests close (less than 1.2 km) and visible to their neighbours, while 16 were not visible but close to their neighbours' nests. Twelve nests were visible but far (greater than 1.2 km) from neighbours' nests, while 8 nests were far and not visible. There was no relationship between nearest-neighbour distance and visibility of nests by neighbours (Chi square test: df = 1, χ^2 = 0.908, p > 0.05).

5.2 NEST SITE CHARACTERISTICS

Seventeen (41.5%) out of 41 pairs mapped in the southern Lake Naivasha area nested in *Euphorbia magnicapsular* trees, while 16 (39%) nested in *Acacia xanthophloea* (Figure 5.3). The remainder nested mainly on cliff ledges in Hell's Gate (9.7%), in *Eucalyptus* trees (4.9%) and in *A. drepanolobium* (2%). The nest of one pair could not be found, and it was assumed to be a non-breeding pair. Five (45.5%) of the 11 nests in Hell's Gate were on *E. magnicapsular* trees, 4 (36.4%) were on cliff ledges and the remaining 2 (18%) were in *A. xanthophloea* and *A. drepanolobium* trees respectively (Figure 5.4).

Twelve nests found in Mundui were all constructed in *A. xanthophloea* trees while of the 21 nests in Sulmac-Oserian, 13 (61.9%) were in *E. magnicapsular* trees, 6 (28.6%) in *A. xanthophloea* trees and 2 (9.5%) in *Eucalyptus* trees (Figure 5.4).
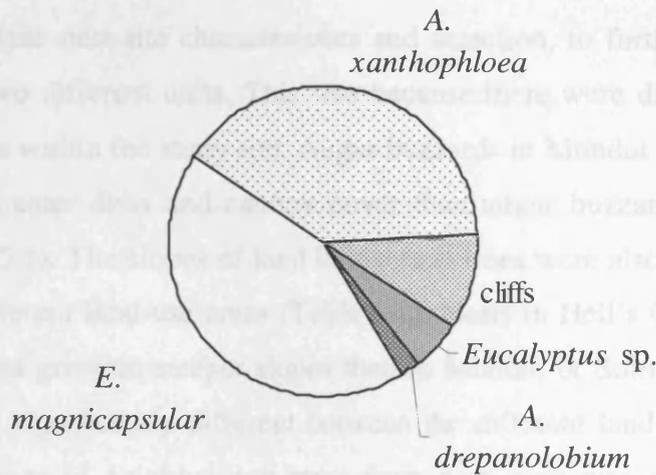
Figure 5.3: Proportion of different nest types constructed on various substrates in the southern Lake Naivasha area (1995-1998) (n = 40 nests).
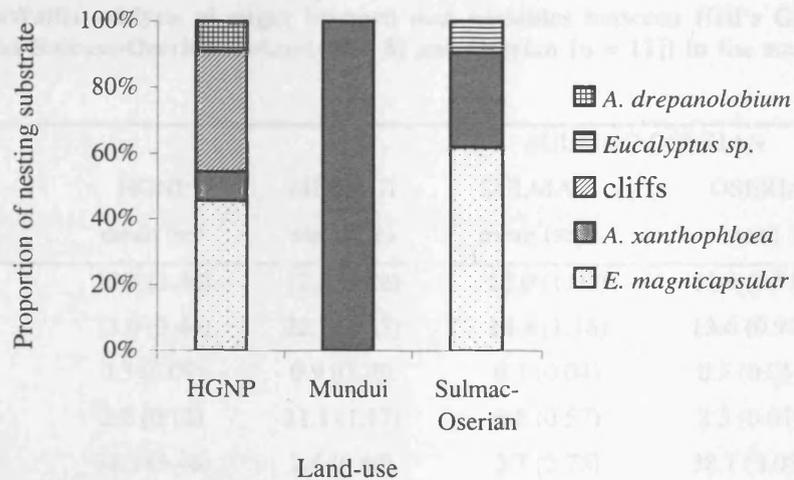
Figure 5.4: Proportions of nesting substrates for augur buzzard nests in each of the three land-use areas (1995-1998) (n = 11 [Hell's Gate], n = 12 [Mundui], n = 21 [Sulmac-Oserian]).

Mean nest heights and nest-tree heights were not significantly different between the different land-use areas (Table 5.2), although in Mundui, nests were built on taller trees. Mean diameter at breast-height (dbh) and canopy cover values of nest trees were significantly different between the different land-use areas (Table 5.2). It was necessary in order to analyse nest-site characteristics and selection, to further subdivide Sulmac-Oserian in to two different units. This was because there were differences in nest trees and slope values within the study site. Augur buzzards in Mundui and Sulmac built nests on trees with greater dbhs and canopy cover than augur buzzards in Hell's Gate and Oserian (Table 5.2). The slopes of land below nest trees were also significantly different between the different land-use areas (Table 5.2). Nests in Hell's Gate and Oserian were built on trees that grew on steeper slopes than in Mundui or Sulmac. The aspects of the slopes were not significantly different between the different land-use areas (Table 5.2). The mean distance of neighbouring trees from nest trees was significantly greater in Sulmac and Mundui than in Hell's Gate and Oserian (Table 5.2). There were no significant differences in each of the nest site variables when Hell's Gate nest trees were compared with those of Oserian; and also when Mundui was compared with Sulmac.

Table 5.2: Kruskal-Wallis analysis of augur buzzard nest variables between Hell's Gate (n = 7), Mundui (n = 12) and Sulmac-Oserian (Sulmac [n = 8] and Oserian [n = 11]) in the southern Lake Naivasha area.

VARIABLE	HGNP mean (se)	MUNDUI mean (se)	SULMAC-OSERIAN		H	p
			SULMAC mean (se)	OSERIAN mean (se)		
nest height (m)	10.3 (3.46)	17.3 (3.26)	12.0 (1.02)	11.4 (0.91)	2.74	0.433
nest tree height (m)	13.0 (3.44)	22.1 (3.83)	14.3 (1.18)	13.6 (0.90)	5.94	0.115
dbh (m)	0.3 (0.09)	0.9 (0.20)	0.7 (0.04)	0.5 (0.05)	11.11	**0.011**
canopy cover (m)	2.2 (0.12)	11.1 (1.17)	8.8 (0.57)	2.5 (0.07)	16.85	**0.001**
slope (degrees)	34.3 (5.46)	2.4 (0.40)	3.3 (2.75)	38.1 (3.03)	15.86	**0.001**
aspect (degrees)	70.0 (27.5)	270.0 (40.5)	153.3 (69.4)	121.0 (49.8)	5.09	0.166
inter-tree distance (m)	8.3 (1.38)	16.5 (3.49)	29.9 (3.57)	7.1 (0.92)	14.87	**0.002**

df = 3

5.2.1 Nest trees vs. randomly selected trees

Nest trees in Hell's Gate were significantly taller than reference trees (Table 5.3). The slopes of land below the nest trees and their mean inter-tree distances were significantly steeper and closer respectively than those of reference trees (Table 5.3). The mean dbh and canopy cover values of nest trees were not significantly different from reference trees (Table 5.3). The aspects of the slopes of nest trees, which faced an easterly and north-easterly direction (mean = 70, se = 27.5) were significantly different from aspects of reference trees (Table 5.3). The mean inter-tree distances from nest trees were significantly closer than those of reference trees (Table 5.3).

In Mundui, nest trees had significantly greater dbh and canopy cover than reference trees (Table 5.4). All other variables were not significantly different from those of reference trees.

In Sulmac, dbh, and inter-tree distance of nest trees were significantly greater than reference trees (Table 5.5). The slopes of reference trees were significantly greater than nest trees although the p value was very close to the confidence limit (Table 5.5). In Oserian, nest tree height, dbh, and slopes of nest trees, were significantly greater than reference trees, while the inter-tree distances of nest trees were significantly closer than reference trees (Table 5.6). Nests were also constructed on trees that faced eastern slopes (Table 5.6).

Table 5.3: Mann-Whitney-U-test analysis of nest variables between nest trees (n = 7) and reference trees (n = 10) in Hell's Gate.

VARIABLE	Nest tree mean (se)	Reference tree mean (se)	U	p
tree height (m)	13.0 (3.44)	5.4 (0.24)	35.0	**0.022**
dbh (m)	0.30 (0.09)	0.11 (0.02)	33.0	0.052
canopy cover (m)	2.2 (0.12)	2.1 (0.22)	26.0	0.446
slope (degrees)	34.3 (5.46)	4.0 (0.70)	36.0	**0.013**
aspect (degrees)	70.0 (27.5)	264.9 (21.6)	6.0	**0.014**
inter-tree distance (m)	8.27 (1.38)	19.0 (3.48)	7.0	**0.032**

Table 5.4: Mann-Whitney-U-test analysis of nest variables between nest trees (n = 12) and reference trees (n = 29) in Mundui.

VARIABLE	Nest tree mean (se)	Reference tree mean (se)	U	p
tree height (m)	22.1 (3.83)	18.7 (0.77)	101.0	0.527
dbh (m)	0.90 (0.20)	0.46 (0.04)	136.0	**0.020**
canopy cover (m)	11.1 (1.17)	8.0 (0.50)	131.0	**0.036**
slope (degrees)	2.4 (0.40)	3.8 (0.52)	68.5	0.358
aspect (degrees)	270.0 (40.5)	226.5 (18.3)	107.0	0.355
inter-tree distance (m)	16.5 (3.49)	22.7 (1.31)	41.0	0.144

Table 5.5: Mann-Whitney-U-test analysis of nest variables between nest trees (n = 8) and reference trees (n = 8) in Sulmac.

VARIABLE	Nest tree mean (se)	Reference tree mean (se)	U	p
tree height (m)	14.3 (1.18)	20.9 (4.88)	39.0	0.476
dbh (m)	0.68 (0.04)	0.41 (0.09)	60.5	**0.044**
canopy cover (m)	8.8 (0.57)	6.4 (1.62)	52.0	0.401
slope (degrees)	3.3 (2.75)	3.5 (0.33)	30.0	**0.049**
aspect (degrees)	153.3 (69.4)	233.0 (53.8)	32.5	0.119
inter-tree distance (m)	29.9 (3.57)	15.1 (3.03)	62.0	**0.033**

Table 5.6: Mann-Whitney-U-test analysis of nest variables between nest trees (n = 11) and reference trees (n = 22) in Oserian.

VARIABLE	Nest tree mean (se)	Reference tree mean (se)	U	p
tree height (m)	13.6 (0.90)	8.5 (0.73)	165.0	**0.002**
dbh (m)	0.53 (0.05)	0.21 (0.09)	175.0	**0.000**
canopy cover (m)	2.5 (0.07)	2.2 (0.22)	140.0	0.078
slope (degrees)	38.1 (3.03)	10.3 (1.46)	182.0	**0.000**
aspect (degrees)	121.0 (49.8)	188.5 (26.0)	77.0	0.161
inter-tree distance (m)	7.1 (0.92)	16.0 (1.47)	40.0	**0.001**

The tree height to canopy cover ratio was highest for nest trees in Hell's Gate and Oserian (*E. magnicapsular* trees) (Figure 5.5). Nest trees in Mundui and Sulmac had low tree height to canopy cover ratios (Figure 5.5). The ratios between nest trees and reference trees in Mundui were similar while those of Sulmac differed by a factor of two.
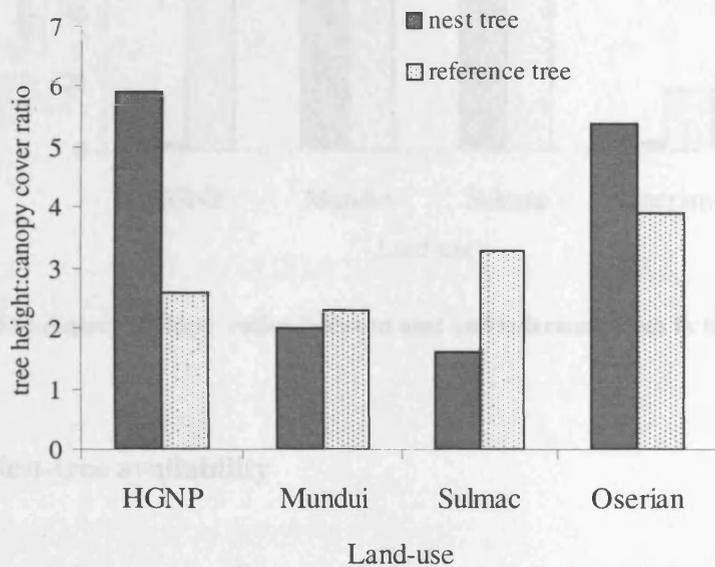
Figure 5.5: Tree height to canopy cover ratios between nest and reference trees in the different land-use areas.

Nest trees in Hell's Gate and Oserian had the lowest aspect to slope ratios while Mundui had the highest (Figure 5.6). Reference trees in Oserian had the lowest aspect to slope ratios while those in Hell's Gate, Mundui and Sulmac had comparatively higher ratios (Figure 5.6).

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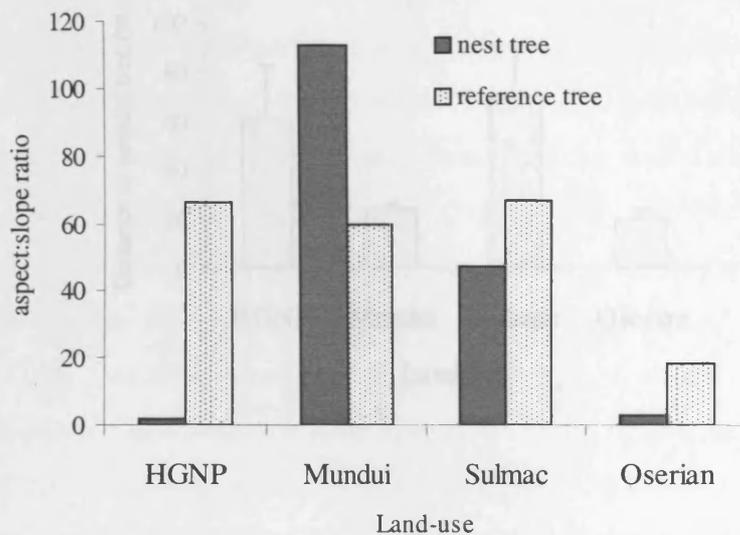
Figure 5.6: Aspect to slope ratios between nest and reference trees in the different land-use areas.

5.2.2 Nest-tree availability

The mean distance to the nearest 'potential nest-tree' from each random point was significantly different among sites (Figure 5.7) (Kruskal-Wallis df = 3, H = 20.17, p < 0.001). In Hell's Gate, the mean distance to the nearest tree from a random point was 60.3 m (range 10 – 256 m, se = 22.3) whilst in Mundui, the mean nearest-tree distance was 24.4 m (range 4 – 50 m, se = 2.10 m). In Sulmac, the mean nearest-tree distance was 69.4 m (range 20 – 200 m, se = 20.8) while for Oserian it was 19.9 m (range 5 – 100 m, se = 4.4). When both Sulmac and Oserian were considered as one unit, the mean nearest-tree distances were significantly different among Hell's Gate, Mundui and Sulmac-Oserian (Kruskal-Wallis, df = 2, H = 7.05, p = 0.03).
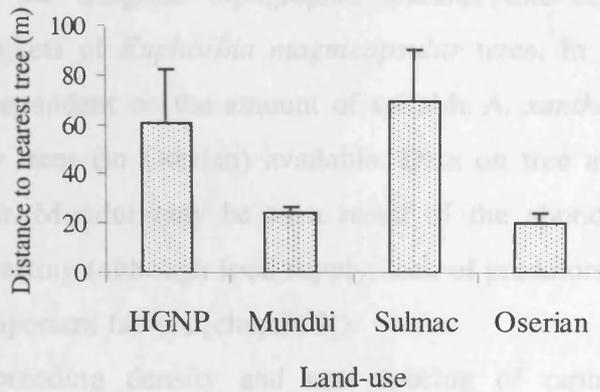
Figure 5.7: Distances (and standard errors) of nearest trees from random points taken at various study sites (1997).

5.2.3 Alternative nests

The mean number of alternative nests used per pair, out of 28 intimately known pairs in the study area, was 2.10 (se = 0.22). Augur buzzards inhabiting Hell's Gate and Sulmac had a mean of 2.50 and 2.22 nests per pair respectively, compared to birds in Mundui and Oserian which had 1.83 and 1.86 nests per pair respectively. Pairs in Hell's Gate and Sulmac constructed more nests although there was no significant difference in the mean number of alternative nests used across study sites (Kruskall-Wallis, df = 3, H = 3.27, p = 0.352).

5.3 DISCUSSION

5.3.1 Nest spacing and density

Mundui had the highest density of augur buzzards that were most closely spaced compared to Hell's Gate and Sulmac-Oserian. Nests in Mundui were built exclusively on *Acacia xanthophloea* trees which were abundant. Nest spacing in Hell's Gate was

dependent on the irregular topographic features like cliffs and steep-sloped hills harbouring pockets of *Euphorbia magnicapsular* trees. In the horticultural areas, nest spacing was dependent on the amount of suitable *A. xanthophloea* (in Sulmac) and *E. magnicapsular* trees (in Oserian) available. Data on tree availability suggests that the high density in Mundui may be as a result of the abundance of suitable nest trees available for nesting (although food supply, lack of predators and reduced human impact may also be important factors [chapter 9]).

Both breeding density and nest spacing of raptors are influenced by the availability of food and nest sites (Newton, 1979), which can in turn be affected by human impacts (Brandl *et al.*, 1985). It follows that raptors should be spaced further apart in areas negatively affected by anthropogenic factors (Brandl *et al.*, 1985). Augur buzzard pairs were more widely spaced in areas where human impacts had increased. Over the 3-year study period, *A. xanthophloea* trees along the southern shoreline were being cleared at an annual rate of approximately 5% (pers. obs), mainly to create and develop horticultural fields. Secondary reasons included provision of fuel wood and building material for horticultural staff. Clearance of these woodlands would reduce the numbers of available nest sites, perch sites and foraging area for augur buzzards. Schmutz (1984) found that agricultural development adversely affected the breeding density of ferruginous hawks *B. regalis* in Alberta, Canada.

The visibility of nests between neighbouring augur buzzard pairs did not affect nest-spacing and hence suggests that the availability of suitable nest sites may have played an important role in the nest spacing of augur buzzards. However, territorial displays and intra/inter-specific interactions were frequently observed and this may have also been important in influencing augur buzzard nest spacing (chapter 6).

Fry *et al.* (1988) suggested that augur buzzard pairs in the Rift Valley in Kenya occupied territories of 1 km² or even less. The overall density estimate of 0.45 pairs per km² was lower than the 0.83 pairs per km² estimated by Muhweezi (1990) in the Impenetrable Forest, Uganda. In Zimbabwe's Matopos hills (a habitat similar to Hell's Gate), Lendrum (1979) estimated augur buzzard density at 0.06 pairs per km², which was 7.5 times lower than that of the southern Lake Naivasha area. This large difference may be as a result of differences in food quality and availability as well as competition for

food and nest sites with the Verreaux's eagle *Aquila verreauxii*, which occurs at high densities in the Matopos hills (Gargett, 1990). This scenario is similar to that found in the rough-legged buzzard *Buteo lagopus*, in the Siberian tundra where their population densities were limited by the diversity of small mammals and the presence of a larger competitor, the snowy owl *Nyctea scandiaca* (Potapov, 1997).

5.3.2 Melansim

The 13% proportion of melanistic birds found in the study area, compared well with the figures given by Lewis and Pomeroy (1989), who estimated its occurrence in Kenya at between 10 and 25% depending on the amount of rainfall (more melanistic birds were found in areas of high rainfall). The southern Lake Naivasha area has lower rainfall compared to other areas in the Kenyan highlands and hence a lower occurrence of melanism was observed.

5.3.3 Nest-site characteristics and selection

Euphorbia magnicapsular and *Acacia xanthophloea* trees were the most common trees in the southern Lake Naivasha area and hence the most likely choice of nest sites. The occurrence of both tree species was mutually exclusive – *E. magnicapsular* grows on steep slopes on hill sides in Hell's Gate and Oserian while *A. xanthophloea*, (which is on average about two and a half times taller) grows on gently sloping land in Mundui and Sulmac close to the lake shore. The variability in tree height to canopy cover ratio and the aspect to slope ratio was reflected in the topography of the different land-uses.

The variability in nest tree characteristics at each site suggested that augur buzzards were adaptable to a wide range of nest sites. For example, in Hell's Gate, one pair (H7) built a nest on an *A. drepanolobium* tree at a height of 3.5 m, as this was the only 'suitable' tree available for nesting in their territory. In Hell's Gate, augur buzzards nested in *E. magnicapsular* although cliffs were present. This was observed with at least two pairs (H5A and H5B) both of which nested on *E. magnicapsular* trees, which grew at the base of large cliffs. Cliffs apparently are the last choice for augur buzzards, selected

in the absence of suitable trees. This may be because other raptors such as Verreaux's eagles *Aquila verreauxii* and lanner falcons *Falco biarmicus* nest exclusively on cliffs and thus constant aggressive interactions between these and augur buzzards may negatively affect the latter's breeding performance. Augur buzzard eggs and young on cliff nests are also more vulnerable to baboons and other predators.

In Mundui, the growth form of nest trees was similar to those of reference trees suggesting that there was no shortage of nest sites. However in Sulmac, the growth form of reference trees did not conform to those of nest trees suggesting that although trees were available, suitable nest sites may have been limiting. The aspect to slope ratio gave a good indication of nest site availability in Hell's Gate and Oserian. The data suggests that in these areas, *E. magnicapsular* trees were more scarce in Hell's Gate than in Oserian.

Augur buzzards selected *E. magnicapsular* trees that were taller, more mature and those that grew on the steepest slopes. Taller and mature trees were selected as nest sites because these probably had nests in them built by previous occupants and were inherited by present ones. Elevated nests in Hell's Gate and Oserian may also provide vantage points from which hunting areas can be more easily watched (see Tubbs, 1974). These nests were also built on trees with others nearby that provided perching posts for females to defend their nests and for males to 'pluck' prey prior to delivery. Nests on *E. magnicapsular* trees are well concealed from below and probably less conspicuous than those constructed on shorter shrubs such as *A. drepanolobium*. This suggests that nests on *E. magnicapsular* trees are less vulnerable to predators. Nests in Hell's Gate and Oserian were also constructed on trees that grew on eastern-facing slopes. The prevailing winds in East Africa (just below the equator) originate from the south east and hence the advantage of having nests on eastern-facing slopes may enable augur buzzards to fly out of their nests directly against the wind with minimum effort. Nest trees in Hell's Gate and Oserian (by virtue of being on steep-sloped hills) are also on a relatively higher elevation than those in Mundui or Sulmac, and hence are exposed to windy conditions and cooler temperatures (especially at night). Hence another reason for constructing nests in trees on eastern-facing slopes is that the early morning sun can warm the nest contents (either an incubating adult or nestlings) during cold mornings in the cool dry season when egg-

laying peaks (Brown and Britton, 1980) (see also chapter 8 on breeding seasons). This means that adults can spend less time brooding young and more time hunting for food or defending their eggs/young against predators.

Augur buzzards selected the most mature *A. xanthophloea* trees that also had the greatest canopy cover. Nests were built on the large flat crown usually at the edges. Trees with greater canopy cover have large branches and abundant foliage (with thorns), both of which protect the nest from predators and weather. Most nests on *A. xanthophloea* trees had a conspicuous open space immediately adjacent to at least one side of the nest tree (although the canopy usually remained unbroken). This feature may provide an unobstructed flight path to the nest which would be advantageous to the adults while making numerous trips with nesting material (large sticks) and food, and to the young while making their initial flight attempts.

Augur buzzards in Hell's Gate and Sulmac constructed more nests per territory than those in Mundui and Oserian. Although this result was not statistically different, it may be as a result of a low sample size coupled with only three years of observation. The presence of predators in Hell's Gate and high human disturbance in Sulmac probably suggests that augur buzzards in these areas build more nests for back-up purposes in case one fails. This aspect should be investigated in future studies.

The data suggest that augur buzzards choose nest sites on the basis of their overall structural characteristics, and then focus on a particular nest tree. Favourable habitat structure and topography probably trigger the 'settling reaction'. Moore and Henny (1984) point out the additional importance of past experience (success or failure) to nest site selection, but at least for first-time nesters, the role of early experience (Klopfer, 1963) and imprinting to the natal habitat (Hilden, 1965) may be of primary importance, especially in areas with high adult mortalities. Additional factors such as prey density, prey availability, competition and the presence of predators need to be addressed in future studies of nest site selection by augur buzzards.

CHAPTER SIX

BREEDING BEHAVIOUR

6.1 BREEDING BEHAVIOUR

A total of 346 hours was spent observing 8 augur buzzard nests (4 in Hell's Gate and 4 in the lake environs) during different stages of the breeding cycle (Table 6.1) (Figure 6.1).

