# Raptor Communities in Hill Habitats in South-eastern Zimbabwe.

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All the work detailed in this thesis was carried out by the author, except where otherwise stated. No part of this thesis, or the whole thesis has been submitted towards a degree at any other university.

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## Summary

The interrelationships between species composition, resource-use and availability, breeding and competition were studied in two hill habitat raptor communities in a conserved reserve and an unprotected communal land in Zimbabwe in 1995 and 1996.

The conserved Lonestar Study Area (LSA) and the unprotected Communal Land Study Area (CLSA) had 38 and 31 raptor species, high and normal diversities for the area sizes respectively. An estimated 147 pairs of 21 raptor species bred in 40km$^2$ in the LSA, compared to only 26 pairs of 22 raptor species per 40km$^2$ in the CLSA. Six species (African Hawk Eagle *Hieraaetus spilogaster*, Black Eagle *Aquila verreauxii*, Crowned Eagle *Stephanoaetus coronatus*, Little Banded Goshawk *Accipiter badius*, Barn Owl *Tyto alba* and Barred Owl (*Glaucidium capense*) made up 69% of breeding raptors in the LSA, while African Hawk Eagles, Little Banded Goshawks, Barn Owls and Barred Owls made up 58% of the breeding raptors in the CLSA. The abundance of Black, Crowned and African Hawk Eagles in the LSA was linked to abundant hyrax, *Heterohyrax brucei* and *Procavia capensis* (3.8 per ha.) and juvenile bushbuck *Tragelaphus scriptus* prey, and the high reproduction rates of Natal Francolin *Francolinus natalensis* (0.7 per ha. when not breeding). Little Banded Goshawk and Barn Owl abundances were linked to their ability to change prey preferences according to prey availability.

A fairly high rate of breeding attempts by eagles in the LSA in both years (60 - 76% of all pairs per year) was probably also linked to prey abundance. Most breeding failures were predator related, and were more common in areas of relatively low nesting densities indicating lower parental vigilance there. High eagle breeding densities were associated with small mean territory sizes in the LSA (7.7 - 10.7km$^2$ for the main eagle species). Eagles in the LSA usually nested closer to another eagle species than a conspecific, resulting in regular distributions of nests and no territory overlap within species. Differences in daily flight activity of eagles in both study areas, and in the onset of breeding between LSA eagles probably reduced interspecific aggression. Interspecific competition for food and nest sites amongst LSA eagles was possibly lessened by slight differences in resource selection.

Raptor resources were mostly unaffected by human activities in either study area during the study period. Differences in the raptor communities were probably as a result of natural habitat differences. The CLSA raptors potentially face resource loss through forest clearing and hunting. An expansion of the present CAMPFIRE program will protect the CLSA raptors.

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# Chapter One: Introduction & Aims

## 1.1 Introduction

Raptor, and other, communities exist in habitats where sufficient food, nesting and space resources occur (Ricklefs 1980). Habitats with abundant resources should thus support dense raptor communities, which may also be diverse. The identification of a dense and diverse raptor community in the granite Matobo Hills, Zimbabwe (Macdonald & Gargett 1984) and a high eagle nesting density in a small hill area in Kenya (Brown 1952) indicates that these hills have abundant resources. Hartley (1993) has also described a diverse raptor community in the precipitous, hill-like habitat of the Batoko Gorge on the Zambezi River. It is probable that most hill areas in Zimbabwe potentially support similarly dense and diverse raptor communities. This has important implications for raptor conservation in Zimbabwe where vast areas (*c.f.* 78000km$^2$) of granite hill habitat are largely unprotected from over-settlement and over-farming (Hartley *et al.* 1996; Whitlow 1980).

With the exception of the Matobo Hills, hill raptor communities in Zimbabwe have been unstudied until recently (Davison 1995). An understanding of the relationships between raptors, hill habitat resources and man has been limited to Black Eagles *Aquila verreauxii* and their resources in the Matobo Hills (Auman & Chiweshe 1995; Barry 1994; Barry & Barry 1996; Gargett 1990; Gargett *et al.* 1995). Resource utilization and distribution of raptors in microhabitats is better understood in African savannas and forests than in hills (Bataamba 1989; Brandl *et al.* 1985; Hustler & Howells 1990; Simmons 1986; Smeenk 1974; Snelling 1969; 1970; Sorley & Anderson 1994; Thiollay 1975; 1988).