Table 6.1: Summary of observation time (in hours) for 8 pairs of breeding augur buzzards in 1995

Pair no.	Site	Period observed (1995)	Incubation	Early nestling	Late nestling	Total
H1	Hell's Gate	24 May-18 Sep	20	20	12	52
H2A	Hell's Gate	13 May-25 Jun	0	12	16	28
H5A	Hell's Gate	5 Jul-19 Sep	12	16	24	52
H6A	Hell's Gate	30 May-4 Oct	16	12	12	40
K1	lake environs	13 May-13 Jul	18	40	32	80
K3	lake environs	1 Jul-1 Sep	12	24	12	48
R1	lake environs	27 Apr-11 May	0	12	4	16
S5	lake environs	25 Jul-19 Aug	0	8	12	20
Totals			78	144	124	346

Three of the 4 nests observed in Hell's Gate were on cliffs (H1, H2A, H6A) while the fourth (H5A) was on a *Euphorbia magnicapsular* tree. In the lake environs, 3 of the 4 nests were on *Acacia xanthophloea* trees (R1, K1, K3) while the fourth was on an *E. magnicapsular* tree (S5). The male and female of each of the 8 pairs observed were readily distinguishable by either colour morph, "window" marks in their mid-secondary feathers, plumage, and/or rings. Chicks in the nest were usually seen on the third day after hatching, although feeding was observed when chicks were not visible. In Hell's Gate, 2 of the 4 nests (H1, H6A) failed during the incubation period but the parents re-laid within a period of two weeks. Nest H1 failed, apparently because rock climbers were too close to the nest, resulting in the eggs being unattended for a long period, while the eggs of nest H6A were depredated by baboons. All 4 pairs in Hell's Gate plus 2 pairs in the lake environs
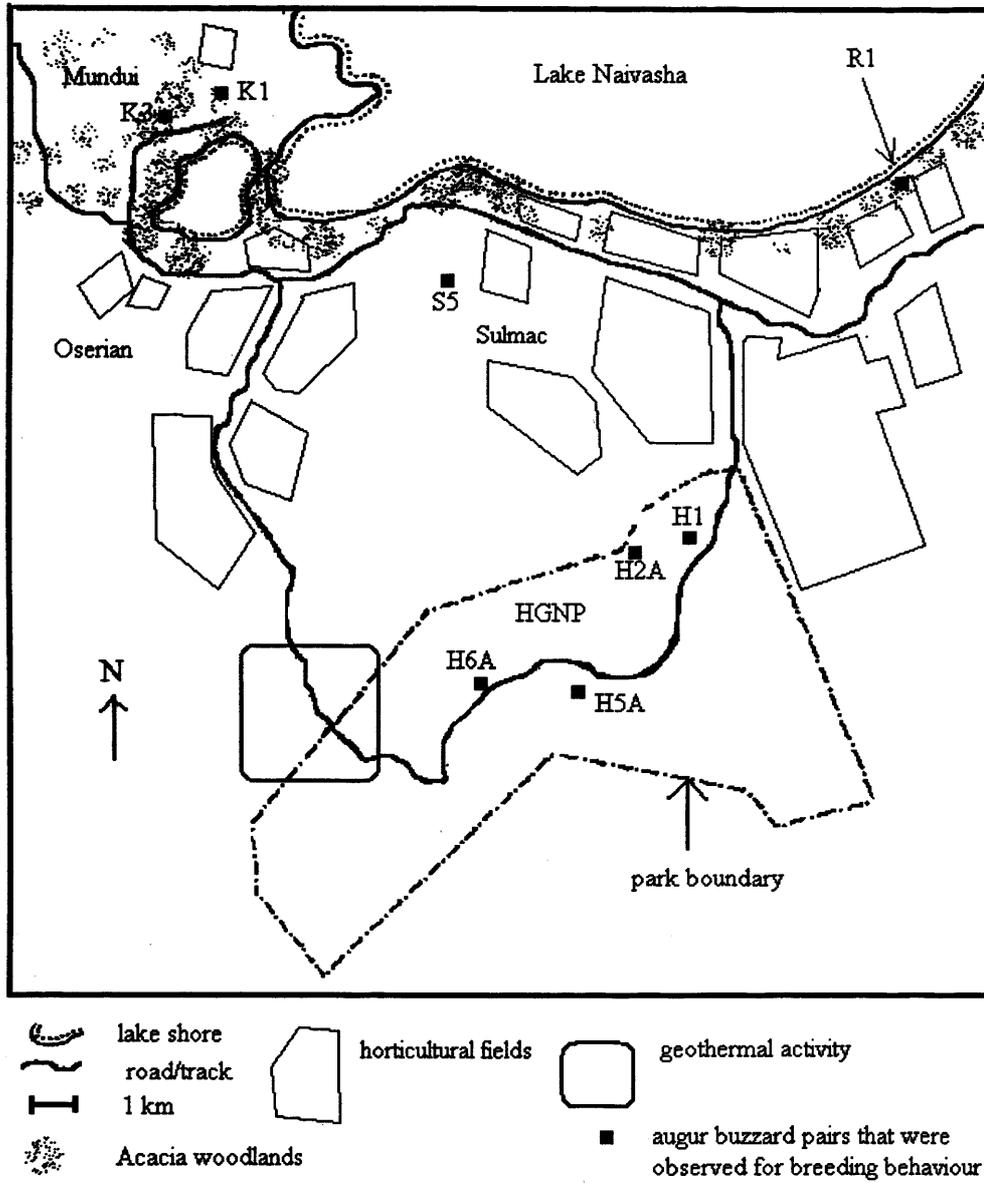
Figure 6.1:Locations of the nests of 8 pairs of augur buzzards observed for breeding behaviour

(R1 and K3) successfully fledged 1 chick each while pairs K1 and S5 successfully fledged 2 chicks each. Siblicide behaviour was observed only in one nest (R1), which resulted in the death of a ten-day old chick. A full account of breeding performance is given in chapter 9.

6.1.1 Location and activity time budget during the breeding cycle

Incubation stage

During incubation, food exchanges occurred without inter-sexual aggression. Males with prey initiated the changeover by either calling from a perch within sight of the nest or perching on the nest itself. Females usually took the prey and flew away from the nest to feed. The male typically initiated incubation once the female left the nest and remained on the nest until the female returned. Female augur buzzards from the lake environs spent 88% ($\pm$ 5.9) of their time at the nest compared with females from Hell's Gate, who spent only 60.7% ($\pm$ 8.29). This difference was not statistically significant, though very close (Mann-Whitney; $U = 168.5$, $p = 0.051$; significance level 0.05) (Figure 6.2). Male augur buzzards from Hell's Gate spent significantly more time (34.9% $\pm$ 8.02) at the nest during the incubation period than males from the lake environs (8.8% $\pm$ 5.06) (Mann-Whitney; $U = 236.5$, $p < 0.05$) (Figure 6.2).
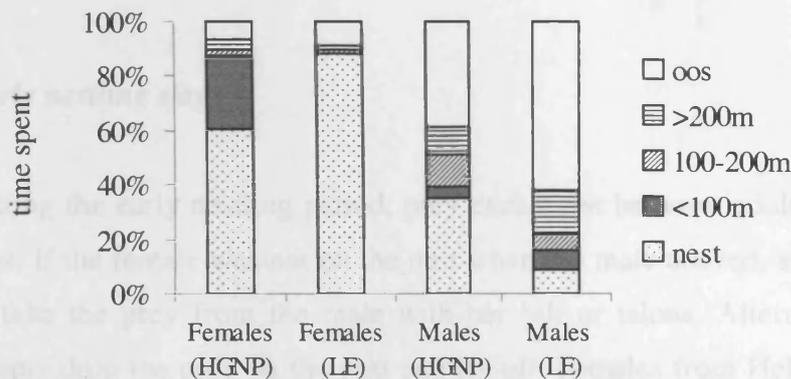
Figure 6.2: Proportion of time spent at various distances from the nest by male and female augur buzzards in Hell's Gate and the lake environs (LE) during the incubation stage (n = 78 hours) (oos = out of sight).

While at the nest, females from the lake environs spent significantly more time attending to eggs (Mann-Whitney; U = 178.5, p < 0.05) than those from Hell's Gate, which spent more time perched close to their nests (Figure 6.3). Males from Hell's Gate spent significantly more time (34.4% ± 8.15) incubating compared to those from the lake environs (7.8% ± 5.18) (Figure 6.3) (Mann-Whitney; U = 235, p < 0.05).
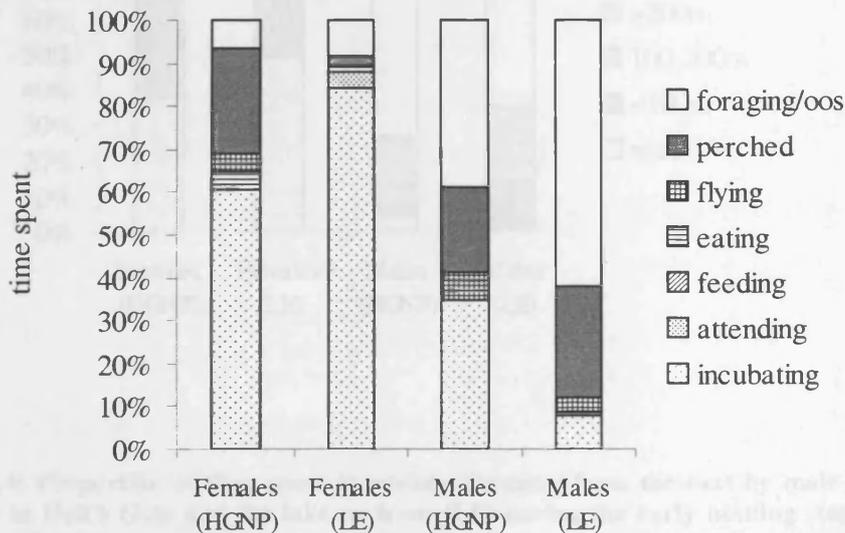
Figure 6.3: Proportion of time spent by male and female augur buzzards in various activities in Hell's Gate and the lake environs (LE) during the incubation stage (n = 78 hours) (oos = out of sight).

Early nestling stage

During the early nestling period, prey exchanges between adults always occurred at the nest. If the female was not on the nest when the male arrived, she flew immediately to it to take the prey from the male with her bill or talons. Alternatively, the male would simply drop the prey on the nest and fly off. Females from Hell's Gate spent more time perched close (< 200 m) to their nests than those from the lake environs, although this difference was not significant (Mann-Whitney; U = 367, p > 0.05) (Figure 6.4).

Males from Hell's Gate spent more time attending to chicks than their counterparts from the lake environs, although this difference was not significant (Mann-Whitney; U = 316.5, p < 0.05) (Figure 6.5).
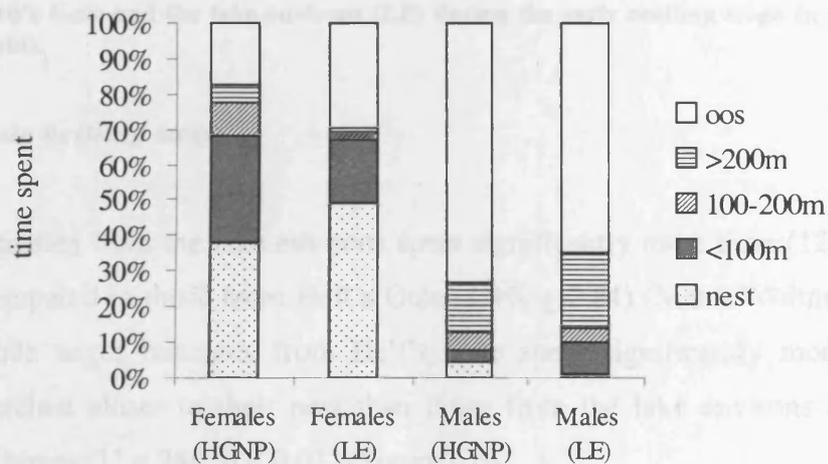
Figure 6.4: Proportion of time spent at various distances from the nest by male and female augur buzzards in Hell's Gate and the lake environs (LE) during the early nestling stage (n = 144 hours) (oos = out of sight).

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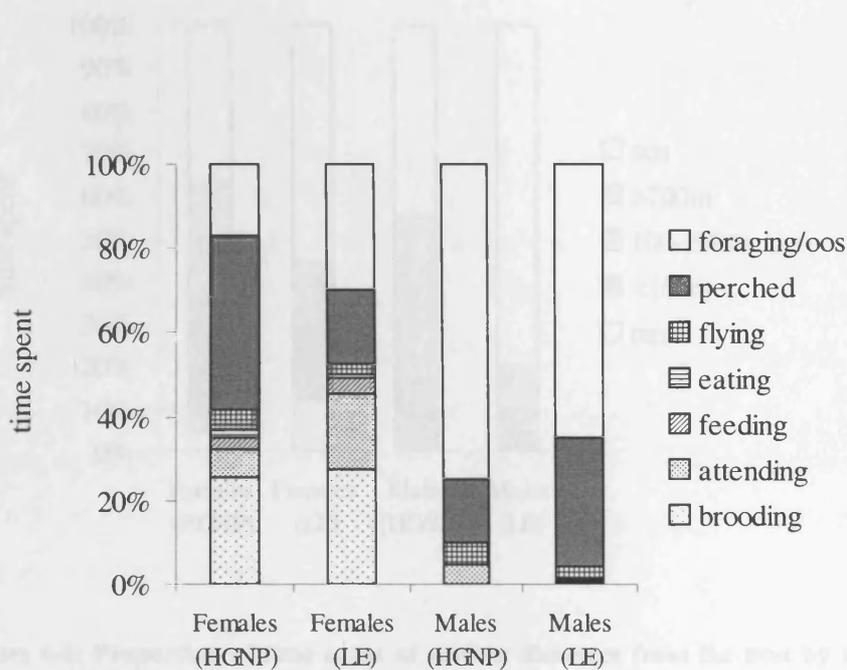
Figure 6.5: Proportion of time spent by male and female augur buzzards in various activities in Hell's Gate and the lake environs (LE) during the early nestling stage (n = 144 hours) (oos = out of sight).

Late nestling stage

Females from the lake environs spent significantly more time (12.3% ± 3.33) at the nest compared to those from Hell's Gate (4.4% ± 2.84) (Mann-Whitney; U = 255, p < 0.05). Male augur buzzards from Hell's Gate spent significantly more time (15.7% ±4.56) perched closer to their nest than those from the lake environs (3.9% ± 2.08) (Mann-Whitney; U = 386, p < 0.01) (Figure 6.6).

Females from the lake environs spent significantly more of their time (6.2% ± 2.94) attending to chicks at the nest as opposed to those from Hell's Gate (0.1% ± 0.1) (Mann-Whitney; U = 266, p < 0.01) (Figure 6.7). There were no significant differences between the respective males and females of both areas in the amount of time spent feeding young, eating and flying (Mann-Whitney; U = 290, p > 0.05).

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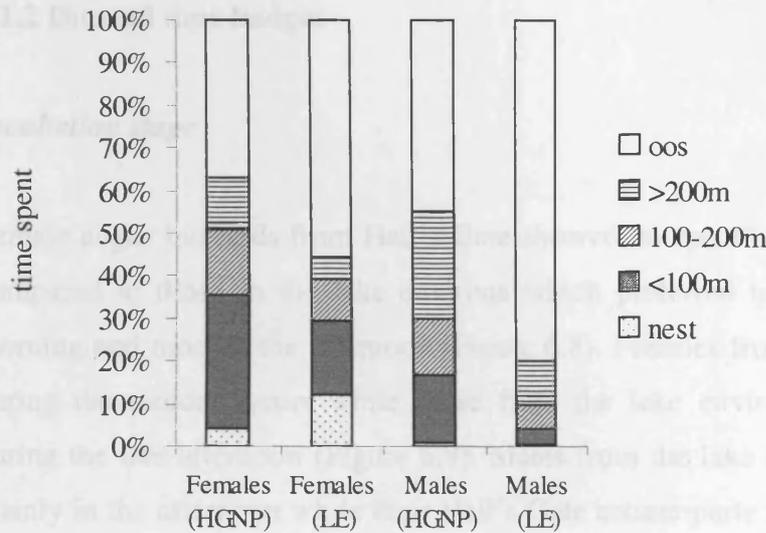
Figure 6.6: Proportion of time spent at various distances from the nest by male and female augur buzzards in Hell's Gate and the lake environs (LE) during the late nestling stage (n = 124 hours) (oos = out of sight).
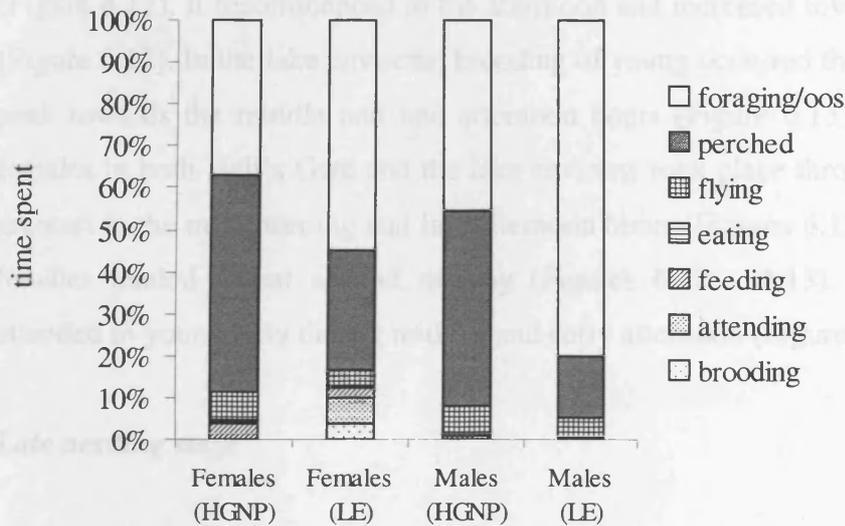
Figure 6.7: Proportion of time spent by male and female augur buzzards doing various activities in Hell's Gate and the lake environs (LE) during the late nestling stage (n = 124 hours) (oos = out of sight).

6.1.2 Diurnal time budget

Incubation stage

Female augur buzzards from Hell's Gate showed no specific time period for incubation compared to those in the lake environs which preferred to incubate during the early morning and most of the afternoon (Figure 6.8). Females from Hell's Gate tended to eat during the midday hours while those from the lake environs fed almost exclusively during the late afternoon (Figure 6.9). Males from the lake environs tended to incubate mainly in the afternoon while their Hell's Gate counterparts showed no preferential time period (Figures 6.10 – 6.11).

Early nestling stage

Females from Hell's Gate showed a preference for brooding young mainly during the early morning hours, which waned towards midday when no brooding took place at all (Figure 6.12). It recommenced in the afternoon and increased towards the end of the day (Figure 6.12). In the lake environs, brooding of young occurred throughout the day with a peak towards the middle and late afternoon hours (Figure 6.13). Feeding of young by females in both Hell's Gate and the lake environs took place throughout the day but was greatest in the mid-morning and late afternoon hours (Figures 6.12 – 6.13). In both areas, females tended to eat around midday (Figures 6.12 – 6.13). In Hell's Gate, males attended to young only during midday and early afternoon (Figure 6.14).

Late nestling stage

Females from Hell's Gate fed young from mid-morning to midday, while in the lake environs, females fed young from mid-morning, through to a peak in the late afternoon (Figure 6.16 and 6.17).
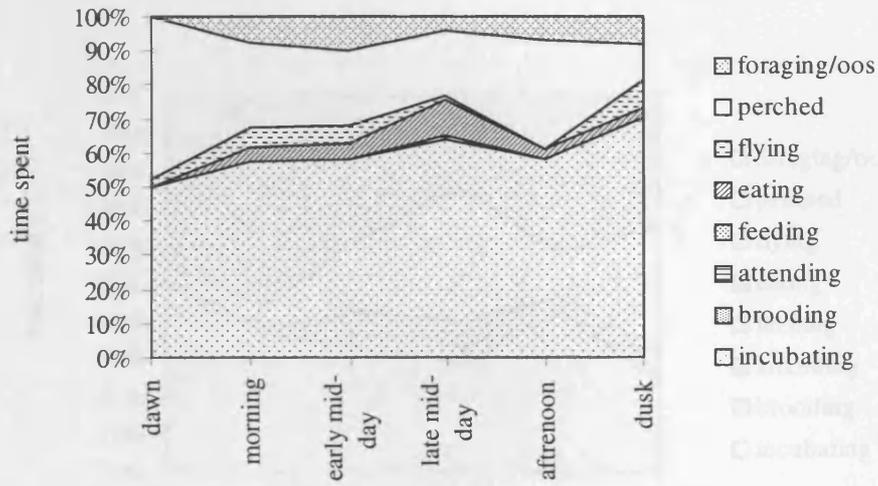
Figure 6.8: Diurnal time budget of augur buzzard females in Hell's Gate during the incubation stage (n = 48 hours) (oos = out of sight).
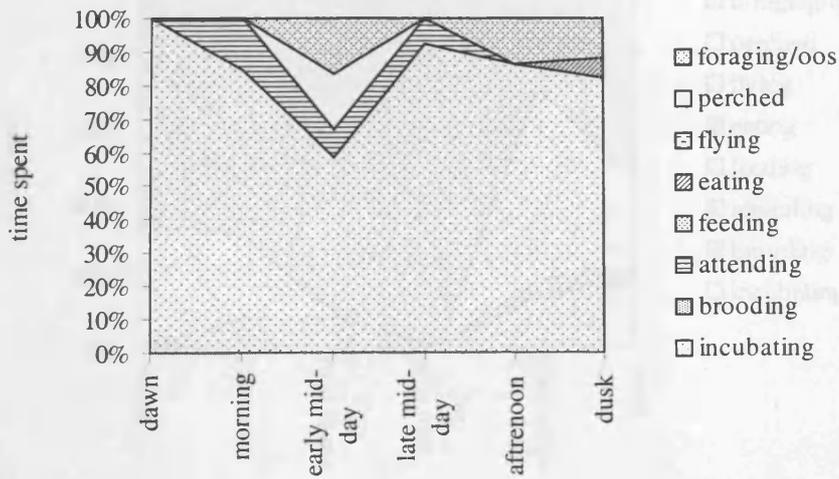
Figure 6.9: Diurnal time budget of augur buzzard females in the lake environs during the incubation stage (n = 30 hours) (oos = out of sight).
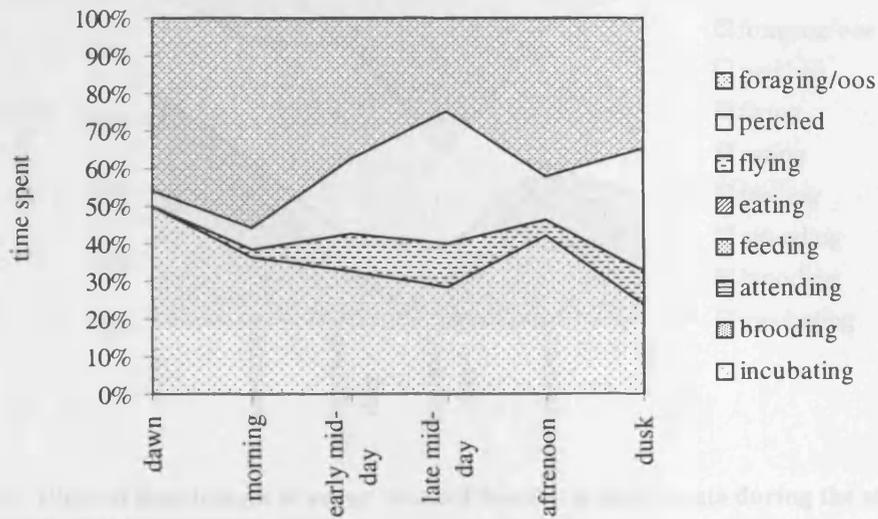
Figure 6.10: Diurnal time budget of augur buzzard males in Hell's Gate during the incubation stage (n = 48 hours) (oos = out of sight).
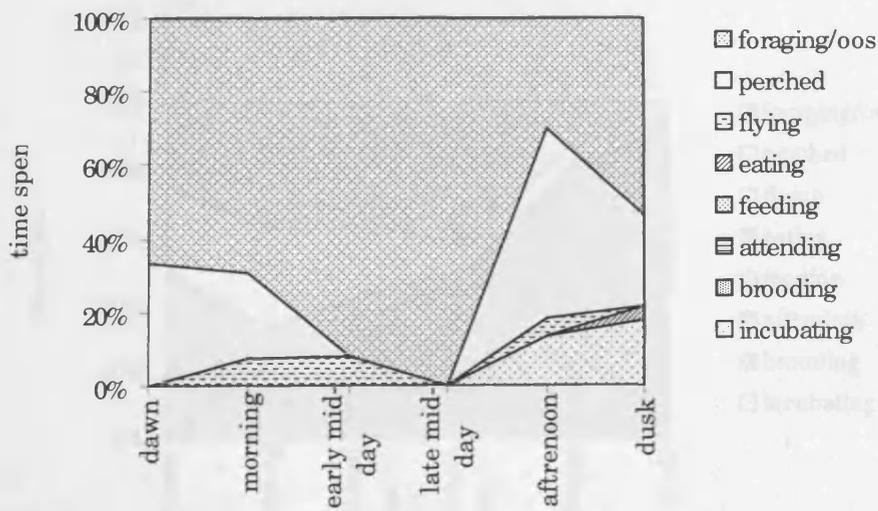
Figure 6.11: Diurnal time budget of augur buzzard males in the lake environs during the incubation stage (n = 30 hours) (oos = out of sight).
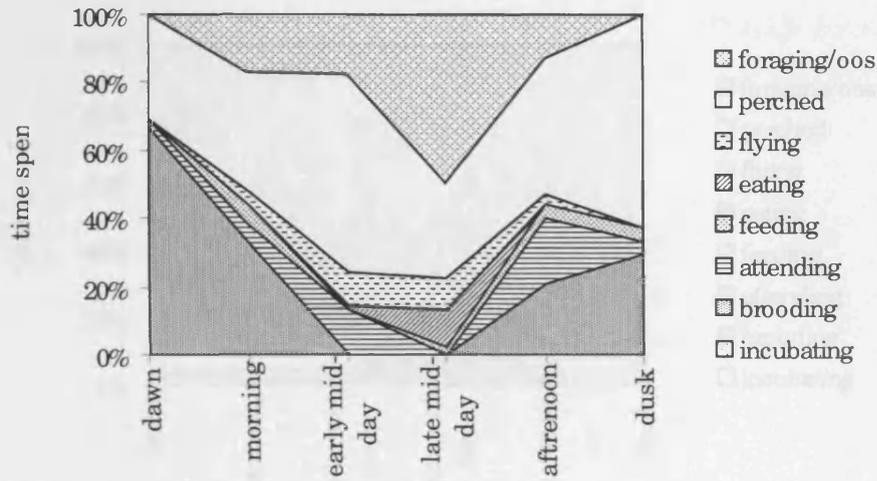
Figure 6.12: Diurnal time budget of augur buzzard females in Hell's Gate during the early nestling stage (n = 60 hours) (oos = out of sight).
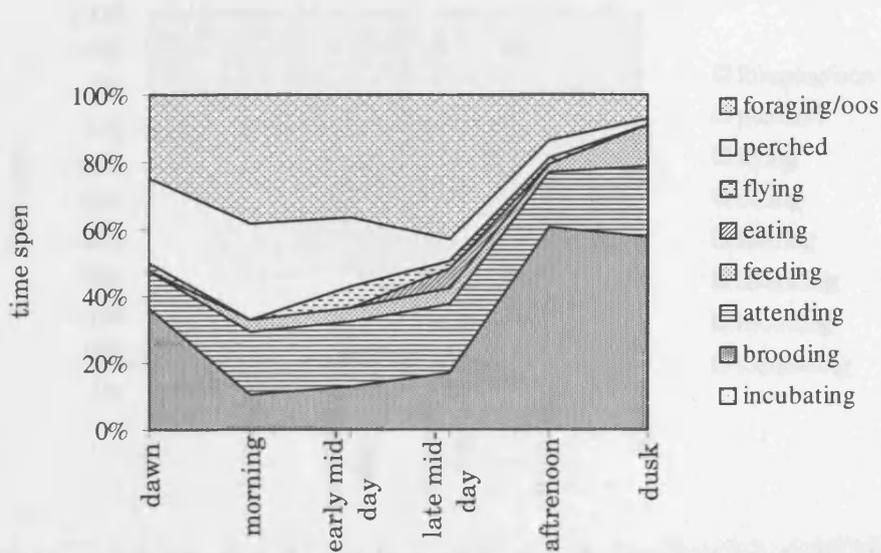
Figure 6.13: Diurnal time budget of augur buzzard females in the lake environs during the early nestling stage (n = 84 hours) (oos = out of sight).
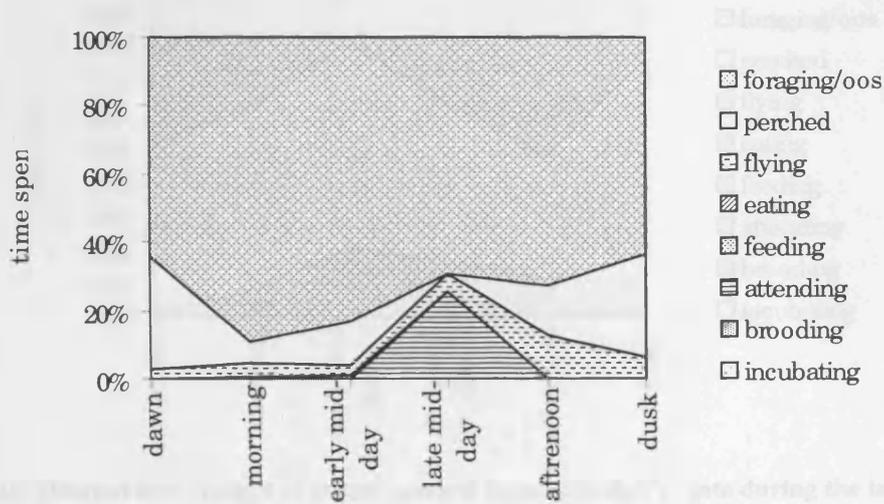
Figure 6.14: Diurnal time budget of augur buzzard males in Hell's Gate during the early nestling stage (n = 60 hours) (oos = out of sight).
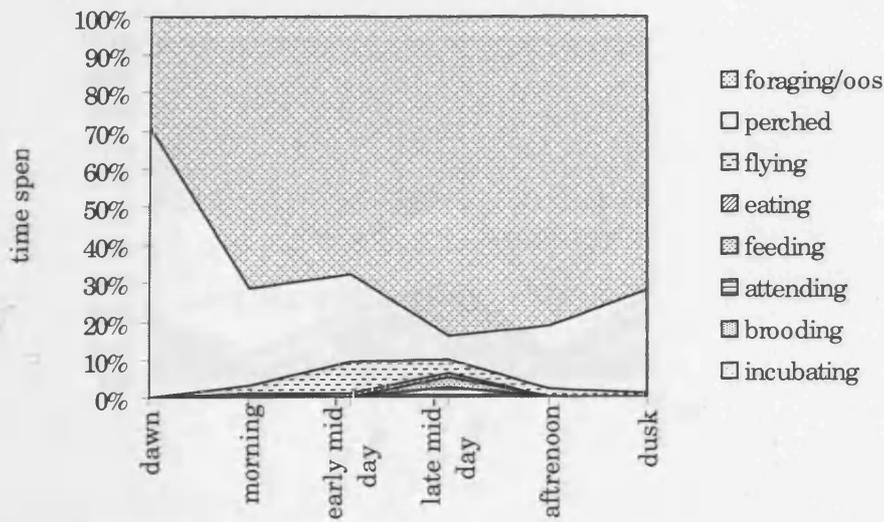
Figure 6.15: Diurnal time budget of augur buzzard males in the lake environs during the early nestling stage (n = 84 hours) (oos = out of sight).

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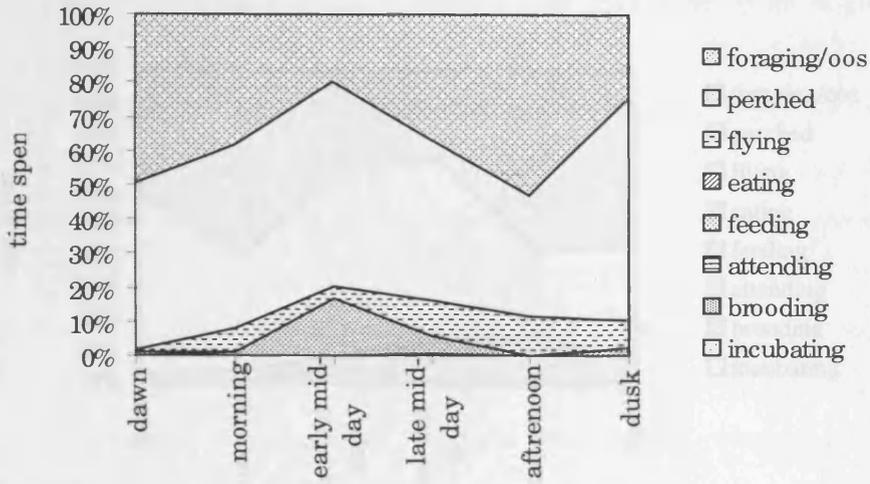
Figure 6.16: Diurnal time budget of augur buzzard females in Hell's Gate during the late nestling stage (n = 64 hours) (oos = out of sight).
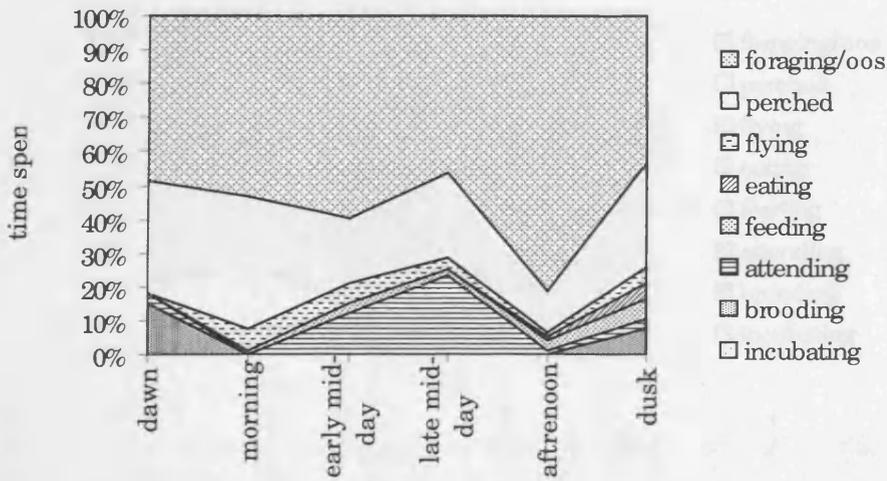
Figure 6.17: Diurnal time budget of augur buzzard females in the lake environs during the late nestling stage (n = 60 hours) (oos = out of sight).

86
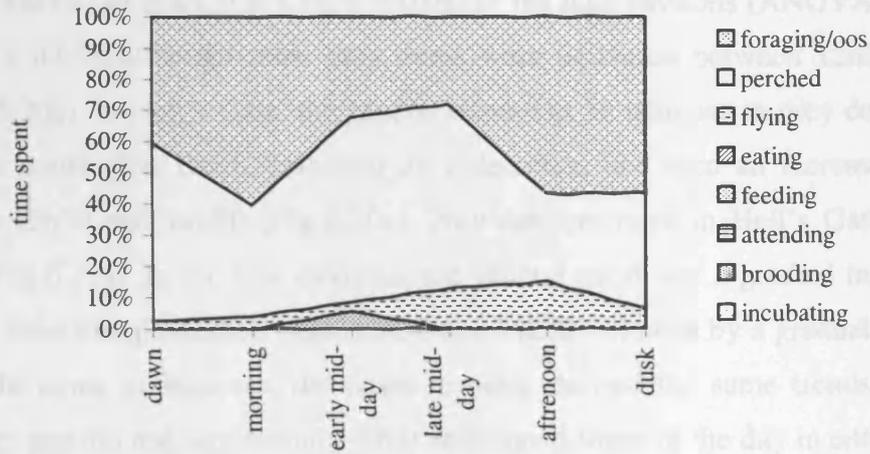
Figure 6.18: Diurnal time budget of augur buzzard males in Hell's Gate during the late nestling stage (n = 64 hours) (oos = out of sight).
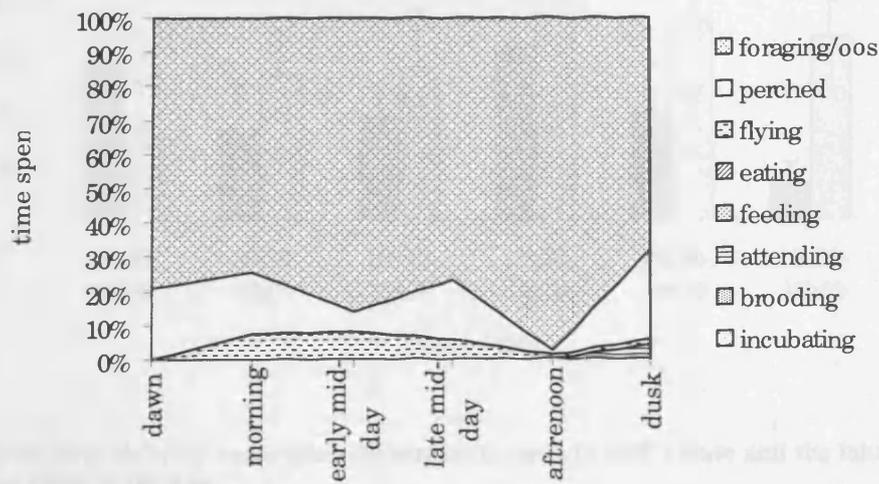
Figure 6.19: Diurnal time budget of augur buzzard males in the lake environs during the late nestling stage (n = 60 hours) (oos = out of sight).

6.1.3 Factors influencing prey delivery rates

Time of the day

Time of the day did not significantly influence prey deliveries to nests in either Hell's Gate (ANOVA; df = 86, F = 1.45, p > 0.05) or the lake environs (ANOVA; df = 83, F = 0.97, p > 0.05), although most prey items were delivered between 12h30 and 14h30 (Figure 6.20a). In Hell's Gate, the general trend was an increase in prey deliveries in the first two hours after dawn, followed by a decrease, and then an increase that peaked between 12h30 and 14h30 (Fig 6.20a). Prey delivery rates in Hell's Gate waned after 14h30 (Fig 6.20a). In the lake environs, the general trend was a gradual increase in prey delivery rates that peaked between 12h30 and 14h30 followed by a gradual decrease (Fig 6.20a). In terms of biomass, deliveries to nests showed the same trends as with prey deliveries and did not significantly differ at different times of the day in either Hell's Gate (ANOVA; df = 86, F = 1.41, p > 0.05) or the lake environs (ANOVA; df = 83, F = 1.43, p > 0.05) (Figure 6.20b).
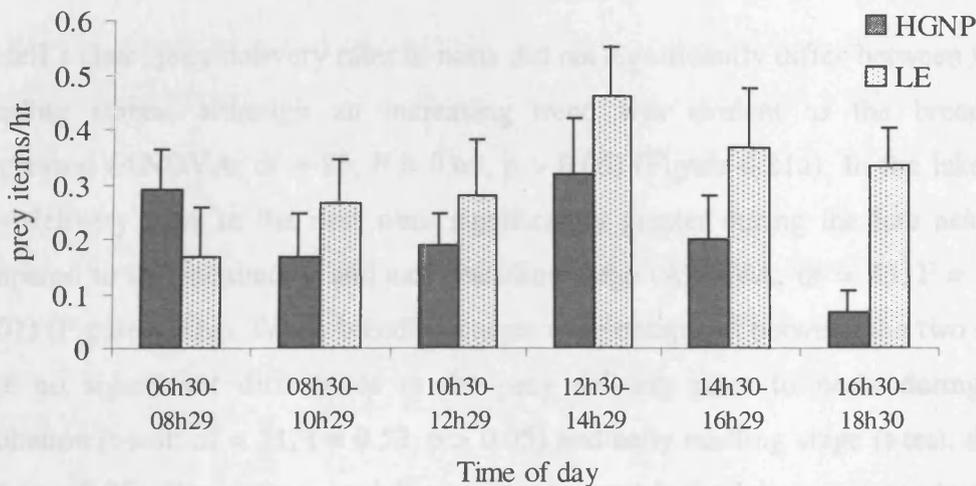
Figure 6.20a: Prey delivery rates (plus std errors) to nests in Hell's Gate and the lake environs (LE) at different times of the day.
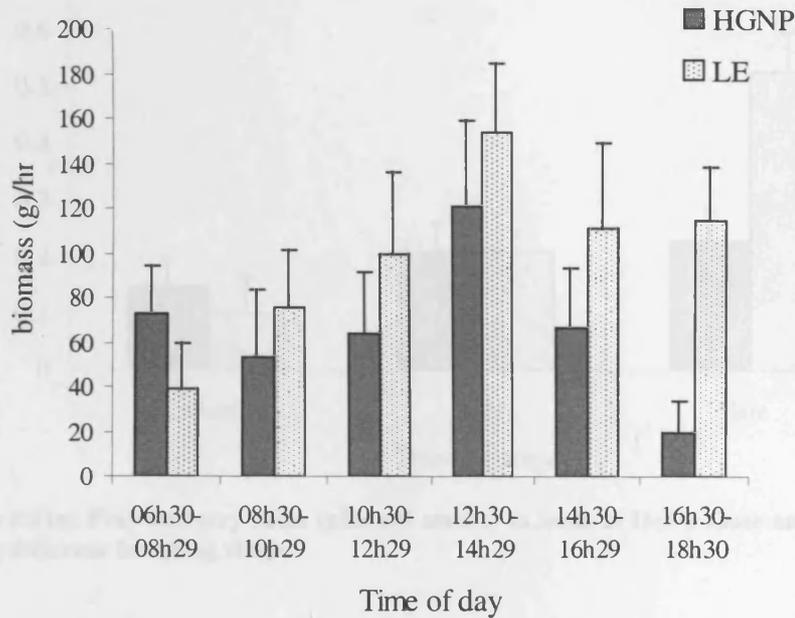
Figure 6.20b: Biomass of prey delivered per hour (plus std errors) to nests in Hell's Gate and the lake environs (LE) at different times of the day.

Breeding stage

In Hell's Gate, prey delivery rates to nests did not significantly differ between the various breeding stages, although an increasing trend was evident as the breeding cycle progressed (ANOVA; df = 86, F = 0.65, p > 0.05) (Figure 6.21a). In the lake environs, prey delivery rates to the nest were significantly greater during the late nestling stage compared to the incubation and early nestling stage (ANOVA; df = 83, F = 11.46, p < 0.001) (Figure 6.21a). When breeding stages were compared between the two sites, there were no significant differences in the prey delivery rates to nests during both the incubation (t-test; df = 21, t = 0.53, p > 0.05) and early nestling stage (t-test, df = 63, t = 0.08, p > 0.05). However, prey delivery rates to nests in the lake environs, during the late nestling stage were significantly greater than in Hell's Gate (t-test, t = -3.18, p < 0.01).
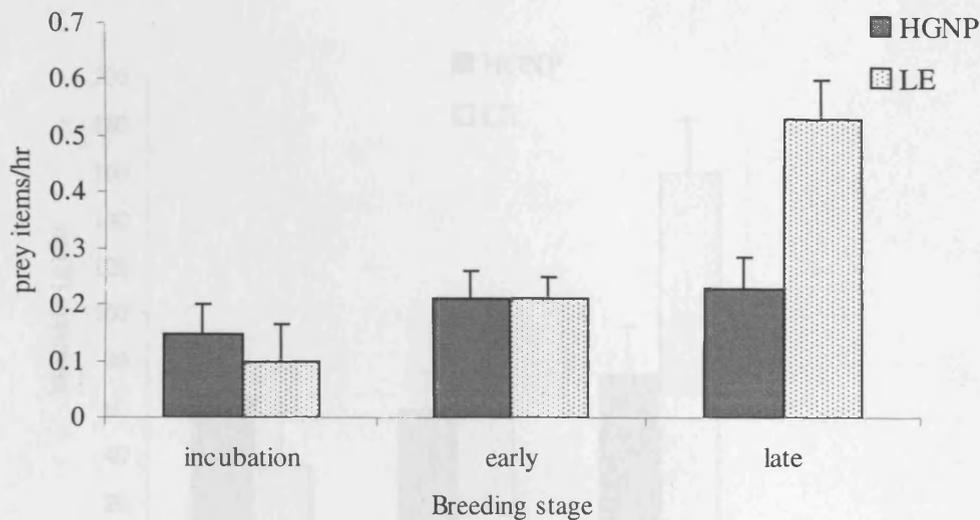
Figure 6.21a: Prey delivery rates (plus std errors) to nests in Hell's Gate and the lake environs (LE) during different breeding stages.

Biomass deliveries to nests also showed the same trends as with prey deliveries. In Hell's Gate, biomass delivered to nests did not significantly differ during the various breeding stages (ANOVA; df = 86, F = 0.167, p > 0.05) (Figure 6.21b). However in the lake environs, biomass delivered to nests was significantly greater during the late nestling stage compared to the incubation and early nestling stages (ANOVA; df = 83, F = 7.42, p < 0.001) (Figure 6.21b). Between the two sites, biomass delivered to nests was not significantly different during the incubation (t-test; df = 33, t = 0.719, p > 0.05) and early nestling stage (t-test; df = 74, t = -0.65, p > 0.05) (Figure 6.21b). However, biomass delivered to nests in the lake environs during the late nestling stage was significantly greater than in Hell's Gate (t-test; df = 60, t = -2.75, p < 0.01) (Figure 6.21b).
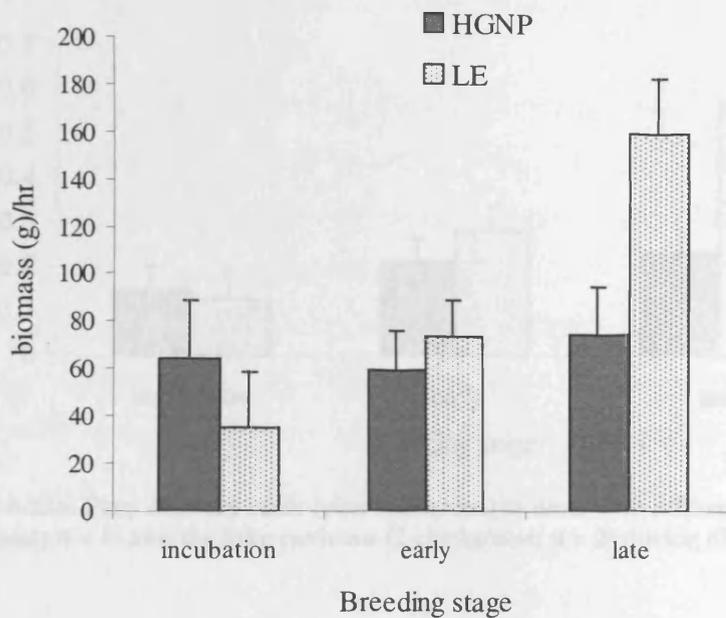
Figure 6.21b: Biomass of prey delivered per hour (plus std errors) to nests in Hell's Gate and the lake environs (LE) during different breeding stages.

Brood size

Prey delivery rates to nests with different brood sizes in Hell's Gate and the lake environs did not significantly differ during the incubation (t-test; df = 3, t = -0.06, p > 0.05) and the early nestling period (t-test; df = 43, t = 1.60, p > 0.05). However, during the late nestling stage, prey delivery rates to nests in the lake environs were significantly greater than in Hell's Gate (t-test; df = 36, t = 1.60, p < 0.01) (Figure 6.22a). Also in the lake environs, nests with single chicks had significantly greater prey delivery rates compared to those in Hell's Gate during the late nestling period (ANOVA; df = 32, F = 3.69, p < 0.05).

Biomass delivered to nests with different brood sizes showed same trends as with prey deliveries (Figure 6.22b). In the lake environs, biomass delivered to nests that contained two chicks was significantly greater during the late nestling stage compared to the incubation and early nestling stages (ANOVA; df = 50, F = 2.33, p < 0.05) (Figure 6.22b).
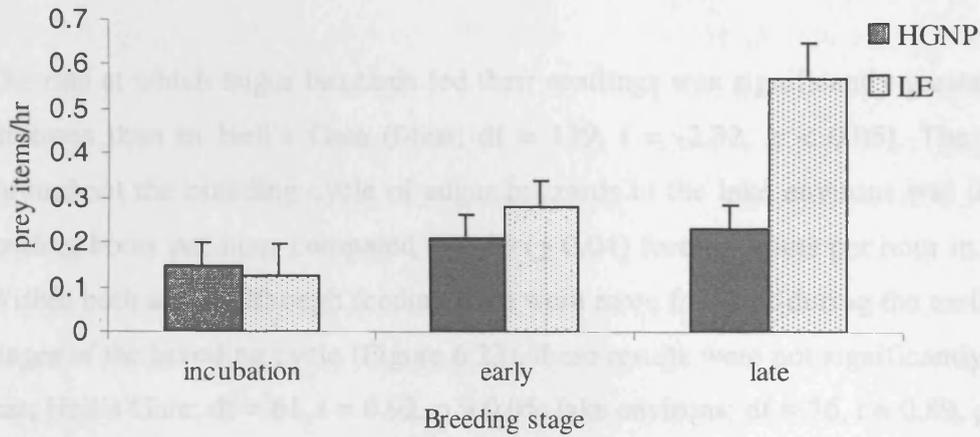
Figure 6.22a: Prey delivery rates (plus std errors) to nests with different brood sizes in Hell's Gate (1 chick/nest; n = 4) and the lake environs (2 chicks/nest; n = 2) during different breeding stages.
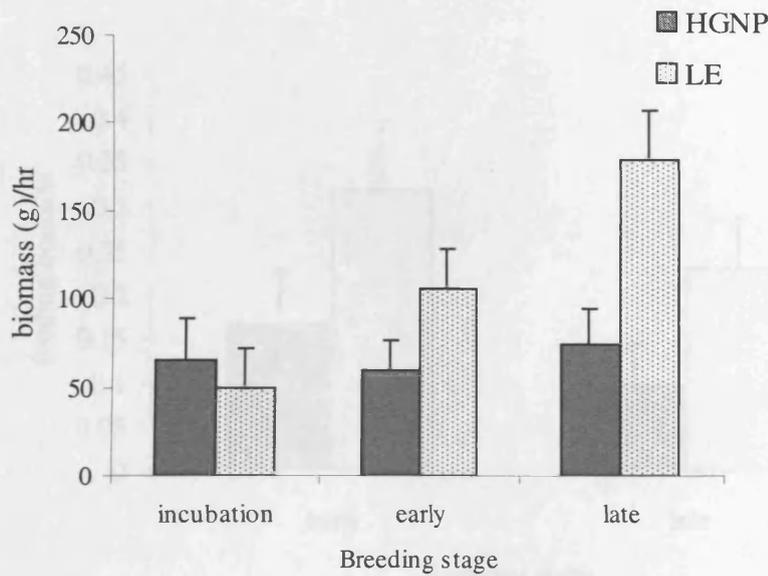
Figure 6.22b: Biomass of prey delivered per hour (plus std errors) to nests with different brood sizes in Hell's Gate (1 chick per nest; n = 4) and the lake environs (LE) (2 chicks per nest; n = 2) during different breeding stages

6.1.4 Factors influencing nestling feeding rates

The rate at which augur buzzards fed their nestlings was significantly greater in the lake environs than in Hell's Gate (t-test; df = 139, t = -2.32, p < 0.05). The feeding rate throughout the breeding cycle of augur buzzards in the lake environs was 0.28 (± 0.05) feeding bouts per hour compared to 0.13 (± 0.04) feeding bouts per hour in Hell's Gate. Within both areas, although feeding rates were more frequent during the earlier than later stages of the breeding cycle (Figure 6.23), these results were not significantly different (t-test; Hell's Gate: df = 61, t = 0.92, p > 0.05; lake environs: df = 76, t = 0.89, p > 0.05).