Studies outside Africa have used the concept of guilds to describe the ecology of raptor and other bird communities (e.g. Adams 1985; Hawkins & MacMahon 1989; Holmes *et al.* 1979; Marti *et al.* 1993a&b; Simberloff & Dayan 1991). Guilds are sets of organisms, within a community, which use the same important resource in a similar way (Root 1967). Food is considered to be the limiting resource for most raptors, and prey-based guilds are viewed as the most ecologically meaningful, although food may not be limiting for some Afro-tropical birds (Brown & Brown 1984, Jacksic 1981, Newton 1979; Nilsson *et al.* 1982, Root 1967, Smith & Murphy 1979, Steenhof & Kochert 1988). Guilds describe communities in terms of processes of resource utilization, rather than merely the component species. Applying this concept to hill raptor communities should explain the structure of community in terms of resource availability and utilization, a more ecologically meaningful explanation than the species lists and densities which are usually given. Understanding raptor - resource dependency and interactions is vital for raptor conservation (Watson 1991).

Between February 1995 and November 1996, I studied the raptor communities in two hill areas, one a conserved area and the other an unprotected communal farming area in the south-east of Zimbabwe. I attempted to describe the community structures in terms of resource availability and utilization, and interactions with man.

### 1.2 Aims

1) Enumerate the diversity and density of raptors in both study areas, to test if distinct communities occur in hill habitats.

2) Evaluate the resources utilized in terms of nesting, prey and space resources.

3) Study the nature, extent and effects of resource sharing on competition and resource partitioning.

4) Investigate the effects of human activities in and around the hill habitats in the study areas on raptor resources and community structure, and suggest land management strategies in the two study areas to enhance raptor community conservation.

# Chapter Two: Study Areas

## 2.1 Lonestar Study Area (LSA)

The Lonestar Reserve was formerly a cattle ranch, and is now a privately owned reserve managed for tourism, game sales, education, and limited hunting. The reserve covers 400km$^2$ in the south-eastern lowveld of Zimbabwe (Fig. 1a) and the terrain is seldom more than 350 metres a.m.s.l. except in the hills. The average rainfall is approximately 500 - 550mm p.a. (Stalmans 1994).

The study area within the reserve is made up of ca. 40 km$^2$ of Stormberg sandstone outcrops, known as the Malilangwe Range (Fig. 1b). The terrain in the LSA consists of ridges of sandstone outcrops about 50 metres above the floor of the valleys which are narrow and incised, or broad and sandy. The Nyamasikana River cuts through the mountains in a north - south direction and most of the larger incised valleys are associated with this river and its tributaries. On top of some of the ridges flat areas form small plateaus. In other areas not associated with river drainage, undulating areas of rocky outcrops exist (Fig. 2).

The vegetation on the ridges and rocky areas is mostly *Brachystegia glaucescens* and *Androstachys johnsonii* thickets, interspersed with *Adansonia digitata* on the slopes where *Kirkia acuminata, Gyrocarpus americanus* and *Newtonia hildebrandtii* are also sometimes common. *Terminalia sericea* and *Acacia nigrescens, A. tortilis, Tabernaemontana elegans, Spirostachys africana* are sandveld trees which are commonly associated with the broad sandy valleys in the hills. In the northern section, *Julbernardia globiflora - Diospyros usambarensis* assemblages exist (Stalmans 1994). The plant species occurring in the communities mentioned are listed in full in Stalmans (1994).

The hills receive higher rainfall on average than the plains to the south and east of the hills. Between 1951 and 1977, a weather station in the south-eastern portion of the hills received on average 565 mm per annum compared to an average of 363 mm per annum between 1968 and

1972 on the isolated Hartebeest Hill in the southern portion of the reserve, the difference possibly due to orographic rain in the eastern section of the hills. The south-eastern hills have numerous springs which flowed throughout the dry season in 1996 following an exceptionally good 1995-1996 rainy season when approximately 745 mm of rain fell in the hills, whereas the surface water in the plains disappeared in the dry season except where artificially supplied. The hills had one large and four small dams which created artificial aquatic habitats and influenced the river courses downstream (J. Anderson pers. comm.).