Nests with two chicks had a feeding rate of 0.35 (± 0.07) feeding bouts per hour compared to those with single chicks which had a rate of 0.13 (± 0.03) feeding bouts per hour, a highly significant difference (t-test; df = 139, t = -3.48, p < 0.001).
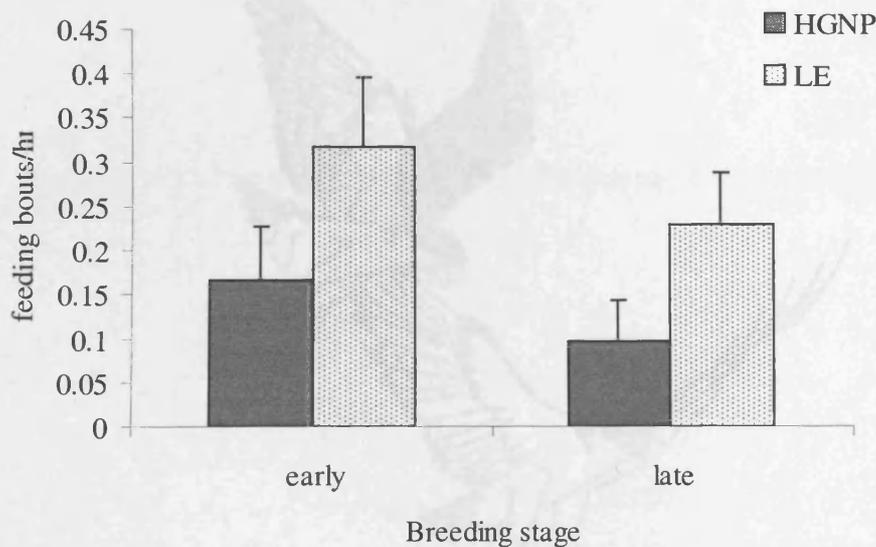
Figure 6.23: Feeding rates (plus std errors) of augur buzzard nestlings by parents in Hell's Gate and the lake environs during the early and late nestling stages.

6.1.5 Intra and inter-specific interactions

Breeding augur buzzards showed two types of behavioural patterns in response to the presence of conspecifics or other species in their territories. These were territorial displays and aggressive interactions. Territorial displays involved both individuals of a pair circling close together above their territory, with legs dangling downwards, whilst at the same time calling (Plate 6.1). Aggressive interactions involved one or both individuals of a pair, flying towards a potential intruder (or intruders). This was followed by one (or both) individual 'dive-bombing' the intruder (sometimes grappling talons or making contact) and chasing it away from the pair's territory. Calling did not usually take place during aggressive interactions.

Plate 6.1: A pair of augur buzzards during territorial display.

The majority of territorial displays in both Hell's Gate and the lake environs occurred in response to other augur buzzards intruding in to occupied territories. In Hell's Gate, this was 42% of the territorial displays, while the rest were in response to adjacent augur buzzard pairs (14%), immature augur buzzards (5%), other raptors (15%) and baboons (10%) (Figure 6.24). In the lake environs, 59% of the territorial displays were in response to intruding augur buzzards while during the rest of the displays, no species were seen within the occupied territories (Figure 6.25).
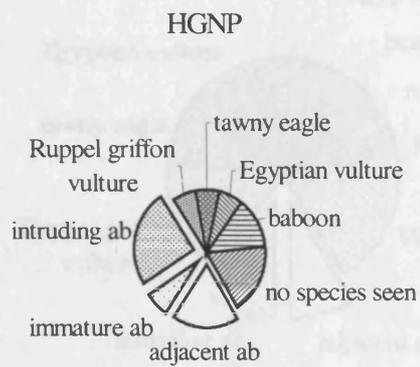
Figure 6.24: Proportion of territorial displays by augur buzzards (ab) in response to the presence of conspecifics and other species in Hell's Gate
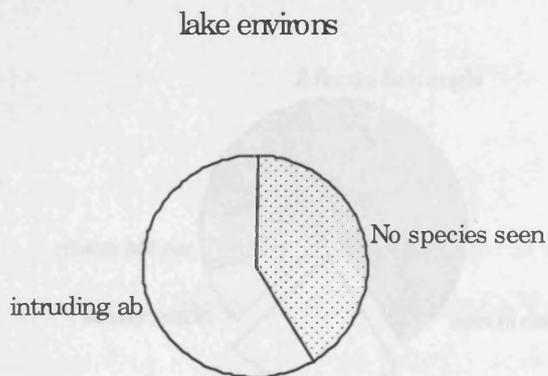
Figure 6.25: Proportion of territorial displays by augur buzzards (ab) in response to the presence of conspecifics and other species in the lake environs.

In Hell's Gate, aggressive interactions took place against other raptors - eagles (30%), vultures (30%), conspecifics (18%), as well as baboons (7%) (Figure 6.26). In the lake environs, aggressive interactions took place mainly against the African fish eagle (51%), conspecifics (21%) and serval cats (14%) (Figure 6.27).

HGNP
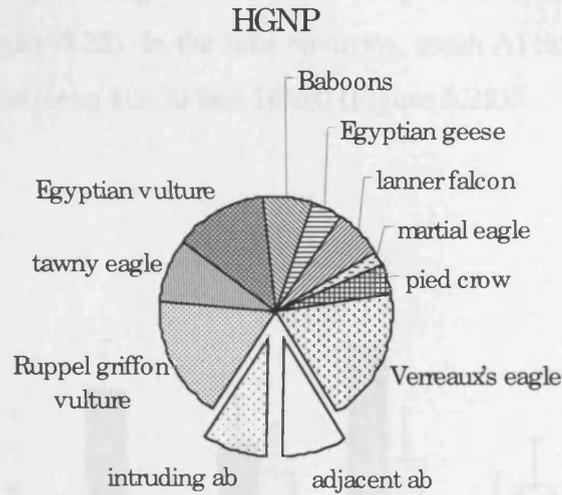
Figure 6.26: Proportion of aggressive interactions by augur buzzards (ab) in response to the presence of conspecifics and other species in Hell's Gate.
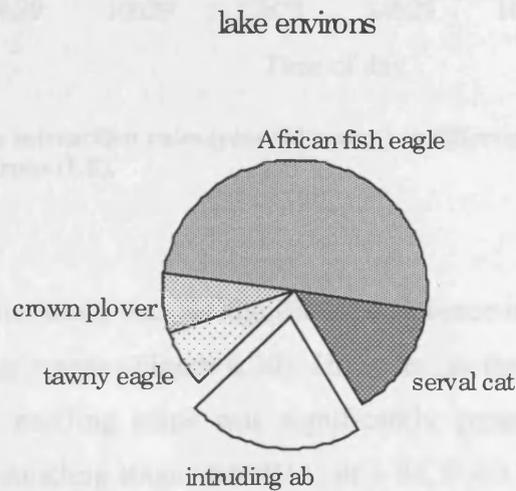
lake environs

Figure 6.27: Proportion of aggressive interactions by augur buzzards (ab) in response to the presence of conspecifics and other species in the lake environs.

The mean aggressive interaction rate (AI rate) for Hell's Gate (0.38 $\pm$0.05 interactions per hour) was significantly greater than the rate for the lake environs (0.18 $\pm$0.04 interactions per hour) (t-test, df = 159, t = 3.12, p < 0.01). There were no significant differences in the mean AI rate between the different time phases of the day in Hell's Gate and the lake environs (ANOVA; df = 86, F = 1.06, p > 0.05). In Hell's Gate, mean AI rates were high throughout the day with peak interactions occurring between 12h30 and 14h30 (Figure 6.28). In the lake environs, mean AI rates were relatively lower and mainly occurred between 10h30 and 16h30 (Figure 6.28).
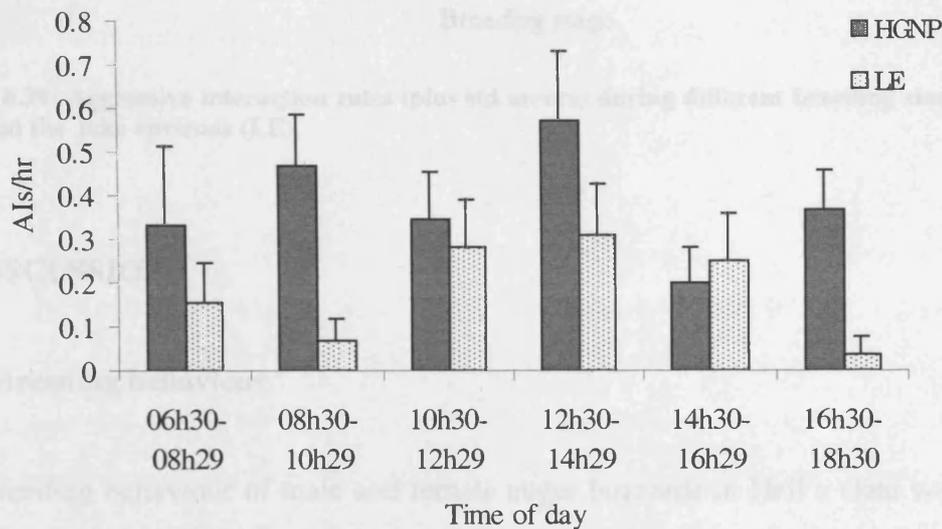
Figure 6.28: Aggressive interaction rates (plus std errors) at different time phases of the day in Hell's Gate and the lake environs (LE).

In Hell's Gate, there was no significant difference in the mean AI rates between the different breeding stages (Figure 6.29). However, in the lake environs, the mean AI rate during the late nestling stage was significantly greater than AI rates during the incubation and early nestling stage (ANOVA; df = 84, F = 3.78, p < 0.05) (Figure 6.29).
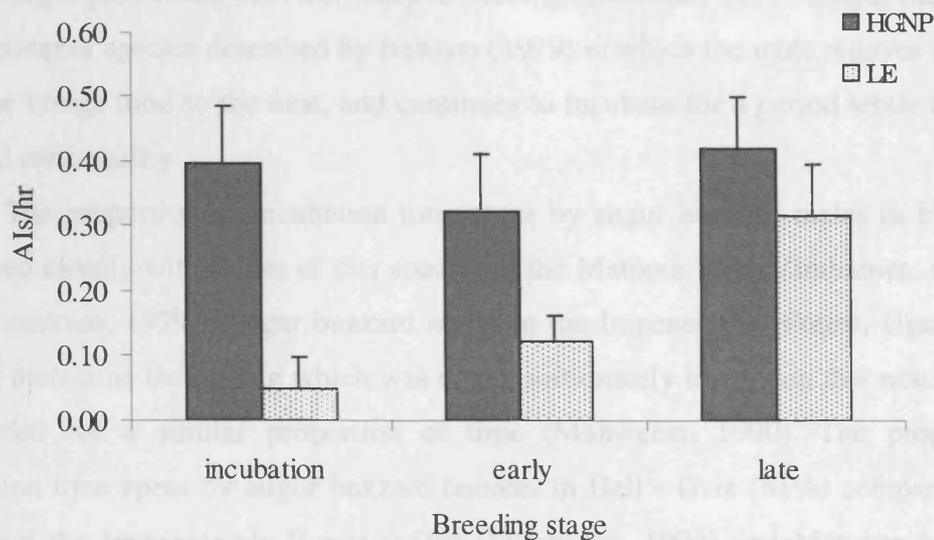
Figure 6.29: Aggressive interaction rates (plus std errors) during different breeding stages in Hell's Gate and the lake environs (LE).

6.2 DISCUSSION

6.2.1 Breeding behaviour

The breeding behaviour of male and female augur buzzards in Hell's Gate was different to those of the lake environs. Males in Hell's Gate spent up to 4 times more incubating compared to those from the lake environs. Males in Hell's Gate also spent more time attending to nestlings and perched closer to their nests during the nestling period. Females in Hell's Gate spent less time incubating and attending to chicks than females from the lake environs. These breeding behavioural differences imply a functional response to habitat characteristics. Food quantity and quality, predation pressure, human disturbance (persecution and habitat alteration) and intra/inter specific interactions are factors which can influence parental breeding behaviour.

Reversed sexual dimorphism in raptors is usually associated with differences between the sexes in parental roles during the breeding season. For example, females are reported to spend more time than males in protection of nestlings and less time in hunting for food for early stage nestlings (Newton, 1979). Furthermore, females are reported to

deliver larger prey items than the males to nestlings (Newton, 1979). Augur buzzards fall in the group of species described by Newton (1979) in which the male relieves the female when he brings food to the nest, and continues to incubate for a period while the female eats and rests nearby.

The proportion of incubation time spent by augur buzzard males in Hell's Gate compared closely with males of this species in the Matopos hills, Zimbabwe, which was 27% (Lendrum, 1979). Augur buzzard males in the Impenetrable Forest, Uganda, spent 18% of their time incubating which was disproportionately low given that nests were left unattended for a similar proportion of time (Muhweezi, 1990). The proportion of incubation time spent by augur buzzard females in Hell's Gate (61%) compared closely with both the Impenetrable Forest (65%) (Muhweezi, 1990) and Matopos hills (66%) (Lendrum, 1979).

My data, plus available literature on augur buzzard incubation time, suggest that the incubation behaviour of Hell's Gate males is the norm and that of males in the lake environs is influenced by other factors. One explanation is that reduced predation pressure from baboons, ravens, crows and other raptors in the lake environs means that females can expend more energy raising chicks and less energy defending their territories against potential predators and/or intruders. Augur buzzards in Hell's Gate spent more time interacting with conspecifics and other raptor species compared to those of the lake environs. This probably reflects a pattern determined by more predators in Hell's Gate than in the lake environs and not a function of the augur buzzards' diurnal cycle. Thiollay and Meyer (1978) attributed low breeding success in the African fish eagle in Uganda to high breeding densities associated with greater interactions between pairs. Increased inter and intra-specific interactions may also be construed as a sign of increased predation pressure. Lendrum (1979) reported high inter-specific interactions between augur buzzards and other large raptors in the Matopo hills where predation pressure was apparently high. Female raptors are usually associated with nest defence, and given that both Hell's Gate and the Matopo hills harbour a rich diversity of raptors (Lester, 1981; Gargett, 1990), it would be logical to suggest that males spend more time incubating in these areas because females are constantly on the alert to ward off potential predators and/or intruders. The paucity of inter-specific interactions in the lake environs implies

that female augur buzzards can spend longer periods incubating, attending to chicks and feeding young, while males can spend more time hunting. Greater maternal care (feeding rates, brooding, incubation) and paternal provisioning in the lake environs would result in greater breeding performance in the lake environs. Breeding performance is examined in chapter 9.

6.2.2 Prey delivery rates and its correlates

Prey deliveries to nests were highest between 10h30 and 14h30 in both areas. Rodents were mainly delivered to nests between 10h30 and 16h30 (chapter 7) and their foraging activity times coincided closely with the time prey were delivered to augur buzzard nests (Jarvis, 1969; Kingdon, 1974). The principal prey items of augur buzzards in Naivasha are mole-rats (Smeenk, 1974; Kingdon, 1974; Brown and Britton, 1980; this study), and their activities outside their burrows are confined to between 10h00 and 19h00 (Jarvis, 1973). Augur buzzards are also a major predator of vlei rats *Otomys angoniensis* which spend long hours feeding but show no preference for particular time periods (Kingdon, 1974). This study found that vlei rats were mainly delivered to nests during the early and late afternoon periods. The time period of most prey deliveries to nests was comparable to that for augur buzzards in the Impenetrable Forest, where 76% of prey were delivered between 09h00 and 13h00 (Muhweezi, 1990). Mountain buzzards *Buteo oreophilus* in the Impenetrable Forest also delivered the majority of their prey to nests between 10h00 and 15h00 (Muhweezi, 1990). My data showed that peak prey delivery rates in both sites coincided with peak aggressive interaction rates. These were mainly conspecific territorial displays between augur buzzard or adjacent pairs and intruding augur buzzards.

Prey deliveries and biomass to nests increased as the nestling period progressed. This was significant in the lake environs where there were also more chicks per nest than in Hell's Gate. In many studies of peregrine falcons *Falco peregrinus*, marsh harriers *Circus* sp., ospreys *Pandion haliaetus*, kestrels *Falco tinnunculus* and some sparrowhawks *Accipiter* sp., the number of prey items and biomass increased during the nestling period, as the young grew, and differed between nests with various brood sizes (Tinbergen, 1940, 1946; Enderson *et al.*, 1973; Johanesson, 1975; Green, 1976). In

peregrine falcons, male provisioning rates were positively correlated with brood size and fledging success, but that of females was unrelated to brood size, fledging success or male delivery rate (Olsen *et al.*, 1998). In the Madagascar buzzard *Buteo brachypterus*, prey delivery rates to nests did not significantly differ between the early and late nestling stages probably as a result of the birds being generalist feeders (Berkelman, 1994). If augur buzzards in Hell's Gate were delivering larger prey, then prey delivery rates would be fewer. This study found no evidence to show that biomass was different between the two sites (although it differed between different breeding stages and nests with different brood sizes). The differences in prey delivery and biomass could be attributable to their abundance (next chapter). The greatest growth in wing and tail length in augur buzzard nestlings occurred between 21 and 42 days after hatching (Lendrum, 1979) and therefore the nutritional requirements of chicks would be greatest between this period. Thus if a pair of augur buzzards have two chicks to feed during the late nestling period, then prey delivery and biomass rates to their nest will be significantly greater, as with the augur buzzards in the lake environs. More chicks per nest in the lake environs also meant that overall feeding rates there were significantly greater compared to Hell's Gate. Reduced aggressive interaction rates in the lake environs means that female augur buzzards can assist males in raising larger broods by helping to hunt. Larger broods in peregrine falcons were fed more regularly than smaller broods, and were fed at peak rate longer into the nestling period (Olsen *et al.*, 1998). Feeding rates were more frequent during the early nestling stage, and suggests that early stage nestlings were more dependent on being fed by females. As nestlings grow older, they begin to feed by themselves, thus leaving females more time to help males in hunting food.

Augur buzzard pairs in the lake environs spent more time caring for chicks than their counterparts in Hell's Gate. This was shown by increased maternal care and paternal foraging which resulted in larger broods and more prey deliveries respectively. The factors responsible for these are reduced predation pressure and inter/intra-specific interactions. Prey quality and availability are also important factors which are examined in the next chapter.

CHAPTER SEVEN
DIET, HUNTING SUCCESS AND FACTORS INFLUENCING PREY AVAILABILITY

7.1 DIET

7.1.1 Prey deliveries

In the overall study area, rodents formed the principal prey item delivered to nests (73.5% n = 87) with the commonest being the mole-rat (c. 42% of the total) (Table 7.1). In Hell's Gate, the proportion of rodents delivered to nests was 54%. Augur buzzards exploited a wider range of additional prey that included birds (14%), rock hyraxes *Procavia capensis* (3%), plus unknown prey items (Table 7.1). In the lake environs, prey comprised 88% rodents, while only 4% was reptiles and arthropods (Table 7.1)

Males delivered 70 (80.5%), while females delivered 17 (19.5%) prey items to nests during the overall breeding cycle (n = 87). In Hell's Gate, a total of 37 prey items were delivered to nests, 28 (76%) by males and 9 (24%) by females (Table 7.1). In the lake environs, 50 prey items were delivered to nests, 42 (84%) by males and 8 (16%) by females (Table 7.1). There were no significant differences in the proportions of prey items delivered by males and females between the two sites and in the type of prey items delivered by each parent (Fisher's Exact test, p = 0.415; p = 0.569). Females at both sites delivered more prey during the late compared to the early nestling stage. This was not analysed statistically as the sample of prey delivered by females was too small. The mean biomass per prey item were 152.9 g ($\pm$ 16.62) and 164.2 g ($\pm$ 7.20) in Hell's Gate and the lake environs respectively, and were not significantly different (t-test; df = 84, F = 7.4, p > 0.05).

The majority of the 64 rodents delivered to nests during the study period were delivered between 10h30 and 16h30 (Figure 7.1). Grass rats *Arvicanthis niloticus* were mainly delivered to nests during the mid-morning period, while mole-rats were delivered in the middle of the day (Figure 7.1). Vlei-rats *Otomys angoniensis* were mainly delivered to nests during the early and late afternoon periods (Figure 7.1). However, there

was no significant association between the type of rodent delivered and the time of the day (Chi-square test; df $= 10$, $\chi^2 = 5.166$, $p > 0.05$). The proportion of rodent prey delivered at nests in the lake environs was significantly greater than that delivered at nests in Hell's Gate (Fisher's exact test, $p < 0.001$).

Table 7.1: Proportions and biomass of prey items delivered at by augur buzzards in Hell's Gate and the lake environs during the breeding period April – October 1995 (observations based on 8 nests)

PREY TYPE	HELL'S GATE % (n)	HELL'S GATE biomass (g)	LAKE ENVIRONS % (n)	LAKE ENVIRONS biomass (g)
mammalian non-rodents				
hyrax *Procavia capensis*	2.7 (1)	500		
mammalian rodents				
mole-rat *Tachyoryctes splendens*	27.0 (10)	2000	52.0 (26)	5200
vlei rat *Otomys angoniensis*	24.3 (9)	1350	28.0 (14)	2100
Nile grass rat *Arvicanthis niloticus*	2.7 (1)	120	8.0 (4)	480
birds				
swift *Apus* sp.	8.1 (3)	120		
francolin *Francolinus* sp.	5.4 (2)	700		
reptiles				
chameleon *Chamaeleo* sp.	2.7 (1)	60		
puff adder *Bitis arietans*	2.7 (1)	250		
lizard *Latastia longicaudata*	2.7 (1)	30	2.0 (1)	30
arthropods				
dung beetle Scarabidae			2.0 (1)	
unknown arthropods	8.1 (3)	30		
unidentified prey items	13.5 (5)	500	8.0 (4)	400
TOTAL	100.0 (37)	5660	100.0 (50)	8210
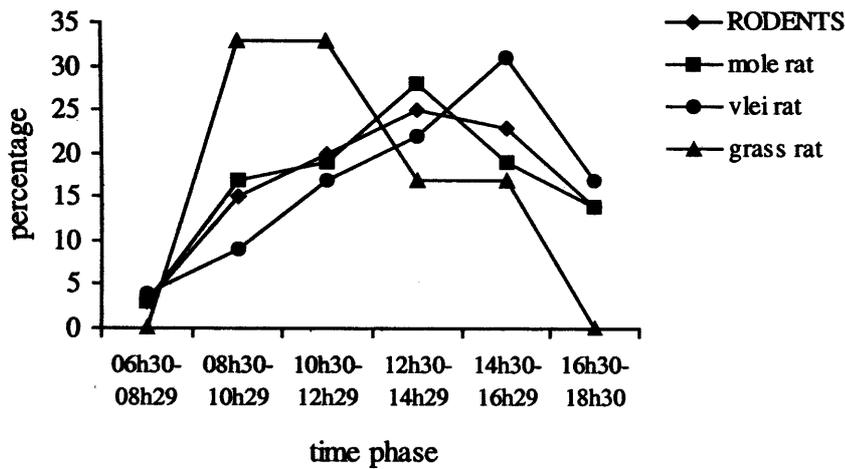
Figure 7.1: Proportion of total rodents (mole-rats, vlei rats and grass rats) delivered to nests at different times of the day (n = 64 rodents)

7.1.2 Prey remains

Rodents comprised 86.5% of the 156 prey remains collected at augur buzzard nests or feeding areas in the overall study area (Table 7.2). In Hell's Gate, rodents comprised 81.7% while in the lake environs they comprised 93.7% where mole rats formed the majority (77.8%) (Table 7.2). The Hell's Gate augur buzzards exploited a wider range of prey that included hyraxes, birds and more arthropods (Table 7.2)

Table 7.2: Proportions of various prey items determined from 156 prey remains collected from augur buzzard nests and feeding areas in the southern Lake Naivasha area (January-September 1995).