## 2.2 Communal Land Study Area (CLSA)

The study area consists of ca. 80 km$^2$ of gneissic granite outcrops in communal farming areas and CAMPFIRE conservation areas in the Ndowoyo and Sangwe Communal Areas of Chipinge and Chiredzi districts of Zimbabwe (Fig. 1c). The CLSA lies on the bank of the Save River. The lower catchment area of this river has been quoted as being some of the most drought-prone and over-utilized agricultural land in Zimbabwe and it is severely degraded in places, where human densities are typically 40-50 people per km$^2$ (Campbell 1994). Average annual precipitation is less than 500mm with most rainfall between November and March.

The terrain is dominated by the Mutandahwe Hill which rises 220 metres above the surrounding plains to a height of 572 metres a.m.s.l. The Bandai Hills consist of broken rocky outcrops. The Save River gorge in the Mahenye area is incised 100 metres in places. To the east of the gorge ridges of basalt hills rise up to 100 metres above the surrounding plains; these have no large rock outcrops.

The vegetation in the outcrop areas is largely *Brachystegia glaucescens*, with some *Androstachys johnstonii*, *Adansonia digitata*, *Newtonia hildebrandtii* and *Kirkia acuminata*. The basalt ridges lack the *Brachystegia glaucescens* stands which exist only on sandy, well drained soils. Numerous springs at the bases of hills exist, and these have been modified and utilized by humans and livestock.

The surrounding areas are flat or associated with the riverine habitat along the Save and smaller rivers. The dominant vegetation is *Colophospermum mopane*, which in the vicinity of Mutandahwe Hill occurs in stands of scrub due to heavy utilization by the local populace.

# Chapter Three: Raptor Diversity, Density and Breeding

## 3.1 Introduction

The assemblage of raptors resident in an area is a result of either random processes or historical accident, or because the birds actively select the particular habitats within the area. Hills and mountainous areas provide specific prey and nesting resources which differ from those in other habitats (Gargett 1990). The diversity of resident raptors in hill habitats should be determined by the ability of the birds to utilize the resources available. Their density should depend on the abundance of these resources, and tolerance by individuals of conspecifics and other neighbours (Newton 1979).

The questions asked in this chapter are; did the hill habitats in this study contain distinct raptor assemblages in terms of diversity, and did they occur at different densities than in surrounding habitats, indicating differences in available resources? I have compared my results with other raptor community enumerations in southern Africa and elsewhere, and discussed the effect of differences in habitat. The structure of the communities were probably limited by resource availability and utilization which are investigated in Chapter 4.

## 3.2 Materials & Methods

The richness of raptors in the two study areas was estimated by noting all sightings of raptors during frequent trips through the study areas. Although more time was spent in the LSA, both study areas were extensively covered on foot, and the surveys in both areas are thought to be accurate and comparable.

Breeding densities of large raptors in the two study areas were estimated from counts of nests. Some of the nests on the LSA were known to the staff of the Malilangwe Conservation Trust and were shown to me. Kim Wolhuter actively sought eagle nests in the Lonestar Reserve in November and December 1994 and had plotted their coordinates using a Garmin Geographical

Positioning System (GPS). A more systematic search of the LSA was conducted in an attempt to find all nests, and a further seventeen nest sites were located. An aerial search of the hills from a microlight aircraft provided good visibility of nests, although no additional nests were found in this manner. The location statistics of all known nest sites on the Lonestar Reserve are given in Appendix 1.

Breeding density was calculated for eagles and eagle-sized raptors breeding within the hill habitat by dividing the number of known breeding pairs during each breeding season into the area of the hill habitat in both study areas, to give a first estimate of breeding density. Pairs of eagles and adult individuals seen regularly outside the estimated territories of known breeding conspecifics were assumed to be potential breeders and added to the estimate of breeding densities. Gymnogenes *Polyboroides typus* were included in the estimates because this species is nearly eagle-sized, and eagle-like in its flight, territorial and nesting behaviour (Steyn 1982).

Barn Owl densities in the two seasons are expressed as the number of known occupied roosts instead of nests which were difficult to locate in caves and crevices. Roosts were often occupied by single birds. Because raptor density indicates the extent and impact of resource utilization, single birds must be included in density estimates as well as breeding pairs.