PREY TYPE	HELL'S GATE % (n)	LAKE ENVIRONS % (n)	TOTAL % (n)
mammalian non-rodents			
hyrax *Procavia capensis*	4.3 (4)		2.6 (4)
mammalian rodents			
mole-rat *Tachyoryctes splendens*	62.4 (58)	77.8 (49)	68.6 (107)
vlei rat *Otomys angoniensis*	12.9 (12)	12.7 (8)	12.8 (20)
Nile grass rat *Arvicanthis niloticus*	3.2 (3)	3.2 (2)	3.2 (5)
mouse *Mus* sp.	3.2 (3)		1.9 (3)
birds			
swift *Apus* sp.	4.3 (4)		2.6 (4)
francolin *Francolinus* sp.	1.1 (1)		0.6 (1)
arthropods			
dung beetle Scarabidae	6.4 (6)	6.3 (4)	6.4 (10)
bush cricket *Ruspolia* sp.	2.1 (2)		1.3 (2)
TOTAL	100 (93)	100 (63)	100 (156)

7.1.3 Pellets

Rodents also formed the major prey item (75.6%) out of 115 pellets collected at augur buzzard nests or feeding areas in the southern Lake Naivasha area (Table 7.3). Forty-two (66.7%) of the 63 pellets collected from Hell's Gate, contained rodents, while birds (14.3%), arthropods (15.9%) and reptiles (3.2%) formed the rest (Table 7.3). In the lake environs, augur buzzard pellets (n = 52) contained predominantly rodents (86.5%), but also some arthropods (7.7%) and reptiles (5.8%) (Table 7.3). The augur buzzards of the lake environs showed no evidence of birds in their diet. The proportion of rodents in prey remains and pellets was significantly larger for augur buzzards of the lake environs compared to those of Hell's Gate (Fisher's exact test; remains and pellets, p < 0.05).

Table 7.3: Proportions of various prey items (by group) determined from 115 pellets collected from augur buzzard nests and feeding areas in the southern Lake Naivasha area (January-September 1995).

PREY TYPE	HELL'S GATE % (n)	LAKE ENVIRONS % (n)	TOTAL % (n)
rodents	66.7 (42)	86.5 (45)	75.6 (87)
birds	14.3 (9)	0 (0)	7.8 (9)
reptiles	3.2 (2)	5.8 (3)	4.3 (5)
arthropods	15.9 (10)	7.7 (4)	12.2 (14)
TOTAL	100 (63)	100 (52)	100 (115)

7.1.4 Direct observations of kills

Arthropods comprised the majority of the prey observed killed by augur buzzards in Hell's Gate (38.9%) whilst rodents (55.6%) formed the majority in the lake environs (Table 7.4). Hyraxes and birds formed almost a quarter of the prey killed in Hell's Gate (22.2%) (Table 7.4). Thirty (83.3%) of the 36 prey animals killed were observed when the augur buzzards were breeding. Non-breeding augur buzzards predominantly killed arthropods (83.4%), while mole-rats formed the rest (n = 6 kills). The proportion of rodent prey killed by augur buzzards was significantly larger in the lake environs than in Hell's Gate (Fisher's exact test, $p < 0.05$).

The mean biomass per prey item killed were 110.0 g (+ 36.35) for Hell's Gate and 117.8 (+ 19.09) for the lake environs. These results were not significantly different (t-test; df = 34, t = -0.189, p > 0.05).

Table 7.4: Proportions and biomass (g) of prey killed by augur buzzards in Hell's Gate and the lake environs (February – September 1996).

PREY	HELL'S GATE		LAKE ENVIRONS	
	% (n).........biomass (g)		% (n)..........biomass (g)	
mammalian non-rodents				
hyrax *Procavia capensis*	11.1 (2)	1000		
mammalian rodents				
mole-rat *Tachyoryctes splendens*	5.6 (1)	200	38.9 (7)	1400
vlei rat *Otomys angoniensis*	16.7 (3)	450	16.7 (3)	450
birds				
swift *Apus* sp.	11.1 (2)	80		
reptiles				
chameleon *Chamaeleo* sp.	5.6 (1)	60		
lizard *Latastia longicaudata*	11.1 (2)	120	16.7 (3)	180
arthropods				
dung beetles Scarabidae	16.7 (3)	30	5.6 (1)	10
unknown arthropods	22.2 (4)	40	16.7 (3)	30
unidentified prey items			5.6 (1)	50
TOTAL	100 (18)	1980	100 (18)	2120

7.2 HUNTING SUCCESS

7.2.1 Hunting success and its correlates

The hunting success rate of augur buzzard males in the southern Lake Naivasha area was 28.8% (n = 125). Males of Hell's Gate made 1.77 ± 0.38 hunting attempts per hour (n = 41) while those of the lake environs made 1.05 ± 0.17 hunting attempts per hour (n = 70). The hunting attempt rates were significantly different between the males of the two areas (t-test; df = 30, t = -2.22, p < 0.05). The hunting success rate for males in Hell's Gate was 28.8% ± 0.09 compared to 33.1% ± 0.07 for those in the lake environs. These differences were not significant (t-test, df = 43, t = 0.38, df = 43, p > 0.05). Monthly rainfall, mean monthly rainfall, monthly temperature range, mean monthly temperature range, weather

and quarterly periods showed no significant correlation with hunting success (Table 7.5). Breeding augur buzzard males had a significantly higher hunting success rate of 56% $\pm$ 0.08 compared to non-breeding males which was 7.1% $\pm$ 0.03 (Table 7.5).

Table 7.5: Results of statistical tests relating augur buzzard hunting success rates (log transformed) to various parameters.

PARAMETER	df	test-statistic*	p value
monthly rainfall (1996)	26	$r^2 = 0.039$	0.326
mean monthly rainfall (1995-97)	26	$r^2 = 0.026$	0.204
monthly temperature range (1996)	26	$r^2 = 0.031$	0.382
mean monthly temperature range (1995-97)	26	$r^2 = 0.023$	0.452
weather (sunny/overcast)	20	$t = -1.41$	0.170
quarterly (Jan-Mar, Apr-Jun, Jul-Sep)	26	$F = 0.74$	0.488
breeding status (breeding/non-breeding)	34	$t = -2.96$	**0.018**

$*r^2$ (correlation analysis); t (t-test); F (ANOVA).

7.3 PREY AVAILABILITY AND ITS CORRELATES

7.3.1 Prey availability, grass height and soil softness

Data were collected for pairs H1, H3, H4A and H5A in Hell's Gate, pairs K1 and K3 in Mundui and pairs R1, R2, R3, R4, S5, O2, and O4 in Sulmac-Oserian (Figure 7.2). The mean mole-rat index was highest in Mundui (3.10 $\pm$ 0.59 mounds per are), whilst for Hell's Gate and Sulmac-Oserian they were 1.10 $\pm$ 0.19 and 2.70 $\pm$ 0.60 mounds per are respectively (Figure 7.2). These means were significantly different (ANOVA, df = 26, F = 4.86, p < 0.01).
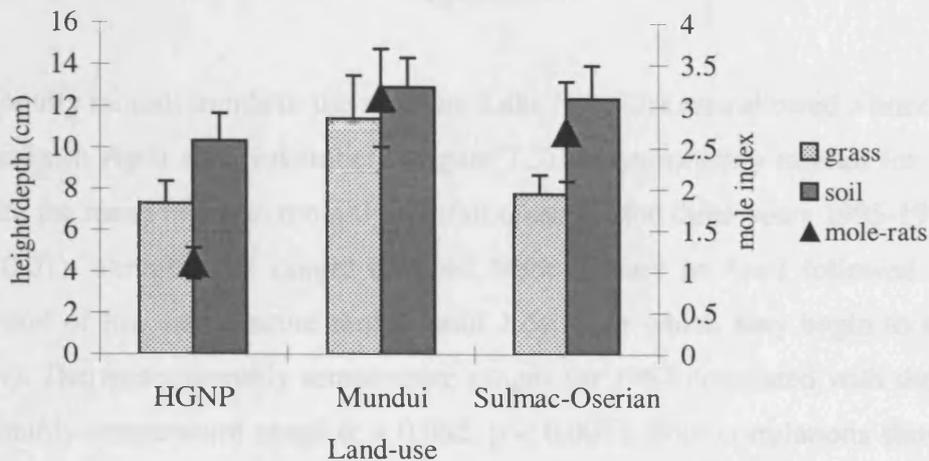
Figure 7.2: Mean soil softness, grass height and mole-rat index for the three different land-use areas in the southern Lake Naivasha area (January-September 1997).

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 7.2). The mean soil softness between the three areas were not significantly different (ANOVA; df = 26, F = 1.02, p > 0.05) (Figure 7.2).

The mean annual mole-rat indices, soil softness and grass height did not significantly differ between adjacent pairs in any of the different land-use areas (Table 7.6). The only exception was mean grass height in the territory occupied by pair R4 in Sulmac which was significantly taller than that growing in the territory occupied by an adjacent pair (R3) (Table 7.6).

Table 7.6: Student's t-test analysis of mean soil softness, grass height and mole-rat index between adjacent pairs in the southern Lake Naivasha area (January-September 1997).

Land-use	Pair	Adjacent pairs	soil softness	grass height	mole-rat index
Hell's Gate	H1	H2, H8			
""	H3	H2, H4A			
""	H4B	H4A, H5A	ns	ns	ns
""	H5A	H4B, H5B	ns	ns	ns
Mundui	K1	K2, K3	ns	ns	ns
""	K3	K1, K2	ns	ns	ns
Sulmac	R1	R2	ns	ns	ns
""	R2	R1, R3	ns	ns	ns
""	R3	R2, R4	ns	*	ns
""	R4	R3, S1	ns	*	ns
Oserian	O2	O3, O4	ns	ns	ns
""	O4	O4, O5			
""	S5	S4, S6	ns	ns	ns

* p < 0.05; ns = non significant

7.3.2 Influence of environmental parameters

Monthly rainfall trends in the southern Lake Naivasha area showed a bimodal distribution (peaks in April and November) (Figure 7.3). Mean monthly rainfall for 1997 correlated with the mean of mean monthly rainfall taken for the three years 1995-1997 (r = 0.841, p < 0.01). Temperature ranges dropped from January to April followed by a consistent period of low temperature ranges until July, after which they begin to increase (Figure 7.4). The mean monthly temperature ranges for 1997 correlated with the mean of mean monthly temperature range (r = 0.952, p < 0.001). Both correlations showed that annual rainfall and temperature range patterns were similar during the entire study period.
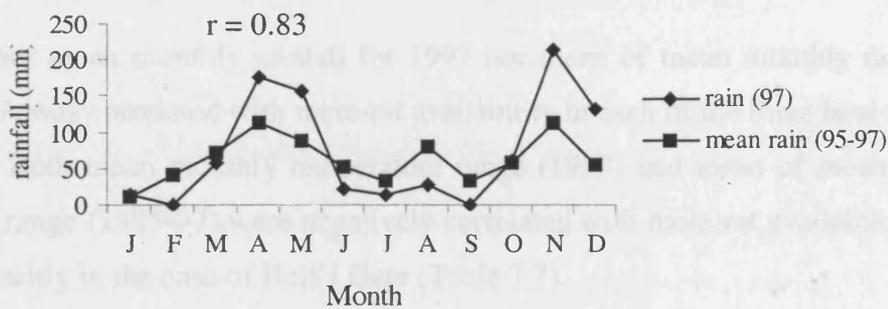
Figure 7.3:Trends in mean monthly and mean of mean monthly rainfall for the southern Lake Naivasha area for 1997 (Source: Sulmac Ltd.)

Figure 7.4: Mean monthly and mean of mean monthly temperature ranges for the southern Lake Naivasha area for 1997 (Source: Sulmac Ltd.)

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 7.7). Both mean monthly temperature range (1997) and mean of mean monthly temperature range (1995-97) were negatively correlated with mole-rat availability (Table 7.7), significantly in the case of Hell's Gate (Table 7.7).

Table 7.7: 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).

Although there were no statistically significant correlations between rainfall patterns and mole-rat availability, there was an apparent trend in that an increase in rainfall was followed approximately one month later by an increase in mole-rats in all the three different land-use areas (Figure 7.5).
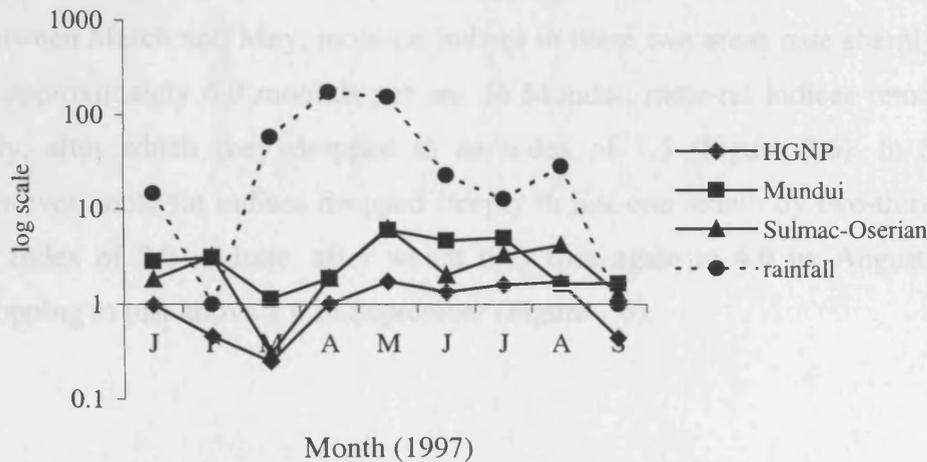
Figure 7.5: Trends in mean monthly rainfall and mean monthly mole-rat index for Hell's Gate, Mundui and Sulmac-Oserian for 1997.

7.3.3 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 7.6). 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 7.6). 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 7.6). 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) (Figure 7.7). 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) (Figure 7.7).

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Mean mole-rat indices in Hell's Gate dropped from 1.0 in January to approximately 0.2 in March (Figure 7.6). 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 7.6). In Mundui and Sulmac-Oserian, mole-rat indices rose gently in February but dropped to minimum levels in March (Figure 7.6). 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 7.6). 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 7.6).
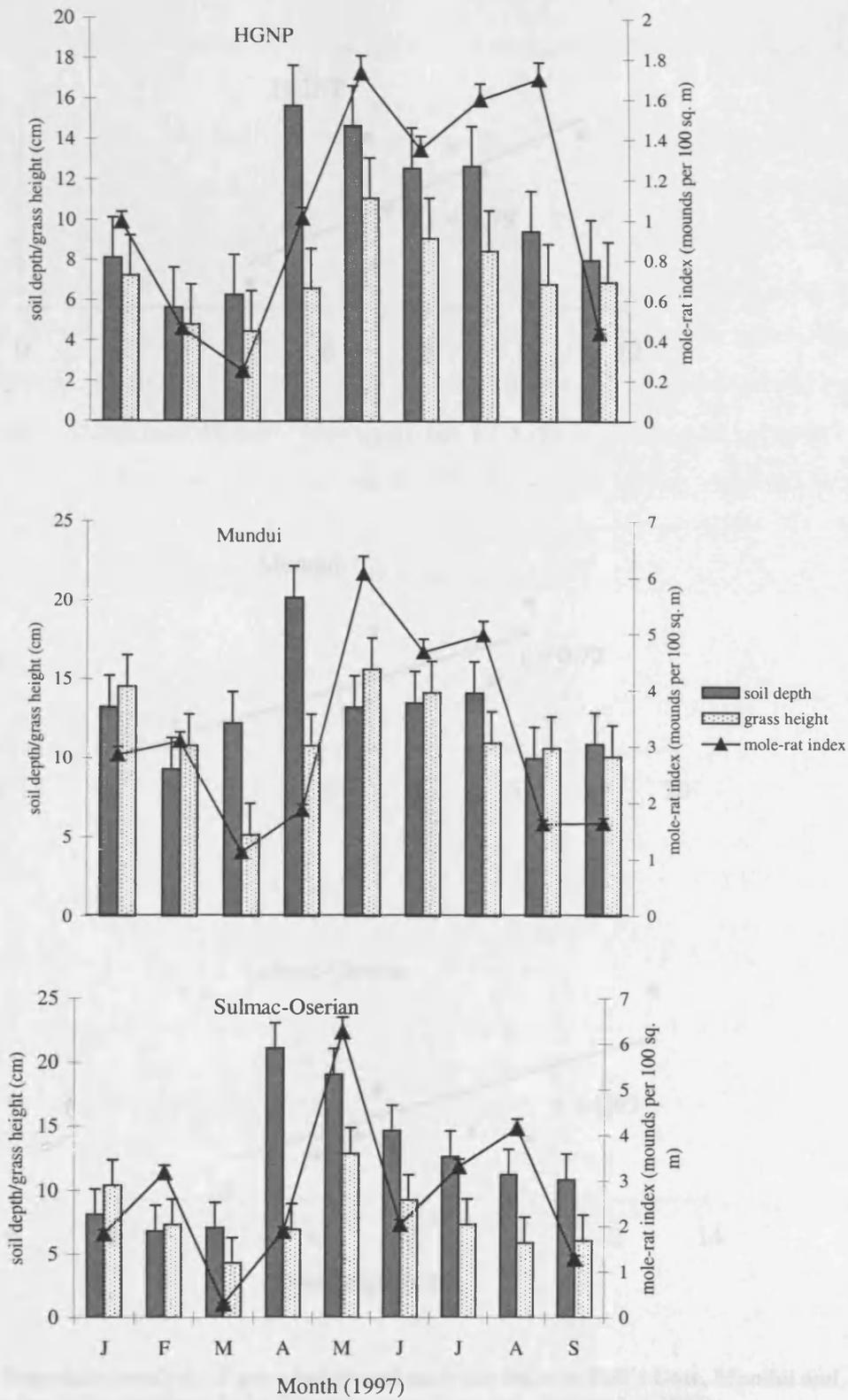
Figure 7.6: Trends in soil softness, grass height and mole-rat index for Hell's Gate, Mundui and Sulmac-Oserian (January to September 1997)

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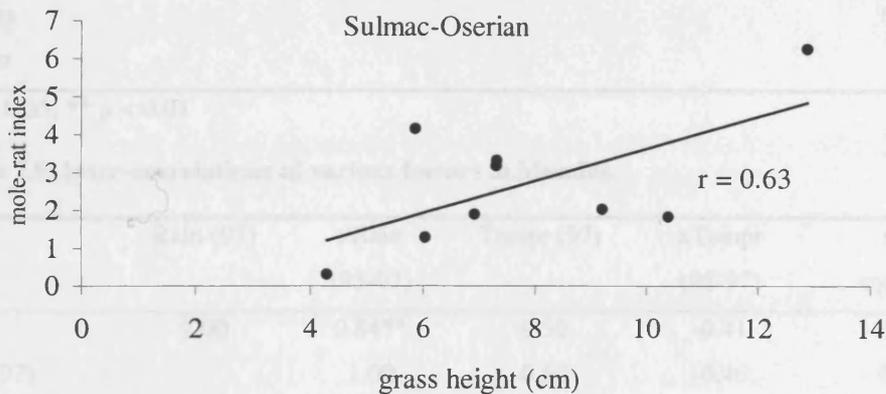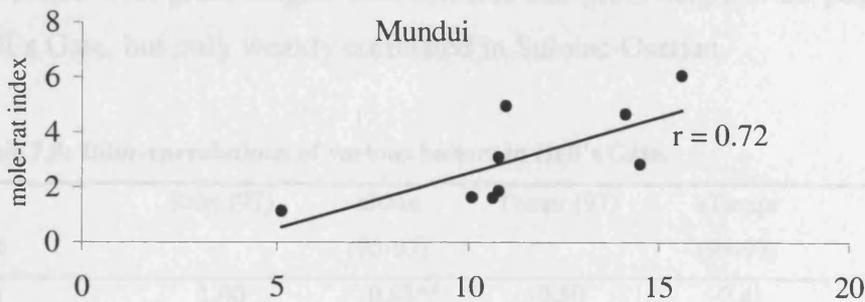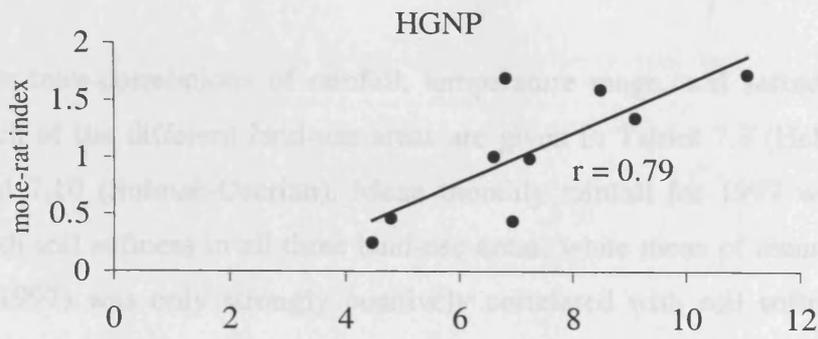
Figure 7.7: Regression analysis of grass height and mole-rat index in Hell's Gate, Mundui and Sulmac-Oserian in the southern Lake Naivasha area (January – September 1997).

7.3.4 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 7.8 (Hell's Gate), 7.9 (Mundui) and 7.10 (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.

Table 7.8: Inter-correlations of various factors in Hell's Gate.

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*	0.32
xRain (95-97)		1.00	-0.50	-0.46	0.55	0.08
Tempr (97)			1.00.	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 7.9: 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 7.10: 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).

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 7.11). 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 7.11). However the p value for the model in the Sulmac-Oserian was 0.071 (Table 7.11).

Table 7.11: 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).

7.4 DISCUSSION

More prey was available to augur buzzards in the lake environs than to those in Hell's Gate where birds had to work harder to obtain their prey. Mole-rats were the augur buzzards' most important food item and were significantly more available in Mundui and Sulmac-Oserian than in Hell's Gate. The main factor influencing mole-rat availability in all three sites was the height of the grass, which in turn is influenced by rainfall, grazing pressure and probably local traditions such as grass burning by pastoralists. Prey availability in turn influences breeding performance. Three reasons may explain the relative paucity of mole-rats in Hell's Gate compared to Mundui and Sulmac-Oserian:-

- Hell's Gate is different from the other two sites because it is a protected area that supports a full suite of mole-rat predators (reptilian, avian and mammalian). These include carnivores such as zorilla *Ictonyx* sp., leopard *Panthera pardus,* striped weasel *Poecilogal* sp. and serval cat *Felis serval* (Kingdon, 1974). These, along with a greater diversity of raptors in Hell's Gate than the lake environs, may potentially help to keep the mole-rat population to low levels. Another predator, the mole snake *Pseudaspis cana,* is quite common in Hell's Gate; but due to the advance of modern agricultural techniques, coupled with local residents' fear of snakes, this species has been almost eradicated in the horticultural areas in the lake environs. This may have considerably helped the mole-rat population to reach high densities (Brown, 1970). Jarvis (1969) suggested that high predation pressure in mole-rats resulted in higher incidences of embryonic resorption. This could further account for relatively lower densities in Hell's Gate.

- Secondly, the abundance of plains game herbivores in Hell's Gate has resulted in parts of the park being overgrazed. This affects mole-rat diet as they are dependent on the roots and shoots of grasses (Kingdon, 1974). In consequence, mole-rat abundance (as well as that of other rodents) and breeding performance may be affected. In contrast, Mundui had the highest mean grass height and is moderately grazed thus creating a suitable mole-rat habitat.

- Thirdly, mole-rats have expanded their range and numbers close to cultivated areas (Kingdon, 1974; Smeenk, 1974) and because of the expanding horticultural fields in

the southern Lake Naivasha area, mole-rat densities have increased to high levels. Rahm (1971) estimated mole-rat density at 0.7 mounds per are. This figure compares with densities in Hell's Gate but is four times lower than mole-rat densities in Mundui and Sulmac-Oserian. It is possible that mole-rat densities in Hell's Gate are limited by a combination of all the above factors. Hell's Gate is also a drier area compared to the lake environs where moisture from the lake may also influence vegetation and rodent numbers (Smeenk, 1974).

7.4.1 Diet

In the southern Lake Naivasha area, rodents formed c. 75% of the diet of nestlings. This figure compares closely with nesting augur buzzards of the Impenetrable Forest, where rodents formed 70% of nestling diet (Muhweezi, 1990). In contrast, augur buzzards of the Matopo hills fed their chicks primarily on reptiles (60%), rodents being a secondary source of food (30%) (Lendrum, 1979).

The nesting location of augur buzzards in the southern Lake Naivasha area affected overall composition of prey types in their diet. Augur buzzards in the lake environs fed their chicks on significantly more rodents compared to those in Hell's Gate, where nestling diet comprised a wider (but limited) array of prey items. This study found no evidence that augur buzzards in Hell's Gate were feeding on significantly larger prey. Augur buzzards in Hell's Gate had a generalist diet while those in the lake environs specialised on rodents, particularly mole-rats. These are abundantly distributed throughout the Rift Valley, central and western highlands of Kenya, (Kingdon, 1974). In the alluvial plains southwest of the Lake Naivasha area, Kingdon (1974) described mole-rats as "being very numerous, favouring open grassland, thinly treed upland savanna, moorland and cultivation which has replaced forest". Brown and Britton (1980) hypothesised that rodents such as mole-rats and grass rats (Arvicanthis sp. and Mastomys sp.) were important, if not staple foods of medium sized hawks in East Africa. Smeenk (1974) found that the density of rodents was significantly greater in a moist agricultural area in the Rift Valley compared to a nearby dry ranch land area. He attributed this to differences in moisture content and precipitation between the two areas. Mole-rats are

most active between 10h00 and 19h00 (Jarvis, 1973) and this explained why the majority of these were delivered to nests during the middle of day.

Augur buzzard prey composition based on prey remains and pellets, yielded similar results compared to prey items seen delivered to nests. The high proportion of mole-rat remains collected from both areas was probably because these were more easily seen under nests and feeding perches. In Hell's Gate, this may have over-inflated the proportion of mole-rats in augur buzzard diet. Hyrax skulls collected confirmed that these did form part of their diet and that the single hyrax delivered to a nest during the breeding cycle was not a chance occurrence. Smeenk (1974) found that 94% of augur buzzard pellets collected at Elementeita (north of Lake Naivasha) consisted of rodents, 70% of which were mole-rats. This compared with my study where rodents made up 87% of the pellets collected from the lake environs. More arthropods were detected in pellets from Hell's Gate than in the lake environs, and augur buzzards in Hell's Gate were observed to kill more arthropods compared to those in the lake environs. The high arthropod content seen in pellets and kills of augur buzzards from Hell's Gate can be explained by the presence of large concentrations of plains game herbivores. These produce large amounts of dung which attracts scarabid dung beetles, an important food source for augur buzzards and other predators during wet periods in Hell's Gate (Cook, 1997).