Other raptors (accipitrines, owls, falcons and kestrels) were enumerated for density calculations by noting and mapping sightings or where vocalizations were heard. Sightings in the same territories were assumed to be the same birds, members of the same pair (if the birds were breeding) or replacement birds in the same territory. Small raptor nests were difficult to find as the nests are often concealed by foliage since the breeding periods coincided with the start of the rains, or in the case of small owls, were in tree holes and also difficult to locate.

## 3.3 Results

### *3.3.1 Diversity*

The LSA had a higher diversity of raptors seen during the study period (38 species) compared to the CLSA (32 species, Table 1). However there were more species which probably breed in the CLSA than in the LSA (23 species compared to 21 species). The difference is slight, as the CLSA is approximately twice the size of the LSA. However, a greater proportion of its raptor assemblage breeds in the area, whereas in the LSA many of the raptors using resources in the hill habitat nest elsewhere (26% compared to 7% in the CLSA). Many of these used the margin of the hills only, and were seldom seen further into the hills. Twenty-four species were commonly seen within the LSA boundaries, the rest were seen in marginal or ecotonal habitat. The scientific names of all raptors seen in the study areas are given in Table 1.

The LSA had a greater number of eagle species (including Gymnogenes) in the hill habitat (14 species) than the CLSA (11 species) but had a lower breeding diversity (9 species) than the CLSA (11 species). Bateleur and Black Breasted Snake Eagles nest and probably nest in the CLSA, but nest outside the LSA. Since the study areas differ in size and the differences are accounted for by one nesting pair per species, these differences cannot be regarded as significant.

Small accipitrines occur in the same diversity (11 species) in both areas. Seven species breed, or probably breed in the CLSA compared to six in the LSA. Bat Hawks were not seen in the CLSA but were possibly in the Save River gorge, and Rock Kestrels were not recorded in the LSA.

Nine owl species have been seen or heard in the LSA compared to the six in the CLSA. Pels' Fishing, Scops, Wood and Grass Owls were not seen in the CLSA but were present in low numbers in the LSA.

### 3.3.2 *Nesting densities of eagles*

In the LSA 51 nest sites belonging to eagles and Gymnogenes were found. These nests were of differing ages and states of repair. From observations at these nests and noting when and where adult birds were seen, an estimate of the number of pairs was made (Table 2).

African Hawk Eagles were the commonest eagle species in both areas, followed by Crowned Eagles. Black Eagles were relatively common in the LSA, but only one pair, which were not known to nest, were seen in the CLSA. The CLSA had more eagle species nesting, but fewer abundant species than the LSA, which was dominated by African Hawk, Crowned and Black Eagles.

There were more eagles nesting in the LSA than the CLSA despite the differences in area. The totals were cumulative over nearly two years. In the case of two of the Crowned Eagle nests, no nest use was seen during the study period, although an adult Crowned Eagle was seen close enough to a nest to assume that the nest belonged to it. Including this sighting, an estimate of 31 pairs or territories, which may have been occupied some of the time during the study, was made. Three African Hawk Eagle nests, which were probably independent and not alternate nest sites, showed no sign of use. One nest had a pair of African Hawk Eagles close to it on many occasions and a juvenile was seen near the nest in the 1995 breeding season indicating that the pair used the nest but the nesting attempt was not noted. No breeding was noted at another nest, although this nest was not observed frequently. All Black Eagle pairs were observed to breed, and nesting or nest building activity was noted at all but one nest. A minimum of 26 breeding pairs of raptors was noted in the LSA during the study period.

In the CLSA, only a few incidents of nesting activity were noted in a pair of Gymnogenes, Crowned and Wahlberg's Eagles in 1996.

### *3.3.3 Eagle breeding and breeding territories*

Probably all eagle territories were maintained between years during the study, with the exception of a Black Eagle territory which was not defended by the female after the male was shot in 1996. Nesting was a definite indication that territories were held. Crowned Eagles, which appeared mostly to breed only every second year in the LSA, were infrequently seen when they were not nesting. It was therefore difficult to ascertain whether some territories were occupied when nests were not in use. In these cases (n=2) it was assumed that the territories were still occupied when an adult was seen or heard within the estimated boundaries of the territories.

The same number of eagle and Gymnogene pairs attempted breeding in each year (18) although not all pairs bred in both years (Table 3). Sixty percent of eagle and Gymnogene pairs in 1995 and 62% in 1996 attempted nesting. The proportion of the population breeding may have been as high as 73 % and 76 % in each year respectively as it was not known whether breeding was attempted at three African Hawk Eagle nests which were infrequently observed or were difficult to see onto. Crowned Eagles showed the greatest variation in the number of breeding attempts in each season. Equal numbers of African Hawk Eagles were thought to nest in each of the years, although not all the same pairs bred between the two years. One pair of Black Eagles did not breed in 1995, but bred in 1996, and another pair which bred in the 1995 season did not breed in 1996 (when the male was shot).

Fewer chicks fledged in 1995 than 1996 due to more nesting failures at Crowned, African Hawk, African Fish and Wahlberg's Eagle nests (Table 3). Overall, 72% of breeding attempts in 1995 were successful, and 40% of all the eagle and Gymnogene pairs in the LSA successfully reproduced. In 1995 only 28% of breeding attempts were known to have been successful, and 17% of the resident pairs successfully reproduced. African Fish Eagles had the highest rate of fledgling production in any year, which was due to one pair successfully raising two chicks in one breeding attempt in 1995 (breeding rate = 1.5 young per pair). Of the three main eagle species in the LSA, African Hawk Eagles had the highest rate of successful breeding attempts and the highest production of fledglings per pair (including non-breeding pairs) in each year (0.5 young per pair in 1995 and 0.33 young per pair in 1996). Crowned Eagles had a high breeding success (75% of attempts) and attempt rate (66.7 % of all pairs) in 1994/1995, when 0.5 young per pair were produced. Black Eagles had low breeding success in both years (25% and 33% of attempts respectively; reproductive rate = 0.2 young and 0.25 young per pair per year respectively). So did Crowned Eagles in 1996/1997 (an estimated 0% of breeding attempts succeeded) although the outcomes of the breeding attempts were not definitely known.

### *3.3.4 Approximate densities of small raptors*

Accipitrines made up 94 % of all small diurnal raptor territories counted (Table 4). Little Banded Goshawks were the commonest accipitrines. Ovambo Sparrowhawks were more commonly seen in 1996 than 1995, and overall were about as common as Gabar Goshawks. African Goshawks and Little Sparrowhawks were not commonly seen (Fig. 3d & e). Other small diurnal raptor groups such as falcons/kestrels, kites and harriers did not use the Malilangwe Hills much, and only one Peregrine Falcon, Blackshouldered Kite and Bat Hawk individual or pair held territory or home range over the hills. Other small diurnal raptors occasionally seen in the LSA included Dark Chanting Goshawks and Yellow-billed Kites.

Owl territories were 23% more common than diurnal raptors in the LSA. Barn Owls were the most numerous raptor in the LSA (Fig. 3i; Table 4) but were only slightly more common than Little Banded Goshawks. Many of the Barn Owls counted at roosts may have been non-breeding immatures, whereas all the sightings of Little Banded Goshawks were of adults. Barn Owl roosts which were in current use or had been recently used were actively searched for as part of a concurrent study on their diet, and as a result a higher proportion of their population was probably found than the other owl species, which were sighted by chance. Barred Owl territories were three times more commonly located overall than the ecologically similar (but slightly smaller) Pearlspotted Owl. Both of these species were vocal during the day and usually easily identified en. Pearlspotted Owls were seen as often as they were heard, while Barred Owls were seen often than they were heard. The difference in the sighting rates between the two was ably not influenced by different vocalization patterns. Large owls, *i.e.* Spotted and Giant Owls and Pel's Fishing Owls were not abundant in the LSA, although Spotted Eagle Owls ifficult to locate during the day as they usually roosted on the ground in dense vegetation ky areas. One pair of Giant Eagle Owls nested near the Malilangwe Hills and possibly within the hills. One pair of Pel's Fishing Owls were limited to the Malilangwe Dam (Fig.

With the exception of Ovambo Sparrowhawks, similar numbers of territories of each species were located in both of the study years. However, only 62% of territories were be occupied in both years (Table 4). Most territories were probably maintained between ut I failed to see 38% of the territory-holding birds in each year. The population count l raptors which held territories in the LSA was about 68 in each year, but could have been as 116 over the two years.