7.4.2 Hunting success

The limited food supply available to augur buzzards in Hell's Gate meant that they had to work harder to obtain prey compared to those in the lake environs. This may explain why augur buzzards in Hell's Gate had significantly more hunting attempts compared to those in the lake environs. Another plausible explanation is that the abundance of arthropod prey such as dung beetles in Hell's Gate during wet periods may have resulted in an increase in augur buzzard strike rates, since they had to catch more food to feed their chicks. The availability of suitable perch sites also plays an important role in influencing hunting behaviour (Widen, 1994). This study did not investigate the influence of perch sites but the evidence obtained from nest-site selection on tree heights and distances from random points (chapter 5) suggested that augur buzzards in Hell's Gate had poor perch-

site quality. Hunting success rates in Hell's Gate and the lake environs were similar and may have been as a result of the adaptability of augur buzzards (particularly those in Hell's Gate) to habitat variations in prey quantity and quality, although other factors such as perch quality and inter-specific competition may have been acting in concert. Smeenk (1974) found that augur buzzards in two areas near Nakuru (one agricultural and one ranch land) occurred at similar densities although other raptor densities differed between these areas. The similar densities were attributed to the special ability of the augur buzzard to hunt mole-rats by watching the earth mounds pushed up by the animals until a slight movement of the soil indicates that a mole-rat is very close to the surface; the bird then swiftly pounces down and extracts the prey from its burrow (Smeenk, 1974; pers obs.). The requirement of this specialised hunting technique from a perch or a hover, coupled with the fairly large size of the mole-rats probably render the augur buzzard the only important diurnal avian predator of these rodents. It is not known whether the tawny eagle *Aquila rapax* is able to utilise the same food source; only Brown (1970) mentions mole-rats as prey of this eagle, but does not give any source references. No other raptors apart from augur buzzards and the nocturnal Verreaux's eagle owl *Bubo lacteus* have been recorded to hunt mole-rats (Smeenk, 1974; Smart and Taylor, 1990). There have been anecdotal reports of African fish eagles hunting mole-rats along the shores of Lake Naivasha (S. Thomsett, pers. comm.).

Breeding augur buzzards were 8 times more successful at hunting than non-breeders. This may be reflected by the greater amount of prey made available to breeding (compared to non-breeding) augur buzzards. The fact that over 80% of the kills were made by breeding augur buzzards suggests that they timed their breeding when prey was not only abundant, but also most readily available. This will be further examined in the next chapter.

7.4.3 Prey availability and its correlates

Grass height emerged as the most important factor that best predicted mole-rat density 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.

Rainfall did not statistically influence mole-rat availability although there was a clear trend that an increase in rainfall resulted in a subsequent (month later) increase in mole-rat densities. 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 limiting factors 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). The effect of prey availability on the timing of breeding in augur buzzards is discussed in the next chapter.

Mole-rat availability in Hell's Gate increased when temperatures were cooler. 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, mole-rats in Hell's Gate may be responding to subtle temperature regimes which trigger their breeding activity and hence their densities. In the lake environs, 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 penetrability probably enable easier burrowing for mole-rats and hence increased activity resulting in greater mole-rat avaialbility. 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).

7.4.4 Implications for augur buzzard ecology

This study has demonstrated that there are differences in diet (quantity and quality), hunting behaviour and prey availability between augur buzzards in Hell's Gate and the lake environs. Augur buzzards in Hell's Gate live in a semi-arid environment, have limited food supply and expend more energy in hunting. They have therefore adapted to hunting diverse prey such as hyraxes, birds, reptiles and arthropods. This adaptation indicates a level of opportunism. Augur buzzards in the lake environs live in cooler, moister conditions, have abundant food supply, exploiting mainly mole-rats and other rodents. The availability of prey at peak populations should have a significant influence on the timing of breeding in augur buzzards (examined in the next chapter) as well as on their breeding performance (chapter 9).

CHAPTER EIGHT

BREEDING SEASONALITY AND FACTORS INFLUENCING EGG-LAYING

8.1 BREEDING SEASONALITY

8.1.1 Influence of climatic factors in the entire study area

Seventy-seven breeding attempts were recorded during the study period (22 in 1995, 30 in 1996 and 25 in 1997). Sixty-nine (89.6%) were first clutches while 8 were second clutches as a result of first-clutch failures. Averaged over the three-year study period, 46.2% of breeding attempts occurred between May and July, with a peak in June (22%) (Figure 8.1a).
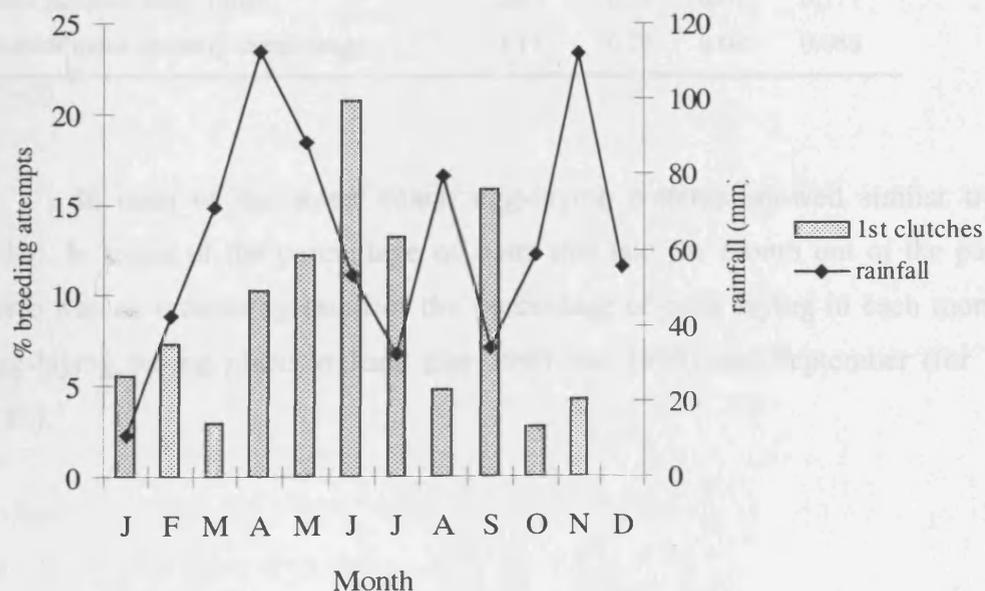
Figure 8.1a: Mean monthly trends in percentage of first clutch breeding attempts in relation to rainfall patterns over the three-year study period in the southern Lake Naivasha area.

A significantly high proportion of breeding attempts (76.9%) were initiated between the 6-month period April to September compared to the period October to March where only 23.1% occurred (t-test; n = 76; t = -3.54; p < 0.001). A significantly larger proportion of breeding attempts (43.2%) occurred during the second quarter (April-June) than at any other quarter in the year (Kruskal-Wallis; df = 3, H = 12.53, p < 0.01). Mean monthly rainfall and mean of mean monthly rainfall for the three years had no influence on the timing off egg-laying across the study area (Table 8.1). The general trend was a peak in rainfall followed by a peak in egg-laying (Figure 8.1a). Mean monthly temperature range and mean of mean monthly temperature range were negatively correlated with timing of egg-laying but the relationship was weak and not significant (Table 8.1).

Table 8.1: Correlation analysis of various environmental parameters on the timing of egg-laying in augur buzzards in the southern Lake Naivasha area (1995-1997).

PARAMETER	F	r	r^2	p
mean monthly rainfall	0.00	0.00	0.00	0.962
mean of mean monthly rainfall	0.44	0.11	0.01	0.514
mean monthly temp. range	2.67	-0.27	0.07	0.111
mean of mean monthly temp. range	3.13	-0.29	0.08	0.086

df = 35

In each of the three years, egg-laying patterns showed similar trends (Figure 8.1b). In terms of the percentage of pairs that laid per month out of the pairs available, there was an increasing trend of the percentage of pairs laying in each month with peak egg-laying taking place in June (for 1995 and 1996) and September (for 1997)(Figure 8.1b).
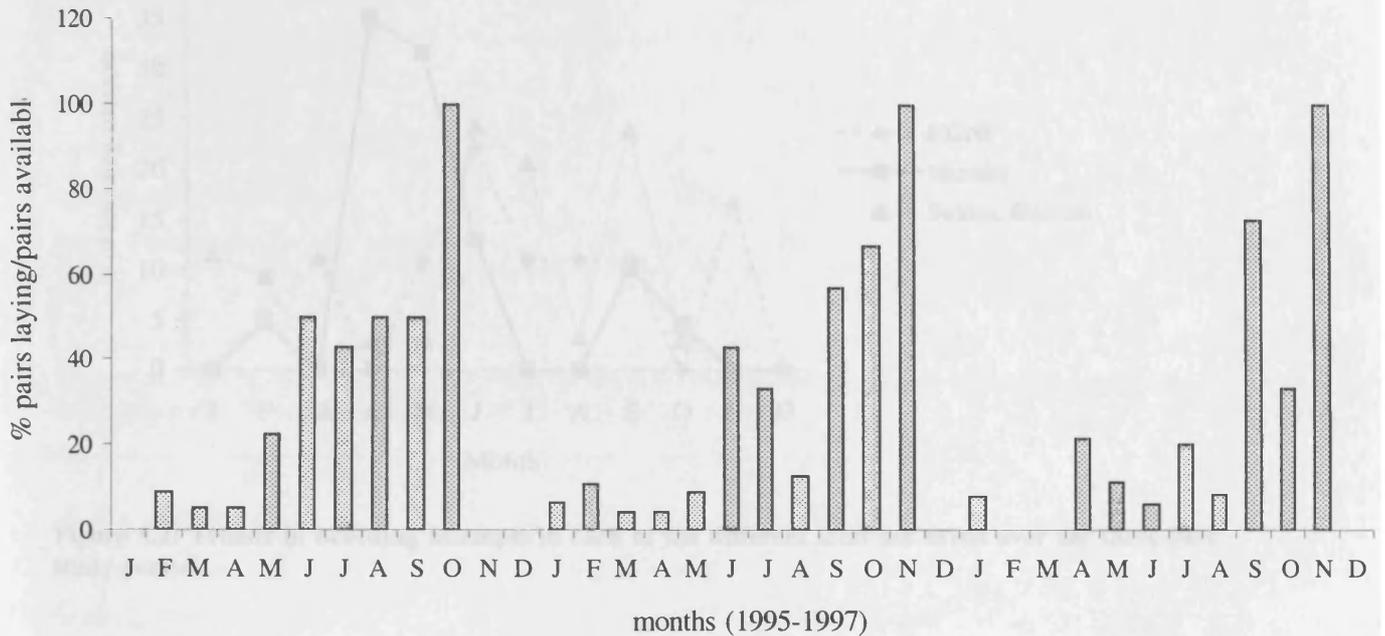
Figure 8.1b: Cumulative chart showing mean percentage of augur buzzard pairs laying per month (out of those available to lay) in each of the three years 1995 (n = 22 attempts), 1996 (n = 30 attempts) and 1997 (n = 25 attempts).

8.1.2 Influence of climatic factors in the different land-use areas

In Hell's Gate, peak egg-laying occurred in June and continued until September (Figure 8.2), while in Mundui, it occurred in April and May and then again in September (Figure 8.2). In Sulmac-Oserian, egg-laying began early in January but dropped by March and later two peak egg-laying periods were evident – one in June and the other in September (Figure 8.2). Basically, Hell's Gate and Sulmac-Oserian showed three egg-laying periods in a year while Mundui showed two (Figure 8.2).

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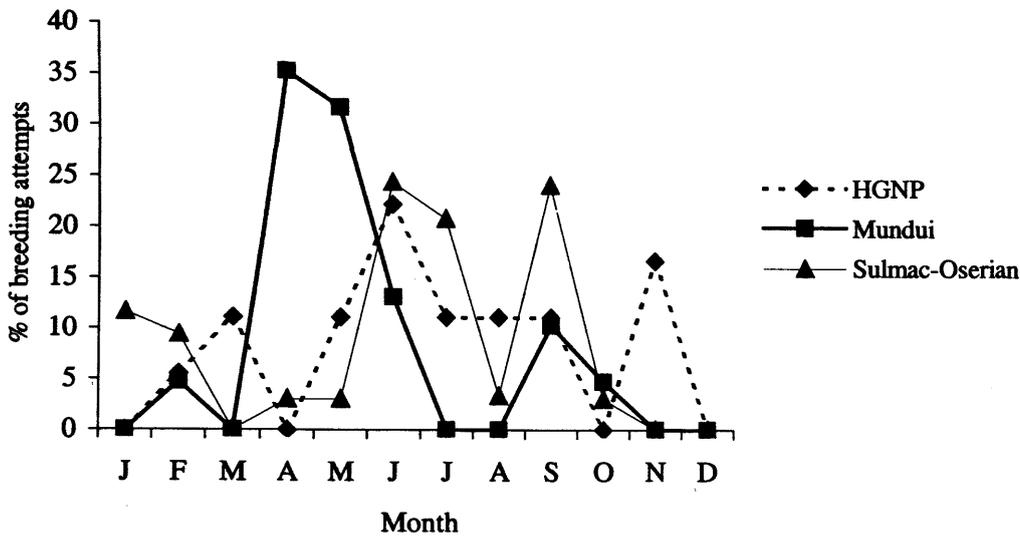
Figure 8.2: Trends in breeding attempts in each of the different land use areas over the three-year study period.

Mean monthly rainfall was not significantly correlated with egg-laying in each of the three land-use areas (Tables 8.2 – 8.4). However, mean of mean monthly rainfall was significantly correlated with egg-laying in Mundui and Sulmac-Oserian although the relationship was weaker in Mundui (Tables 8.3 and 8.4). Mean monthly temperature range and mean of mean monthly temperature range significantly influenced egg-laying only in Hell's Gate although the relationships were also weak (Table 8.2).

Table 8.2: Correlation analysis of various environmental parameters on the timing of egg-laying in augur buzzards in Hell's Gate (1995-1997).

PARAMETER	F	r	r^2	p
mean monthly rainfall	0.09	0.17	0.03	0.764
mean of mean monthly rainfall	0.40	0.11	0.01	0.530
mean monthly temp. range	6.68	-0.40	0.16	**0.014**
mean of mean monthly temp. range	4.71	-0.35	0.12	**0.037**

df = 35

Table 8.3: Correlation analysis of various environmental parameters on the timing of egg-laying in augur buzzards in Mundui (1995-1997).

PARAMETER	F	r	r²	p
mean monthly rainfall	1.98	0.23	0.06	0.169
mean of mean monthly rainfall	4.49	0.34	0.12	**0.041**
mean monthly temp. range	1.53	-0.21	0.04	0.224
mean of mean monthly temp. range	2.90	-0.28	0.08	0.097

df = 35

Table 8.4: Correlation analysis of various environmental parameters on the timing of egg-laying in augur buzzards in Sulmac-Oserian (1995-1997).

PARAMETER	F	r	r²	p
mean monthly rainfall	1.37	0.20	0.04	0.250
mean of mean monthly rainfall	9.06	0.46	0.21	**0.005**
mean monthly temp. range	0.04	0.03	0.00	0.836
mean of mean monthly temp. range	0.11	0.05	0.00	0.739

df = 35

8.1.3 Influence of soil, grass and prey availability

Mean soil softness, grass height and prey availability were not correlated with the mean percentage of augur buzzards pairs laying in each of the three areas (Tables 8.5 – 8.7). Soil softness was significantly positively correlated with timing of egg-laying in Mundui (Table 8.6).

Table 8.5: Correlation analysis of soil softness, grass height and prey availability on the timing of egg-laying in augur buzzards in Hell's Gate.

PARAMETER	F	r	r²	p
soil softness	0.05	0.08	0.00	0.835
grass height	1.13	0.37	0.14	0.323
prey availability	0.47	0.25	0.06	0.516

df = 8

Table 8.6: Correlation analysis of soil softness, grass height and prey availability on the timing of egg-laying in augur buzzards in Mundui.

PARAMETER	F	r	r^2	p
soil softness	3.90	0.80	0.64	**0.009**
grass height	1.18	0.38	0.14	0.314
prey availability	0.62	0.28	0.08	0.458
df = 8				

Table 8.7: Correlation analysis of soil softness, grass height and prey availability on the timing of egg-laying in augur buzzards in Sulmac-Oserian.

PARAMETER	F	r	r^2	p
soil softness	0.06	0.09	0.00	0.812
grass height	0.03	0.06	0.00	0.864
prey availability	0.33	0.21	0.05	0.582
df = 8				

8.1.4 Combined effect of rainfall, temperature, soil softness, grass height and prey availability on timing of egg-laying - 2 multiple regression models

Between the period January to September 1997, mean monthly rainfall and mean monthly temperature range were correlated with timing of egg-laying in Hell's Gate, although the results were weak and not significant (Pearson's correlation: df = 8, r = 0.51 [rainfall], r = -0.36 [temperature range], p > 0.05). In Mundui, only mean monthly rainfall was significantly correlated with timing of egg-laying (Pearson's correlation; df = 8, r = 0.77, p < 0.05). No correlations could be found between rainfall and temperature range, and the timing of egg-laying in Sulmac-Oserian.

Two best-fit step-wise multiple regression models were developed to determine which of the climatic and natural variables best predicted the timing of egg-laying in augur buzzards. The variables for Model 1 were mean monthly rainfall and temperature range for the period January to September 1997, plus mean monthly data on soil softness, grass height and mole-rat availability. Model 2 used the same parameters except soil softness as it was highly correlated with rainfall (previous chapter).

For Model 1, rainfall in Hell's Gate and Sulmac-Oserian was the most important variable that best fitted the multiple regression model that predicted peak egg-laying, while soil softness was the best-fit predictor in Mundui (Table 8.8). For Model 2, rainfall was the most important variable that best-predicted peak egg-laying in both Mundui and Sulmac (Table 8.8). Hell's Gate had no best-fit predictor for Model 2.

Table 8.8: Best-fit multiple regression of two models to predict the timing of egg-laying in Hell's Gate, Mundui and Sulmac-Oserian in the southern Lake Naivasha area, 1997.

MODEL[*]	SITE	beta constant	best-fit predictor (beta coefficient)	r^2	F	p
1	Hell's Gate	-7.411	rainfall (-0.152); soil (2.203)	0.67	6.14	0.035
1	Mundui	-60.918	soil (5.564)	0.65	12.79	0.009
1	Sulmac-Oserian	-4.847	rainfall (-0.224); soil (2.232)	0.81	12.84	0.007
2	Hell's Gate	-	-	-	-	-
2	Mundui	-2.115	rainfall (0.253)	0.60	10.30	0.015
2	Sulmac-Oserian	15.578	rainfall (-8.593E-02)	0.35	3.82	0.092

[*]Model 1 predictors: rainfall (1997), temperature range (1997), soil softness, grass height and mole-rat availability;
Model 2 predictors: Model 1 minus soil softness (1997).

8.2 BREEDING STATUS IN RELATION TO PREY AVAILABILITY

In Hell's Gate and Mundui, high mole-rat densities coincided with periods when augur buzzards were breeding while low mole-rat densities coincided with periods of non-breeding (Figure 8.3). In Mundui, mole-rat densities were significantly higher when augur buzzards were breeding (t-test; df = 9, t = -2.66, p < 0.05) while in Hell's Gate, this difference was not significant (t-test; df = 11, t = -1.83, p > 0.05). In Sulmac-Oserian, there was no significant difference in the mean mole-rat density between breeding and non-breeding periods (t-test; df = 10, t = -0.03, p > 0.05) (Figure 8.3).
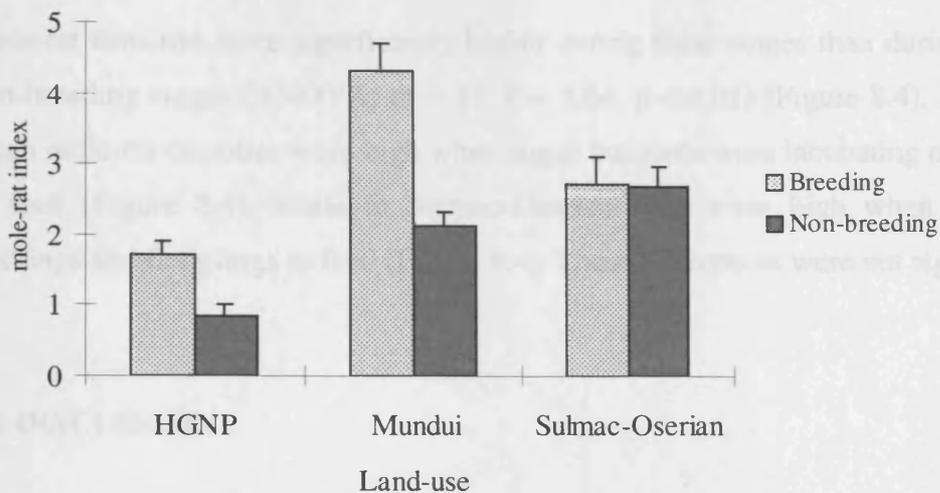
Figure 8.3: Mole-rat availability (plus std errors) in mounds per are plotted against the breeding status of augur buzzard pairs in each of the different land-use areas in the southern Lake Naivasha area.

When the breeding/non-breeding period was further subdivided into 5 specific stages (courtship/display, incubation, nestling, fledgling and non-breeding), high mole-rat densities in Mundui coincided with augur buzzards undergoing courtship feeding, displaying, nest-building and copulation (Figure 8.4).
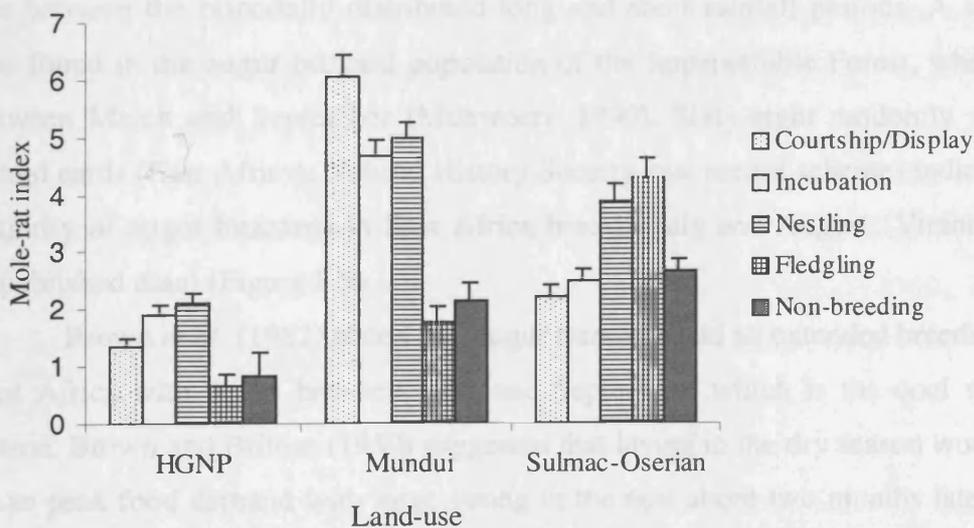
Figure 8.4: Mole-rat availability (plus std errors) in mounds per are plotted against specific breeding stages and non-breeding of augur buzzard pairs in each of the different land-use areas in the southern Lake Naivasha area.

Mole-rat densities were significantly higher during these stages than during fledgling or non-breeding stages (ANOVA; df = 17, F = 7.64, p < 0.01) (Figure 8.4). In Hell's Gate, mean mole-rat densities were high when augur buzzards were incubating or had nestlings to feed (Figure 8.4), while in Sulmac-Oserian, they were high when the birds had nestlings and fledglings to feed (Figure 8.4). These differences were not significant.

8.2 DISCUSSION

Rainfall influenced breeding at all three sites and hence compared well to data analysed from nest-record cards (Brown and Britton, 1980). The general trend shown was that rainfall increased vegetation cover (mainly grasses), which consequently caused an abundance in mole rats (and possibly the abundance of other rodents as well as potential prey species such as reptiles and arthropods).

Augur buzzards in the southern Lake Naivasha area laid eggs throughout the year except in December. The majority laid between the period April to September, with peak egg-laying occurring between May and July (the cool-dry season). This "window" period lies between the bimodally distributed long and short rainfall periods. A similar result was found in the augur buzzard population of the Impenetrable Forest, where 80% laid between March and September (Muhweezi, 1990). Sixty-eight randomly selected nest record cards (East African Natural History Society nest record scheme) indicated that the majority of augur buzzards in East Africa bred in July and August (Virani and Maina, unpublished data) (Figure 8.5).