## scussion

### *iversity*

A positive relationship is expected between the size of an area and the diversity of a set nisms within the area. In terms of African savanna ecosystem raptor assemblages, between the equator and 36° south, this increase in raptor diversity is described by the relationship;

$$y \quad 0.513x \quad 16.861 \quad (n \quad 53)$$

where $y$ is the raptor diversity of visiting migrants and breeding birds, and $x$ is the logarithm of area (data from authors cited in Macdonald & Gargett 1984). Raptor assemblages between the equator and 12° north and south, 13° and 24° south, and 25° and 36° south, show the following relationships between the logarithm of area and raptor diversity:

(0°-12°N&S) $y \quad 0.110x \quad 39.499 \quad (n \quad 6)$

(13°-24°S) $y \quad 0.664x \quad 15.181 \quad (n \quad 23)$

(25°-36°S) $y \quad 0.528x \quad 15.643 \quad (n \quad 24)$

The data for the equation for raptor diversity/area relationship closest to the equator do not include counts of raptor diversity which omit owls (Macdonald & Gargett 1984). There appears to be little increase in raptor diversity with increase in area from locations near the equator, although the sample was small. The greatest increase in raptor diversity with increased area is between 13° and 24° south of the equator, the latitudinal zone within which the two study areas lie. Macdonald & Gargett (1984) do not discuss the differences in these relationships with latitude.

The overall raptor diversity in the LSA is greater than that which would be expected from a 40 km$^2$ area in the same latitudinal zone, or in any part of sub-Saharan Africa (Fig. 4a). Similarly, the raptor breeding diversity in the LSA, and in the rest of the Lonestar Reserve, is higher than expected for the size and location of the areas (Fig. 4b). The breeding diversity in the LSA is exceeded only by one 40 km$^2$ area in the Matopos Study Area where 22 breeding species were found (Macdonald & Gargett 1984). The overall diversity in the CLSA is equal to what would be expected for an 80 km$^2$ area in the same latitudinal zone (Fig. 4a) but the breeding diversity is higher (Fig. 4b).

The high breeding diversity in the LSA and in sample areas in the Matopo Study Area, an area which is " the most diverse community of raptorial birds that has yet been described from an area of comparable size anywhere in the world " (Macdonald & Gargett 1984, pp 299) strengthens the argument that protected hill habitats support diverse raptor assemblages. This also suggests that complete competitive exclusion does not occur in hills where resources are abundant, and where there is topographical complexity providing an array of habitats and reduced intervisibility between nests. Competition probably does not control community structure and resource use where resources are abundant (Simberloff & Dayan 1991). However, hill habitats are often spatially limited, and raptors which are abundant may limit the distribution of less common raptor species.

It was not in the scope of this study to investigate in detail the raptor assemblages in the riverine habitat and plains savannas surrounding the hill study areas. Nest data were however collected by Kim Wolhuter, and augmented by further incidental observations by staff, visitors and the author in these areas and yielded an estimate of 26 breeding species in ca. 360km$^2$. This diversity is high for an area this size in Africa, which indicates that the hills did not support relatively more breeding raptor species than surrounding plains. The raptor diversity in the plains surrounding the CLSA was not studied in enough detail to present results, but indications were that nesting eagles were not common, although Tawny, Bateleur and Brown Snake Eagles were seen relatively frequently over the plains, and kites and kestrels were commonly seen over cultivated and settled areas. Here hills probably did have more breeding raptor species than the surrounding areas.

The high eagle richness in the CLSA is in contrast to their low breeding densities, low food resource availability (see Chapter 4) and human land-use in the area (see Chapter 5). The reasons for this may be,

1) A decreasing density of eagles, or raptors in general, may reduce interspecific competition thus allowing more species to coexist.

2) Human disruptions causing increases in prey may reduce interspecific competition for food, allowing raptor species to coexist. Also, an increase of one prey group may benefit other raptor prey species which feed on it (*e.g.* snakes and mongooses feeding on rodents). A decrease in abundant prey species may result in other prey species becoming more abundant due to lower competition. There is then a more diverse prey base and a more diverse group of raptors may exist.

3) The habitat mosaic may increase when wood cutting and cultivation alter the vegetation and soils in areas, and more habitat niches become available (Simmons 1994a).

4) A greater degree of habitat alteration and degradation outside of the hill area may force eagles to abandon territories and seek refuge in the hill habitats.

5) Eagles may spill over from the neighbouring Gonarezhou National Park.