Brown et al. (1982) stated that augur buzzards had an extended breeding season in East Africa with peaks between June and September, which is the cool mid-year dry season. Brown and Britton (1980) suggested that laying in the dry season would normally mean peak food demand with large young in the nest about two months later, usually in the shorter rainy period, when cover is long and prey more difficult to catch. They hypothesized that the available data for the southern Lake Naivasha area did not accord

well with theoretical conclusions on the availability of food at the time of maximum demand for young in the nest.
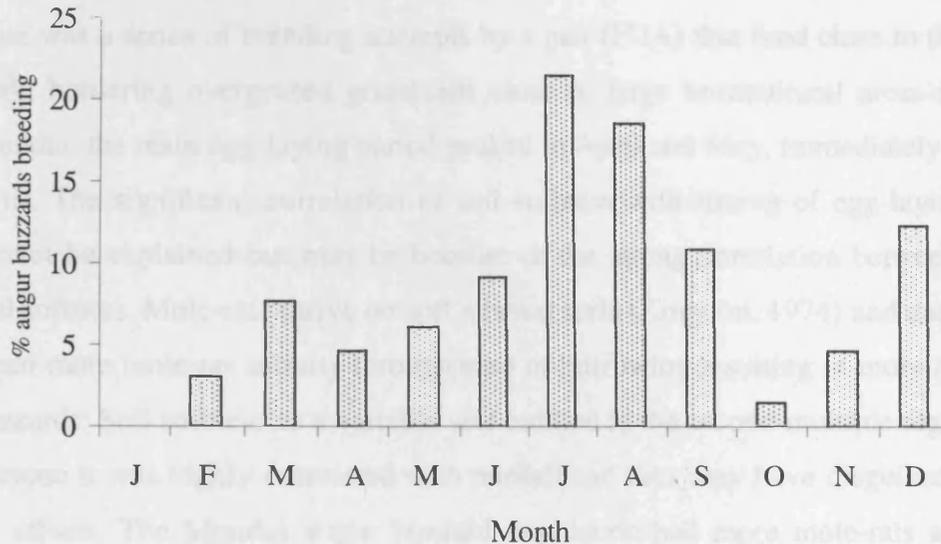
Figure 8.5: Analysis of 68 randomly selected nest record cards (East African Natural History Society) showing the percentage of augur buzzards that bred at various places in East Africa during each month between the period 1929 to 1998. (excluding data from this study).

The factors controlling the season and the breeding behaviour of medium to large sized raptors in East Africa have been reviewed by Brown (1970), and Brown and Britton (1980). Lack's (1954) generally accepted theory is that the breeding seasons of birds have so evolved that young are produced when food is most abundant for them. This theory has been extensively researched and works well for temperate species; but little evidence exists to conclude that tropical raptors, especially those living close to the equator, conform to seasonal breeding patterns (see Brown, 1970). Moreau (1950), hypothesized that large raptors in East Africa, laid in the "cool dry season", supposedly resulting in young when vegetation cover was reduced (often through burning) and prey was easier to catch.

This study found that the long rains in April were followed approximately two months later by a peak in egg-laying. This suggested (as with the factors influencing mole-rat availability) a cause and effect mechanism in play. There were differences in seasonal variations in breeding in each of the different land-use areas. In Hell's Gate,

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breeding peaked in June and July and was consistent with the theory that it occurred about two months after the long rains. The smaller peak in November may have followed from the effects of the short rains (usually in September-October); at this time breeding was mainly attempted by pairs that were successful earlier. The March peak in Hell's Gate was a series of breeding attempts by a pair (H2A) that bred close to the edge of the park, bordering overgrazed grasslands close to large horticultural areas in Sulmac. In Mundui, the main egg-laying period peaked in April and May, immediately after the long rains. The significant correlation of soil softness with timing of egg-laying in Mundui cannot be explained but may be because of the strong correlation between rainfall and soil softness. Mole-rats thrive on soft alluvial soils (Kingdon, 1974) and deeper soils may mean more mole-rat activity through ease of burrowing resulting in more food for augur buzzards. Soil softness as a variable was omitted in the second multiple regression model because it was highly correlated with rainfall and thus may have disguised or concealed its effects. The Mundui augur buzzard population had more mole-rats available, bred earlier and produced more fledglings (this study, discussed in the next chapter). A smaller peak in September may have been induced by unusually heavy rainfall in August of 1996. Another possibility is that even though mole-rats may have been abundant in Mundui, the relatively higher grass there may have protected them from being hunted. Generally, birds that breed earlier in a season, are more successful than late nesters (Newton, 1979). In Sulmac-Oserian, although augur buzzards laid throughout the year, two peak egg-laying periods were evident; one in June-July and the other in September. The June-July peak conforms to the standard accepted theory that augur buzzards breed after the long rains (Brown and Britton, 1980; Brown et al., 1982). The second peak, in September, may have resulted from the unusually heavy rainfall which occurred in August 1996.

Food supply is regarded by most authors on breeding seasons as being the most important ultimate factor for nearly all bird species (Brown and Britton, 1980). In Mundui, high mole-rat densities coincided with early stages of augur buzzard breeding such as courtship feeding and copulating. Unfortunately I could not collect rainfall data at each of the different study sites, but it is a generally accepted notion that Hell's Gate is drier than both Mundui and Sulmac-Oserian, which are cooler and moister (J. Root, pers

comm.; pers obs.). Mole-rats were not the dominant food item for augur buzzards in Hell's Gate since they occurred at significantly lower densities compared to Mundui and Sulmac-Oserian.

Sumba (1986), in his study of African fish eagles at Queen Elizabeth National Park, Uganda, found that significantly more pairs laid when temperatures were low. He offered no explanation stating that temperature ranges in his study area do not normally exceed 5°C, and hence there would be no obvious advantages fish eagles would derive by laying at low temperatures. My results suggest that temperature range may also be an important factor in influencing the timing of breeding in Hell's Gate where food supply is limiting. In addition, augur buzzards in Hell's Gate are constantly defending their nests against predators, and territories against conspecifics and neighbouring pairs. This means that parents spend more time off the nest either hunting or defending while having eggs or young in them. Reduced female nest-attendance in Hell's Gate, coupled with the fact that nests are usually high up on cliff ledges, means that eggs or young are exposed to extremes of temperature and or rainfall. By timing egg-laying during months when temperature range and rainfall are minimal, augur buzzards may have ensured survival for their young. Brown and Britton (1980) suggested that raptors in East Africa tended to select the cool mid-year dry season which may have been connected with a reduced need to spend time on the nest shading the young. I am inclined to believe that this preference may be due more to availability of food (brought about by rainfall) than to low temperatures and cloud cover.

It is evident that rainfall acts as a proximate factor in triggering egg-laying in augur buzzards. Three years of field data is not enough to investigate whether the amount of rainfall in a year has any influence on breeding rates or productivity (discussed in next chapter). The decline in mole-rat densities (after reaching peaks) in all three sites from around July onwards suggests that augur buzzards (along with grazing pressure, predation pressure and anthropogenic influences – each varying among land-use areas) may be having a partial impact on the mole-rat population. As herbivore and livestock grazing reduces grass cover to varying heights in different land-use areas, mole-rats and other rodents may be more visible and hence easier to hunt. Further research is necessary to test this hypothesis since this study has no evidence to confirm whether it is the case.

CHAPTER NINE
FACTORS INFLUENCING BREEDING PERFORMANCE

9.1 OVERALL BREEDING PERFORMANCE

9.1.1 Breeders vs. non-breeders

Breeding was attempted on 65 (73.9%) out of a total of 88 occasions (pair-years) in the southern Lake Naivasha area. This included all known pairs in Mundui (n = 16 pair-years), half of the 32 pair-years in Hell's Gate and 33 (82.5%) of the 40 pair-years in Sulmac-Oserian. There was a highly significant relationship between the type of land-use and the proportion of augur buzzard pairs that attempted to breed (Chi-square; χ^2 = 16.65, df = 2, p < 0.001).

9.1.2 Breeding rates

The mean breeding rate per year in the southern Lake Naivasha area was 0.92 ± 0.08 breeding attempts per pair per year. The overall breeding rate in 1995 was 0.96 ± 0.13 breeding attempts per pair per year, in 1996 it was 1.03 ± 0.16 breeding attempts per pair per year and in 1997 it was 0.78 ± 0.11 breeding attempts per pair per year. There was no significant difference in the annual breeding rate between the 3 years (Kruskal-Wallis; df = 2, H = 1.47, p > 0.05) or between the three years of study within each of the study sites (Table 9.1).

The highest breeding rates occurred in Mundui (1.13 ± 0.09 breeding attempts per pair per year) and Sulmac-Oserian (1.03 ± 0.12 breeding attempts per pair per year), while Hell's Gate had the lowest breeding rate (0.69 ± 0.15 breeding attempts per pair per year). The differences in breeding rates between the three study sites over the three-year period were significant (Kruskal-Wallis; df = 2, H = 7.72, p < 0.05).

Table 9.1: Kruskal-Wallis analysis of breeding rates (breeding attempts per pair per year) (plus std. errors) within the three land-use areas over the study period..

SITE	BREEDING RATE (se)			H value	p value
	1995	1996	1997		
Hell's Gate	0.80 (0.25)	0.73 (0.30)	0.55 (0.21)	0.57	0.752
Mundui	1.00 (0.00)	1.40 (0.25)	1.00 (0.00)	4.71	0.095
Sulmac-Oserian	1.11 (0.20)	1.15 (0.22)	0.86 (0.18)	1.25	0.536
df = 2					

9.1.3 Successful vs. unsuccessful breeders

Fifty-six (72.7%) breeding attempts out of a total of 77 in the southern Lake Naivasha area were successful. All breeding attempts in Mundui were successful compared with 63.6% in Hell's Gate (14, n = 22) and 64.9% in Sulmac-Oserian (24, n = 37). The type of land-use where breeding attempts occurred had a significant influence on the proportion of augur buzzards that bred successfully (Chi-square; χ^2 = 8.82, df = 2, p < 0.05).

Mean annual failure rates per breeding attempt were high but not significantly different between Hell's Gate (36% ± 0.11) and Sulmac-Oserian (35% ± 0.08) (Mann-Whitney; U = 374, p > 0.05). The annual failure rate per pair in Hell's Gate was 26% ± 0.11 while in Sulmac-Oserian it was 36% ± 0.07. This difference was not significant (Mann-Whitney; U = 214, p > 0.05).

Six (75%) out of the 8 breeding attempts that failed in Hell's Gate were due to predation (4 were seen to be depredated by baboons), 1 to rock climbers climbing too close to a nest (resulting in the eggs left unattended), and 1 for unknown reasons (Figure 9.1). The reasons for 6 (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 (Figure 9.1).
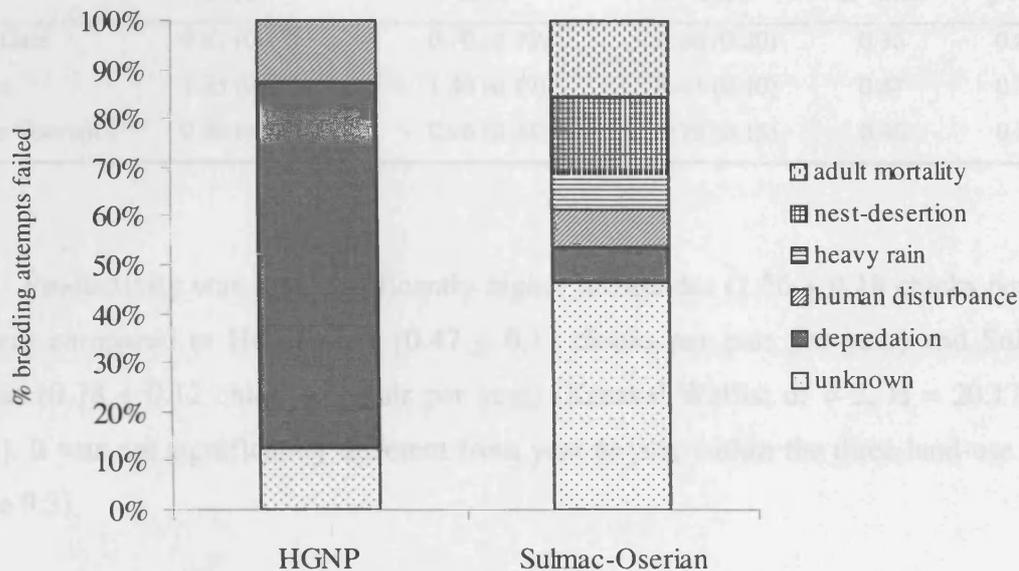
Figure 9.1: Percentages of the various causes of breeding failure in Hell's Gate (n = 8 failed attempts) and Sulmac-Oserian (n = 13 failed attempts).

9.1.4 Breeding success and productivity

The overall breeding success (number of successful chicks fledged per breeding attempt) in the southern Lake Naivasha area was 0.95 ± 0.08 chicks per breeding attempt per year, while the overall productivity (number of successful chicks fledged per pair [including non-breeding pairs]) was 0.81 ± 0.09 chicks per pair per year. This difference was not significant (Mann-Whitney; U = 5755.5, p > 0.05).

Breeding success was significantly higher in Mundui (1.38 ± 0.12 chicks per breeding attempt per year) compared to Hell's Gate (0.72 ± 0.12 chicks per breeding attempt per year) and Sulmac-Oserian (0.85 ± 0.18 chicks per breeding attempt per year) (Kruskal-Wallis; H = 11.73, p < 0.01). It was not significantly different from year to year within the three land-use areas (Table 9.2).

Table 9.2: Kruskal-Wallis analysis of breeding success (plus std. errors) within the three land-use areas over the study period.

SITE	BREEDING SUCCESS (se)			H value	p value
	1995	1996	1997		
Hell's Gate	0.67 (0.17)	0.70 (0.30)	0.80 (0.20)	0.36	0.834
Mundui	1.25 (0.25)	1.40 (0.19)	1.43 (0.20)	0.47	0.792
Sulmac-Oserian	0.88 (0.21)	0.96 (0.24)	0.70 (0.15)	0.40	0.817
df = 2					

Productivity was also significantly higher in Mundui (1.56 ± 0.18 chicks per pair per year compared to Hell's Gate (0.47 ± 0.13 chicks per pair per year) and Sulmac-Oserian (0.78 ± 0.12 chicks per pair per year) (Kruskal-Wallis; df = 2, H = 20.17, p < 0.001). It was not significantly different from year to year within the three land-use areas (Table 9.3).

Table 9.3: Kruskal-Wallis analysis of productivity (plus std. errors) within the three land-use areas over the study period..

SITE	PRODUCTIVITY (se)			H value	p value
	1995	1996	1997		
Hell's Gate	0.50 (0.17)	0.46 (0.28)	0.46(0.21)	0.65	0.722
Mundui	1.25 (0.25)	2.00 (0.45)	1.43 (0.20)	2.01	0.367
Sulmac-Oserian	0.89 (0.20)	0.92 (0.24)	0.57 (0.17)	1.79	0.408
df = 2					

9.2 MORTALITY

Fifteen out of 57 marked and ringed adult augur buzzards were recovered or found missing from their territories over the three-year study period. These were as follows - Nine (60%) in Sulmac-Oserian, 4 (26.7%) in Hell's Gate and 2 (13.3%) in Mundui. The mean annual mortality in the southern Lake Naivasha area was estimated at 8.77%. 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 in Sulmac-Oserian varied from 3.3% in Oserian to 20.8% in Sulmac.

The causes of death of the majority of adult augur buzzards were unknown (Figure 9.2). Human persecution and poisoning were the main causes of death in Hell's Gate and Sulmac-Oserian, while in Mundui, it was drowning (in a cattle trough). Electrocution from power transmission lines was also a cause of death in Sulmac-Oserian.

Mean annual mortality rate was highly positively correlated with the 'Increasing Human Impact' index (IHI) (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) .
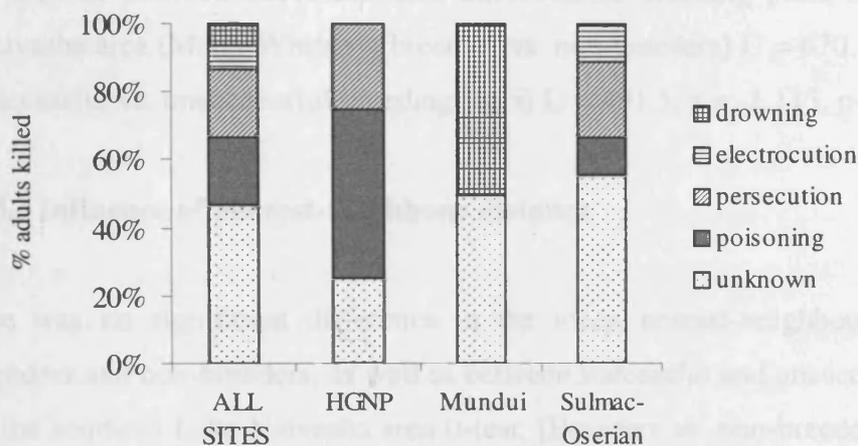
Figure 9.2: Percentages of the various causes of adult mortalities in the southern Lake Naivasha area (n = 15: Hell's Gate [4]], Mundui [2], Sulmac-Oserian [9]).

9.3 FACTORS INFLUENCING BREEDING PERFORMANCE

9.3.1 Influence of nest type

Nests in cliffs had a breeding success rate of 64.7% while nests in *Acacia xanthophloea* and *Euphorbia magnicapsular* trees had breeding success rates of 70.6% and 85.0% respectively. There was no significant relationship between the type of nest used and the

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proportion of successful breeding attempts (Chi-square; χ^2 = 2.17, df = 2, p > 0.05) although nests in *Euphorbia* trees tended to be more successful. There was also no significant difference between the type of nest used and the number of chicks reared per nest (ANOVA; df = 76, F = 0.990, p > 0.05). Twenty (35.1%) out of 52 breeding attempts were successful when new nests were constructed while 17 (32.7%) were successful when old nests were re-used. There was no significant relationship between old/new nests and whether a breeding attempt was successful or not (χ^2 = 1.10, df = 1, p > 0.05).

9.3.2 Influence of increasing human impacts (IHI index)

There was no significant difference in the IHI index between breeders and non-breeders, as well as between successful and unsuccessful breeding pairs in the southern Lake Naivasha area (Mann-Whitney;[breeders vs. non-breeders] U = 670, z = -1.512, p > 0.05; [successful vs. unsuccessful breeding pairs] U = 491.5, z = -1.113, p = 0.266).

9.3.3 Influence of nearest-neighbour distance

The was no significant difference in the mean nearest-neighbour distances between breeders and non-breeders, as well as between successful and unsuccessful breeding pairs in the southern Lake Naivasha area (t-test; [Breeders vs. non-breeders] df = 97, t = 1.20, p > 0.05; [successful vs. unsuccessful breeding pairs] df = 75, t = -1.34, p > 0.05).

9.3.4 Influence of mortality rate

Mortality rates between breeding and non-breeding pairs did not significantly differ in the southern Lake Naivasha area (Mann-Whitney; U = 755.5, z = -0.799, p = 0.424). However, breeding augur buzzards that were unsuccessful had a significantly higher mortality rate in their territories than successful breeders (Mann-Whitney; U = 218.5, z = -4.34, p < 0.0001).

9.3.5 Influence of previous breeding attempt

Thirty-two (65%) breeding attempts that were successful, out of a total of 49, were also successful in their previous attempts, while 8 (16%) that were unsuccessful, followed previously unsuccessful attempts. There was a highly significant relationship between the successful outcome of a previous breeding attempt and the proportion of successful breeding attempts that followed in the southern Lake Naivasha area (Chi-square; χ^2 = 10.55, df = 1, n = 49, p < 0.001).

9.3.6 Influence of soil softness, grass height and mole rat availability

There was a significant linear trend between the grass height (χ^2 = 4.99, p = 0.026) and mole-rat availability (χ^2 = 4.16, p = 0.041) categories and the proportion of augur buzzards that bred in 1997 (Chi-square test for trend; df = 1, n = 34 pairs [25 breeding, 9 non-breeding]). There was no significant linear trend between the soil softness category and the proportion of breeding augur buzzards (Chi-square test for trend; χ^2 = 2.53, p = 0.112). Soil softness was positively correlated with grass height and mole-rat index, but negatively correlated with nearest-neighbour distance (Tables 9.4 and 9.5). Grass height was positively correlated with soil softness and mole-rat availability, while mole-rat availability was positively correlated with both soil softness and grass height, but negatively correlated with nearest-neighbour distance (Tables 9.4 and 9.5).

There was a significant linear trend beteen the grass height category (χ^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 linear trend among the soil softness (χ^2 = 0.01, p = 0.924) and mole-rat availability (χ^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]).

9.3.7 Combined effect of all variables – logistic regression model

Several of the explanatory variables measured at each territory and nest were significantly correlated (Tables 9.4 and 9.5). For breeding vs. non-breeding pairs, 4 out of 15 correlation coefficients exceeded 0.5 and 7 were significantly different from zero ($r > 0.34$, $n = 34$, $p < 0.05$) (Table 9.4). For successful vs. unsuccessful pairs, 4 out of 15 correlation coefficients exceeded 0.5 and 9 were significantly different from zero ($r > 0.39$, $n = 25$, $p < 0.05$) (Table 9.5).

Table 9.4: Correlation coefficients for habitat and competition variables measured at 34 augur buzzard territories in the southern Lake Naivasha area, 1997.

	IHI	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 IHI 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 9.5: Correlation coefficients for habitat and competition variables measured at 25 augur buzzard nests in the southern Lake Naivasha area, 1997.

	IHI	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 IHI 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 9.6: Summary of univariate results of 9 explanatory variables and their relationship to a) breeding vs. non-breeding pairs; and b) 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

Five out of the 6 variables that potentially influenced breeding were considered in the multivariate logistic regression Model 1, while 4 out the 9 variables that potentially influenced successful breeding were considered for Model 2 (p < 0.25) (Table 9.6). This selection was based on univariate test results.

Multiple regression revealed that when considered together, only mortality rate (MR), outcome of previous brood (PB) and grass height (GH) were related to breeding attempts and success (Table 9.7). The most parsimonious model for the multivariate regression of breeders versus non-breeders included only grass height (Model 1B in Table X). Model 1A did not have any significant predictive variables (Table 9.7). The logistic model 1B predicting the probability of a pair breeding $P(\text{Br})$ was

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

..........(Model 1B)

It was only 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.

Table 9.7: 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 χ^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

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 9.7). The logistic model 2A predicting the probability of a pair breeding successfully P(BrSux) was

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

........(Model 2A)

while that of 2B was

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

........(Model 2B)

Both models 2A and 2B contained coefficients different from zero (Wald χ^2 test [Table 9.7]). They were both significantly better than the null model (p < 0.05 [Model 2A]; p < 0.01 [Model 2B] (Table 9.7) 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.

Although the most parsimonious regression models of P(Br) and P(BrSux) were significant, the R^2 value for each model was 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).

9.4 DISCUSSION

9.4.1 Breeding performance

Breeding rates and the proportions of breeding augur buzzard pairs were greatest in Mundui and Sulmac-Oserian compared to Hell's Gate. This could be attributed to higher mole-rat densities and availability of suitable nest-sites in those areas. Hell's Gate had the lowest breeding rate that may be as a result of both limited food supply and nest-sites. Both Hell's Gate and Sulmac-Oserian had similarly high nesting failure rates while Mundui had a zero failure rate. In Hell's Gate, cliff-climbing terrestrial predators such as baboons (and possibly leopards) were important in causing nest failures, as was the limited food supply. In Lendrum's (1979) study of the augur buzzard population in the Matopos hills, eggs were depredated by baboons, white-necked ravens *Corvus albicollis*, and pythons *Python sebae*. The failure rate in Sulmac-Oserian was caused by high adult mortality rates. This meant that surviving parents had to abandon their eggs or nestlings and attract new mates that are usually inexperienced and spend the first year orientating themselves to new foraging areas (Newton, 1979). High food availability in Sulmac-Oserian led to high breeding rates but high adult mortality coupled with lack of breeding experience by new territory holders usually led to increased failures.

Overall breeding performance in the southern Lake Naivasha area was similar to that of the Matopos hills (Lendrum, 1979), but higher than that of the Impenetrable Forest, where breeding success was poor (Muhweezi, 1990 [no figures available]). Annual breeding rates at Hell's Gate, Mundui and Sulmac-Oserian remained constant over the three-year study. Breeding performance was highest in Mundui and lowest in Hell's Gate. The high breeding performance in Mundui is attributable to high mole-rat availability, high nest-site availability, low predation and human persecution pressure, decreased adult mortality (this leads to more experienced birds that can provision better for nestlings) and a low IHI index. It could also be argued that good penetrative soil conditions in Mundui provided for better burrowing for mole-rats, hence their greater availability. The low breeding performance in Hell's Gate was attributable to high predation pressure, limited food supply and nest-site availability and high intra and inter-specific interactions. Nests built on elevated trees and cliffs in Hell's Gate may be subjected to extreme weather conditions and hence could also account for low breeding performance.

In Sulmac-Oserian, breeding performance was low though slightly higher than in Hell's Gate. This low performance could be attributed to high adult mortalities resulting in abandoned nests and/or lack of parental care. In territories where adults have been replaced, the new occupants are usually inexperienced birds that take a few years to identify themselves with prime foraging areas, perching sites, nest trees as well as to develop and maintain a bond with their mates. The influence of human activities in controlling mole-rat populations (when they peak) may also have detrimental effects on augur buzzard breeding performance. Annual breeding performance within sites was constant. This 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 only be detected in studies of 10 years or longer (Gargett, 1990).

9.4.2 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 strong relationship between annual mortality rate and IHI index suggests that human disturbance influenced augur buzzard adult mortality. 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. My observations indicated that dead augur buzzards were usually replaced within one or two days. Brown and Amadon (1968) have also documented this.

The negative correlation with grass height suggests that areas that were extensively grazed experienced greatest 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. I frequently saw cattle and goat herders throw rocks at perched augur buzzards. This would be possible considering cattle and goat herders 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 stated 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, also had a lower adult mortality rate.

Assuming the adult population is stable and that recruitment from the immature population equals that annual mortality (8.77% in the southern Lake Naivasha), then the life expectancy of an augur buzzard in the southern Lake Naivasha area was estimated at 12.5 years per bird (10.9 years [based on the formula by Fry, 1980] + 1.6 years [time period to reach adult plumage – Steyn, 1982]). This estimate compared well with that of Fry *et al.* (1982) which was 13 years per bird. They estimated a juvenile 75% mortality rate before sexual maturity at 3 years and hypothesized that adults would require a breeding life of 10 years; but their observations suggested that this was longer than

normal. Presumably with different mortality rates amongst sites, the average life span of augur buzzards will vary according to the natural and anthropogenic pressures exerted.

The augur buzzard adult annual mortality rate of 8.77% in the southern Lake Naivasha area is much lower than that for adult common buzzards *Buteo buteo* (19 – 20%) (Olsson, 1958; Mebs, 1964) and red-tailed hawks *B. jamaicensis* (21 – 24%) (Henny and Wight, 1972). These latter high mortality rates were based on national ringing recoveries and can be biased (Newton, 1979). Kenward's (in press) radio-telemetry study on common buzzards in the UK has shown that adult mortality rates are presently as low as 9% while those of first-year birds are about 35%. This compares well with adult mortality estimates for the southern Lake Naivasha area although data are still lacking for estimates on juvenile augur buzzard mortalities. The disparity in mortality rates between the pre-1970 era and the present (1992 onwards) can be attributed to greater awareness and protection offered to raptors against human-induced activities such as shooting, trapping, persecution, pesticide poisoning, electrocution and habitat loss

9.4.3 Correlates of breeding performance

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 breeding or not. This study showed that grass height was positively correlated with mole-rat availability, which was in turn was 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 would mean 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.

The type of nesting substrate that a pair used did not influence the success of a breeding attempt. Cliff nests were most vulnerable to predation mainly because baboons were common in Hell's Gate and are skilled at climbing cliffs. All *Acacia xanthophloea* nests in Mundui were successful. They were constructed on tall and mature trees, which offered protection against predators, and were also subject to minimal human

disturbance. In Sulmac-Oserian, local people knew of some of the augur buzzard nest trees and hence influenced their breeding success by either killing adult augur buzzards or cutting down nest-trees. *Euphorbia magnicapsular* trees had the most successful breeding success rates. They (*E. magnicapsular*) grow on steep slopes, usually at a distance from human influences, have fragile fronds that carry a poisonous milky sap, and are difficult to climb. Despite constraints from human disturbances and close distances to neighbouring pairs, augur buzzards established territories and attempted to breed even in areas with high IHI indices.

Success or failure in one year affects breeding performance in the next, but there are other factors involved. Territorial occupancy, boundary changes and/or inter-specific contacts also affect the likelihood that a breeding attempt will be made (Garget, 1990). In addition to augur buzzard adult mortality (discussed above), the logistic regression model showed that the success of a pair's previous breeding attempt was also an important variable in predicting the success of their next breeding attempt. 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 2 out of 3 years because there was a tendency for pairs that bred successfully to not nest the next year. This may be true for raptors such as large eagles with longer breeding periods (including periods of long post-fledgling dependency). In the Verreaux's eagle *Aquila verreauxii*, Garget (1990) found that a successful breeding attempt in one year was almost invariably followed by non-breeding in the following year.

My study was observational rather than experimental, and the multivariate analysis thus exploratory. Also because the breeding population was relatively small (34 pairs considered for the model), the results are based on somewhat limited data. Although the regression models were significant, they did not explain most of the variation in the data. Given the nature and limitations of the study, the results suggest new hypotheses regarding factors influencing breeding success and productivity of augur buzzards. Future

studies should attempt to test these using larger sample sizes from study areas where important explanatory variables are less likely to be correlated.

CHAPTER TEN
OVERALL DISCUSSION AND SYNTHESIS

10.1 INTRODUCTION

This study has demonstrated the ecological adaptation of augur buzzards to different land-use patterns. In chapters 5 to 9, nesting density, nest-site selection, breeding behaviour, diet, prey availability, seasonality and breeding performance were individually discussed in relation to different land-use patterns. The aims of this final chapter are to:

- present an overall study synthesis;
- discuss the factors that influence the overall breeding ecology of augur buzzards, particularly with respect to population size and breeding performance;
- consider management implications and future research priorities.

10.2 OVERALL STUDY SYNTHESIS

The density of augur buzzards in the southern Lake Naivasha area is the highest reliably recorded anywhere in their range. Their behaviour and ecology in response to the ecological variables studied was different between the three land-use areas (Table 10.1). The augur buzzard population of the undisturbed *Acacia* woodland pastures of Mundui had the best nesting habitat, produced the most fledglings (1.6 chicks per pair per year), enjoyed an abundant food supply as the land was not heavily grazed, and suffered the least persecution. In contrast, the augur buzzards of Hell's Gate produced the fewest fledglings (0.5 chicks per pair per year). Their nests were confined to cliffs and short shrubs that were vulnerable to predation. They had a limited food supply, and spent significantly more time than their counterparts in the lake environs interacting with potential predators and defending their territories against conspecifics. The augur buzzards of Sulmac-Oserian were affected by horticultural and pastoral practices. Although their food supply was

Table 10.1: Summary of various ecological variables affecting augur buzzards in different land-use areas in the southern Lake Naivasha area.

Ecological Variable	HELL'S GATE	LAKE ENVIRONS Mundui	Sulmac-Oserian
nesting density	high	very high	high
nest-site selection	cliffs/*Euphorbia* trees tall trees on steep-sloped hills. Nests faced eastern slopes	only *Acacia* trees that were mature with large canopies	mature *Acacia* trees in Sulmac and mature *Euphorbia* trees in Oserian that grew on steep slopes.
parental care	males spent more time incubating while females defended nests against predators and conspecifics	males spent less time incubating while females devoted much more time towards raising chicks.	
prey delivery rates	low	high	high
feeding rates to chicks	low	high	high
inter/intra-specific interactions	very high	low	low
diet	limited food supply but diverse – hence generalist feeder	abundant food supply comprising mainly of mole-rats – hence specialist feeder	
strike rates	high	low	low
egg-laying period	June - September	April - May	June - September
breeding rates	low	high	high
breeding success	moderate	high	moderate
productivity	low	high	moderate
adult mortality rate	moderate	low	high

abundant and they nested on large trees where available, they produced fewer fledglings (0.8 chicks per pair per year) and suffered the highest adult mortalities as a result of human persecution. Augur buzzard foraging areas were (and still are) threatened by horticultural development and overgrazing by domestic livestock, both of which may affect prey quality and quantity.

Mole-rats were the primary food source of augur buzzards in the lake environs, while in Hell's Gate, they exploited a broader spectrum of prey that included limited numbers of mole-rats, but also hyraxes, birds, reptiles and arthropods. Augur buzzards in Hell's Gate spent significantly more time hunting compared to those in the lake environs. This implied that it was more difficult to procure prey in Hell's Gate since a broader prey spectrum requires different hunting strategies, which consequently affects their breeding performance. The difficulty in obtaining prey in Hell's Gate may be attributable to competition with other predators and a suppressed prey base due to semi-arid conditions and the effects of overgrazing by a large mammalian herbivore population restricted within the park. Limited food supply in Hell's Gate meant that prey delivery rates to nests and feeding rates to chicks were much lower compared to the lake environs, hence reducing breeding performance in Hell's Gate. Male augur buzzards in Hell's Gate also spent significantly more time (up to eight times) sitting on eggs than males from the lake environs. This can be attributed to the behaviour of the females whose role is to defend the nest (and its contents) against predators. As predation pressure is high in Hell's Gate, females spend less time incubating and more time driving away potential predators and intruding augur buzzards; an adaptation that may reduce breeding performance. Modern agricultural practices in the lake environs coupled with an increasing human population have probably eliminated other predators of the mole-rat (such as mole-snakes). This has resulted in the lake environs supporting large populations of mole-rats, which have been effectively exploited by augur buzzards, making them probably the most important avian predator of mole-rats. This may explain why the breeding rate of augur buzzards in the lake environs is much higher than in Hell's Gate.

The breeding patterns of augur buzzards are governed by rainfall. There were clear trends illustrating that egg-laying was triggered by an increase in mole-rat density caused by an increase in vegetative cover (mainly grasses) as a result of rain. Peak egg-laying also coincided with the time of the year when temperatures were cool and dry. This may be associated with a need to avoid laying in harsh tropical conditions such as periods of heavy rainfall and extremes of heat, both of which can cause nest failures. The cool dry conditions between June and August is also a period when luxuriant growth of grass following the rains in April is grazed to levels that render prey not only available

but also visible to augur buzzards. High interaction rates which results in reduced nest attendance by females would also make laying in cool dry conditions advantageous as nest contents are less likely to suffer from heat exposure or heavy downpours.

The overall breeding success of augur buzzards depends on the success of previous breeding attempts as well as a low adult mortality rate. Their ability to breed depends on good quality grasslands that are moderately grazed so that prey is visible. Heavily grazed grasslands diminish prey populations and affect augur buzzard breeding. In Hell's Gate, the augur buzzard population is limited by the availability of suitable nesting sites, a general (but limited) food niche, intra-specific competition and high predation pressure. In the horticultural areas of Sulmac-Oserian, their population is limited by high mortality rates caused by human persecution, while in Mundui, their population is probably limited by density dependent factors.

Novel findings from this study are that

- augur buzzards show changes in behaviour and breeding performance in response to different pressures (natural and anthropogenic), such as predation, prey quantity/quality, variable landscape patterns, and changing land-uses caused by human impacts;

- augur buzzards breed (assuming nest-sites are available) in relation to changes in vegetation cover (mainly grasses) which influences prey density and visibility. Vegetation cover is in turn influenced by rainfall and grazing pressure.

- breeding success of augur buzzards is related to mortality of adults and the outcome of previous breeding attempts;

- the life span of augur buzzards was estimated to be 13 years, while juvenile survival was estimated to be 21.5% (section 10.3.5).

One of the limitations of this study was that a larger sample of augur buzzard pairs would have been needed to accurately correlate prey availability with nesting density and breeding performance.

10.3 FACTORS INFLUENCING AUGUR BUZZARD BREEDING ECOLOGY

10.3.1 Rainfall, grass and food supply

This study showed that rainfall was the most important factor in predicting the timing of egg-laying in augur buzzards in the southern Lake Naivasha area. Lack of rainfall data for each of the different study sites was a major limitation of this study as site-specific information on rainfall would have shed more light on its influence on breeding patterns. In the grasslands of Hell's Gate, Kiringe (1993) showed that primary production coincided with rainfall amount and availability. In the southern Lake Naivasha area, this study showed a similar pattern, that is an increase in grass cover immediately following the long rains in April. Grass height (used as an index of primary production) in turn was positively correlated with mole-rat availability. My results support the hypothesis of Brown and Britton (1980) that rodents normally increase during the rainy seasons, sometimes reaching a peak of abundance. My three-year study was too short to determine whether total annual rainfall influenced productivity. In the African fish eagle, their numbers and prey abundance are positively correlated with Lake Naivasha's water level (Virani, unpublished data) – which has been positively correlated with the amount of rainfall (Vincent et al., 1979). Hustler and Howells (1988) also showed that periods of higher rainfall resulted in greater breeding success, earlier laying and larger clutch sizes in the African hawk eagle *Hieraaetus spilogaster*.

Grass height, via its role in influencing food supply (rodents) had a greater role in initiating breeding rather than influencing breeding performance. Basically, fresh grass in May following the rains in April caused an increase in mole-rat numbers. While the grass was kept reasonably short through domestic livestock and wildlife grazing, mole-rats were visible and hence easily available to augur buzzards. Areas that were completely overgrazed or devoid of grass had low mole-rat densities and hence the resident augur buzzard pairs of those areas probably could not get sufficient food to initiate breeding – non-breeding pairs were found in parts of Hell's Gate and Sulmac-Oserian that were heavily grazed. In Mundui, where the grass (and food supply) was higher than in Hell's Gate and Sulmac-Oserian, all pairs bred (and successfully). The high breeding rates in

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Mundui and Sulmac-Oserian support the findings of this study that food supply was plentiful in these areas compared to Hell's Gate where the breeding rate was significantly lower.

Two clear findings emerged from this study of food quality/quantity and breeding success amongst augur buzzards in the southern Lake Naivasha area. Firstly, the population in Hell's Gate had a limited food supply and thus exploited a wide range of food resources making it a generalist feeder, and to do so necessitates a wider range of hunting strategies which may result in reduced hunting efficiency. Secondly, in the lake environs, augur buzzards were probably the most important avian predators of mole-rats. Their abundance, together with vlei rats and Nile grass rats have rendered the augur buzzards to become specialist feeders, requiring uncomplicated hunting techniques. This study showed that male augur buzzards in Hell's Gate made more hunting attempts than their male counterparts in the lake environs. This may be one reason why augur buzzards in Hell's Gate tended to breed less successfully than those in the lake environs. Another factor, which probably contributes to reduced breeding performance in Hell's Gate, is the comparative lack of sufficient prey in the augur buzzards' optimum size range (animals around 150 – 300 g in weight). This has resulted in a dependence on large prey (> 1 kg) such as hyraxes and francolins, or small prey (< 50 g) such as swifts and arthropods, and consequent inefficiencies when such items must be carried to nest sites. Hence, in Hell's Gate, the augur buzzards' broad-spectrum diet is consistent with the findings of this study that conditions there are less than optimal.

10.3.2 Temperature

Temperature is of little consequence to eggs that are properly incubated, or to chicks that are well brooded. In Hell's Gate, augur buzzards mainly laid during the coolest months. This would have made sense for two reasons:

• the high inter and intra-specific interactions coupled with a limited food supply meant that parents spent more time off the nest and would be assured that their eggs or downy chicks would have a lower probability of perishing from extremes of weather;

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• augur buzzards additionally benefit from an increase in mole-rats as their activities are influenced by temperature fluctuations; they are active during the cooler months and inactive during the hot and dry months.

The peak egg-laying period of augur buzzards in the southern Lake Naivasha area adds credence to Brown and Britton's (1980) suggestion that raptors in East Africa tended to select the cool mid-year dry season as this reduced parental needs to spend time on the nest shading the young.

10.3.3 Nest sites, predation and interactions

Augur buzzards in the southern Lake Naivasha area constructed nests on the type of substrates available to them; namely cliffs and trees. Generally, cliffs occurred in the gorge in Hell's Gate, *Euphorbia magnicapsular* trees grew on steep hill faces in Hell's Gate and Oserian, and *Acacia xanthophloea* grew on gently sloping land in Sulmac and Mundui. Augur buzzard distribution in Hell's Gate was limited by the availability of suitable cliffs and trees available. Competition for nest sites with conspecifics and other cliff nesting raptors may have also played an important role in influencing augur buzzard nesting density and breeding performance. Cliff nests were vulnerable to predation whilst some tree nests appeared not to have offered enough protection. Although non-significant, cliff nests had a lower breeding success rate than tree nests. There was no evidence to show that nest-site availability limited the distribution and abundance of augur buzzards in Mundui and Sulmac-Oserian.

The high interaction rate between adjacent augur buzzard pairs suggests that intra-specific interactions play a significant role in the spacing of augur buzzards in the southern Lake Naivasha area. In Hell's Gate, nest spacing appears to be partly related to the irregular terrain features (such as cliffs and steep-faced hills harbouring pockets of *E. magnicapsular* trees). Potential nest-sites in Mundui were plentiful while those in Sulmac and Oserian were restricted to riparian woodlands (close to the lake) and steep-faced hills (between Hell's Gate and the lake) respectively. Augur buzzards in the southern Lake Naivasha area, as elsewhere (Lendrum, 1979; Fry *et al.*, 1988; Muhweezi, 1990), were

strongly territorial, and boundary disputes between pairs were seen frequently throughout all three land-uses. I suspect that territorial behaviour would be the prime cause of nest spacing in the southern Lake Naivasha area. In any further studies, it would be challenging to investigate the strong regular structure of augur buzzard nest dispersion, and to relate nest locations to environmental features.

By virtue of being a national park and protected area, Hell's Gate harbours more natural predators than the lake environs (where many predators have been killed). Predation of augur buzzard nest contents accounted for 75% of all breeding attempts that failed in Hell's Gate. This study has shown that augur buzzards in Hell's Gate spent significantly more time interacting with potential predators and defending their territories against intruding augur buzzards than those in the lake environs. This may contribute towards reduced breeding performance since time spent defending nests or territories is at the expense of time devoted to raising chicks (in an area already limited by food supply).

High nest failures in Hell's Gate and Sulmac-Oserian (mainly in Sulmac) might have caused augur buzzards to have more nests per territory than in Mundui. This probably means more energy is expended in nest construction contributing to reduced breeding efficiency. The number of alternative nests per pair should be studied over a longer period of time to test the hypothesis that more nests are built in territories that are vulnerable to predation or human disturbance.

In early 1999, a troop of baboons in Hell's Gate had attacked and severely injured an augur buzzard (the male of pair H1) as it tried to defend its nest (S. Thomsett, pers. comm). An area with high predation/interaction pressure such as Hell's Gate, may thus also carry the potential risk of increased adult mortalities. Consequently breeding success is affected. New augur buzzards that replace dead ones are usually inexperienced and may take time to establish themselves in to their new surroundings (assuming they last) before breeding can start.

10.3.4 Anthropogenic factors

Anthropogenic factors mainly affected those augur buzzards in Sulmac-Oserian through habitat quality, nest spacing, food supply, breeding performance and survival. In the

southern Lake Naivasha area, augur buzzards were more widely spaced in areas where human impacts had increased. Inter-nest distances in Sulmac-Oserian were greater compared to Hell's Gate and Mundui. Although nest-sites may be limiting, I suspect the reason for greater inter-nest distances in Sulmac-Oserian is because food supply (and probably perching and nesting sites) is affected by human activities. In Sulmac-Oserian, trees were felled and grasslands were cleared at an annual rate of 5% (pers obs.). This was done to make way for horticultural units, and has the potential to affect prey density, perch/nest availability and area for foraging. While food supply may be abundant in some territories at certain times of the year, it is scarce in others where horticultural farms employ pest control methods to curb rodent outbreaks. Consequently, augur buzzards in these areas may start to breed following an increase in food supply, but are forced to abandon nests for lack of food as a result of human interference. One pair, R1, suffered 5 consecutive nesting failures while another, R2, had 2 failures. Both pairs were adjacent to large horticultural farms and the failures were attributed to human disturbance. Local farm workers also trap mole-rats, which forage on their vegetable plots (pers. obs). Some farmers who keep chickens, trap mole-rats and lace them with poison (mainly strychnine) to bait and kill augur buzzards which are suspected of killing chickens (F. Njuguna, pers. comm; pers obs.). All these activities affect augur buzzard breeding performance and survival.

In Mundui, augur buzzards had the lowest breeding rate to breeding success ratio (0.82). This meant that they produced more fledglings compared to the number of times they attempted breeding. In Hell's Gate, the ratio was close to 1 (0.96) which meant that augur buzzards produced fledglings at the same rate at which they attempted breeding. However, in Sulmac-Oserian, augur buzzards had the highest breeding rate to breeding success ratio (1.21), which meant that their breeding rate was greater than the number of successful fledglings produced. This implied that nest failures were frequent but a high breeding rate was maintained, as food supply was usually abundant. Nest failures were caused by human disturbances (felling of nest trees), adult mortalities and nest-desertions (probably because of lack of food, adult mortalities or poisoned mole-rats delivered to nests).

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Not all anthropogenic influences are negative. Some birds of prey such as kites *Milvus* sp. have benefited from increased human populations (Newton, 1979). In the southern Lake Naivasha area, augur buzzards would benefit by the human-induced elimination of mole-rat predators coupled with keeping grass cover at levels where mole-rats are abundant and visible. In Sulmac-Oserian, augur buzzards have also benefited from an abundance of telephone poles, fence posts and power pylons, which have provided useful perching sites from which to exploit their prey more easily (although power pylons carry the potential risk of raptor electrocution). This study did not investigate augur buzzard perch site characteristics and density, an aspect of habitat selection that should be investigated in future studies. There is usually a strong correlation between home range size and numbers of perching posts amongst hawks e.g. pale chanting goshawk *Melierax poliopterus* (Malan and Crowe, 1997). The abundance of man-made structures used by augur buzzards for perching may partly explain their relatively high densities in the southern Lake Naivasha area compared to other parts of Kenya.

10.3.5 Mortality and survival

Knowledge about the mortality and survival of augur buzzards in the southern Lake Naivasha area is crucial in understanding their population dynamics and the species' wider demography. Sulmac-Oserian had the highest adult mortality attributed to human impacts. This study has shown that adult mortality increased in areas where human impacts were greatest. The adult mortality rate was found to be one of the most important variables in predicting the successful outcome of a breeding attempt. Poisoning, human persecution, electrocution and drowning were the main causes of adult mortalities.

The high longevity estimates of augur buzzards may contrast with temperate buzzards where the classic difference between temperate/tropical latitudes is in adult survival (low/high), balanced by brood size (high/low). Based on the annual adult mortality from this study, and assuming that the population in the southern Lake Naivasha area is stable, then the estimated measure of pre-breeing survival (1st and 2nd

year combined) was 21.5% (hence mortality is 78.5%). This estimate is based on the following formula:

$$x_1x_2 = \frac{2m_a}{p_f}$$

where x_1x_2 = multiplicative 1st and 2nd year juvenile survival;

m_a = annual adult mortality;

p_f = annual fledgling production per pair.

The '2' corrects for the fact there are two birds in a pair. My juvenile survival estimate is similar to that given by Fry *et al.* (1988) which was 25%. Although my sample size was small, I speculate that actual juvenile survival would be similar, if not more than my estimate. During the three-year study period, I ringed a total of 67 augur buzzards out of which adults made up 76.2%. All ringed augur buzzards were trapped at random and the proportion of juvenile birds ringed (23.8%) was similar to my estimated juvenile survival. While high breeding success may reflect the health of a population and its habitat, low juvenile survival may affect the entire population over a period of time. Raptors reveal the same trends as other birds, and the greater mortality of younger individuals is readily explained in terms of their lesser experience and social status (Lack, 1954, 1966). This study period was too short to detect whether the augur buzzard population in the southern Lake Naivasha area was acting as a reservoir for surplus birds, as this can only be accurately established by studying dispersal patterns of juveniles either from ringing recoveries or through the use of radio-telemetry.

10.4 MANAGEMENT IMPLICATIONS AND PRIORITIES FOR FUTURE RESEARCH

The efficacy of most ecologically-based raptor studies is limited by small sample sizes and in the case of the east African tropics, a lack of knowledge about the basic biology of most species (Virani and Watson, 1998). This is further compounded if populations have

to be compared along a gradient of different habitats. In East Africa, raptors breed all year round but have peak egg-laying periods (many of which have still to be researched) and hence nests have to be visited frequently.

This study has created a platform upon which future raptor studies in Kenya can be built. It is the most complete single-species study conducted on a relatively large population of raptors in Kenya. It has also contributed to raptor biology in general as little was known about augur buzzards since Lendrum's (1979) controversial study in Zimbabwe, the authenticity of which has since been questioned (Gargett, 1990).

The results of this study will be helpful in contributing to the management plan of the Lake Naivasha Riparian Association (LNRA) and the Kenya Wildlife Services (KWS) in their management plans for Hell's Gate and the lake environs in the following ways:

- the extent of grazing pressure and indiscriminate habitat alteration can be controlled by monitoring augur buzzard nesting density and breeding performance;

- rock-climbing routes on cliffs in Hell's Gate that are close to augur buzzard nest-sites should be closed between May and September, which is the period when the birds are most likely to breed;

- create awareness amongst the horticultural farmers, local schools and communities in the Lake Naivasha area on the importance of augur buzzards as indicators of ecological health and their usefulness in the control of rodents. Farmers should be cautioned and educated about the indiscriminate use of poisons to control rodent outbreaks.

It is imperative that follow-up studies on the augur buzzards continue so as to accumulate long-term data about breeding success (through nest inspections) and longevity and survival (through ringing efforts) to determine whether the population is increasing or declining.

Future studies should concentrate on the following aspects:

- collection of information on breeding success which should be correlated with rainfall, temperature range and prey availability;

- predator-prey relationships – the impacts of augur buzzards on mole-rat populations. This study should be expanded to quantify other small rodents such as vlei rats and Nile grass rats through trapping. The hunting and foraging behaviour of augur buzzards should also be studied in areas where no grazing is allowed to investigate if long grasses inhibit hunting success even though food supply is abundant.

- territory size of augur buzzards through use of radio-telemetry. Territory size should be correlated with perch habitat quality and prey density.

- post-fledgling dispersal studies (via ringing and radio-telemetry) to estimate juvenile survival;

- DNA studies – to compare the augur buzzard population in East Africa with that of southern Africa. DNA studies will also be useful in understanding the evolutionary and behavioural processes that drive co-operative breeding amongst augur buzzards where three birds co-exist in one territory. This was seen in one pair (S1) where two males and one female successfully raised broods in two consecutive years. Simmons (pers comm.) has reported this phenomenon for jackal buzzards *Buteo rufofuscus* in Namibia. DNA studies will also help in investigating the taxonomic relationships between augur buzzards and other African buzzard species;

- brood manipulation experiments to determine if prey delivery rates and feeding rates change in areas where food is not limiting.

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Acknowledgements