6) The eagle diversity may result from some intrinsic quality of the habitat which has not been influenced directly by humans, such as soil fertility or natural vegetation diversity and mosaic (Hustler & Howells 1990).

The raptor assemblages in the LSA and CLSA differed from other areas in southern Africa in that the eagle groups were richer than small diurnal raptors (Table 5). Most areas, including the Matopos Study Area, appear to be more suited to small diurnal raptor species. The LSA and CLSA probably differ significantly from other areas in overall raptor resource availability see Chapter 4). The dominance of Little Banded Goshawks and the relatively low densities of other small diurnal raptors in the LSA and CLSA suggests that the areas were not well suited for most small diurnal species Small raptors, with small territories and needing small amounts of resources, can utilize finer scale differences in resource distributions, whereas eagles with large territory needs can not Small diurnal raptors may be more diverse where there is a patchy mosaic of small habitats The LSA and CLSA had continuous woodland habitat although the topography and tree species distribution varied (Stalmans 1994) In contrast, the Matopos Study Area has about equal proportions of granite outcrops and grasslands which form a mosaic of habitats (Gargett 1990) The Lonestar Reserve outside the hills, and the Sabi-Sands/Timbavati-Klaserie areas have savanna and riverine habitats, and patches of the savanna habitat in both areas have been altered by burning and bush clearing (Simmons 1994a) Also, differences in soils result in a vegetation mosaic in the Lonestar Reserve (Stalmans 1994) These three areas had high breeding diversities of small diurnal raptors, possibly caused by varied micro-habitats and ecotonal areas between habitats where prey resources were diverse (Hustler & Howells 1990; Simmons 1994a)

Owls were fairly diverse in the LSA and CASA, but due to the lack of diversity of habitats, several species which require specific habitats, such as Grass and Marsh Owls, were not present at one or other of the areas As with small diurnal raptors, owls were diverse in areas with diverse habitat, *i.e.* Lonestar Reserve and Sabi-Sands/Timbavati Klaserie The breeding diversity of owls in the Matopos Study Area is probably an underestimate (S & V Tarr pers. comm.) as is the estimate for the Botoko Gorges where few breeding owls were seen (Table 5). I have included small owls seen in the Batoko Gorges by Hartley (1993) as probable territory holders and therefore breeders, as they hold small territories, but large owls (2 species) which may visit the narrow gorges from the plateau were left out.

### *3.4.2 Density, eagles and small raptors*

The density of raptors breeding in an area indicates the availability of resources and suggests the levels of competition. Hill habitats in this study are hypothesised to be rich in nesting and food resources; but limited in space. The relative abundance of habitat resources would be accentuated where surrounding habitat is degraded. Hill raptor communities are expected to be densely populated, with territories being smaller as food and nesting needs are met in smaller areas.

The only comparable hill habitat community study in sub-saharan Africa is that detailed by Macdonald & Gargett (1984) which listed the community components and estimated the breeding densities of raptor species in the $620km^2$ Matopos Study Area in south western Zimbabwe. They did not investigate the resource utilization and availability of the community.

The measured and estimated LSA raptor breeding density was high, while that in the CLSA was about average compared to other areas in Africa (Macdonald & Gargett 1984). High concentrations of raptors often occur in isolated wooded habitats surrounded by open habitat otherwise rich in food (Newton 1979). The LSA did not, however, provide only abundant nesting resources for raptors feeding in the surrounding habitat, but was a closed, complete resource base for many of the raptor species within the area. The density of breeding raptors per unit area in the LSA was higher than any other reported in Africa for a similar sized area (Table 6) which illustrates the influence of certain resources, and provides an opportunity for the study of community processes in an unusually dense and defined raptor community.

The LSA had a substantially larger estimated breeding density than either of the other two hill areas in Table 6, with an almost six fold greater density than the CLSA, and almost seven fold greater than Matopos Study Area (Macdonald & Gargett 1984). Even the greatest breeding estimate in the Matopos, 7.6 pairs per $10km^2$, where breeding estimates in unstudied areas were included (Macdonald & Gargett 1984) is lower than the LSA estimate. Differences in the breeding densities of raptors between the LSA, and the CLSA and the Matopos probably represent real biological differences, despite the greater search effort per unit area in the smaller LSA and CLSA which would reveal a higher proportion of the raptors. This has been recognised by Simmons (1994a) who also indicates that longer study periods generally reveal larger diversities and densities of raptors. Three smaller areas (40km$^2$) in the Matopos gave a higher counted nesting density of between 8.5 and 9.8 raptor pairs per 10km$^2$, nearly twice as high as the count of pairs in the entire Matopos Study Area. The higher estimates in the samples were possibly due to the riverine habitats where two of them were conducted (Simmons 1994a) although another sample area which included other habitat types also had a high counted nesting density of 8.5 pairs per 10km$^2$. The counts from these smaller areas were probably a closer estimate of the raptor density of the entire Matopos area, as river valley habitat is common in the Matopos (pers. obs.).

Simmons (1994a) suggests that only the larger, more visible raptor species should be used in comparisons between areas in order to eliminate biases incurred by incomplete counts of small and nocturnal raptors. However, this assumes that the large raptor component of the community in all areas indicates the relative abundance of all raptors. In this study, small diurnal and owl breeding density estimates were higher than these of eagles in both study areas, and Thiollay (1975) found that small raptors dominated the raptor assemblage in the Lamto Reserve, Côte d'Ivoire. The Matopos, Sabi-Sands and Timbavati-Klaserie studies estimated eagle breeding populations to be larger than the small raptors. Using large raptors as indicative of overall raptor breeding densities would overlook ecological parameters which affect smaller raptors, and therefore the community as a whole. It is also important to compare the relative abundances within areas of all raptor groups, especially when applying the resource utilization based guild concept in describing communities. There is no indication as yet that high large raptor densities correlate positively with high smaller raptor densities within areas. For instance, in the Lonestar savanna area, eagle densities were found to be low, while small diurnal raptors, of the accipiter and falconid groups, were seen more frequently, and owls seen and heard at lower frequencies than in the LSA, where eagles were commoner. A comparison of these two areas using large raptors as indicator species would give estimates of the contribution of small diurnal raptors and owls which were dissimilar to those actually seen.

The finding in this study that small diurnal raptors and owls occur at higher densities than eagles is probably biologically real, as smaller birds require less food and space than eagles, allowing the small raptors to hold more territories within an area. The findings by Macdonald & Gargett (1984) Simmons (1994a) and Tarboton & Allen (1984) as the first two authors point out, probably underestimate the small species. There was probably less error in the LSA where a smaller area was more intensively sampled, although assigning repeated sightings of single individuals to different territories could introduce errors especially as little is known of territory sizes for accipitrines in similar habitats.

In the LSA and the CLSA, African Hawk Eagles territories were the most numerous large raptors, whereas Black Eagles were most numerous in the Matopos Study Area (Macdonald & Gargett 1984). Of the eagles in the LSA and the CLSA, Crowned Eagle territories were the second most numerous, and Black Eagles were third most numerous in the LSA, while in the Matopos, African Hawk Eagles and Wahlberg's Eagles held second and third position respectively. Wahlberg's Eagles were not common in either of the two study areas in this study.

The difference in the relative status of Black Eagles between the Matopos and the LSA (the breeding of a single Black Eagle pair in the CLSA is uncertain) is probably due to the habitat differences between the two areas for the three main resident eagle species. These differences relate to the super-abundant nesting resources in the Matopos Study Area compared to the limited nesting resources for these birds in the LSA, and the abundant nesting resources for the Crowned Eagle in the LSA and CLSA, compared to the dearth of the same in the Matopos (Gargett 1990).

Although Black Eagles are not the most common eagle species in the LSA, the measured density of nesting pairs was 37.7 % higher than that in the Matopos Study Area. This higher density in the LSA is as a result of small territory sizes in the LSA, the large proportion of areas not included in territories in the LSA indicating that this species is not limited by space. This will be discussed in the chapter on resource availability and utilization.

Another indication that there are significant differences between the raptor communities of the LSA and the Matopos Study Area is the higher density of Wahlberg's Eagles in the Matopos Study Area (0.403 territories per 10km$^2$). Only one pair of Wahlberg's Eagles nested on the border of the LSA hill habitat. This may indicate a difference in prey or nesting resources between the two areas, or, if there is interspecific exclusion of Wahlberg's Eagles in the LSA, a biologically effective difference between the eagle assemblages and densities. Wahlberg's and African Hawk Eagles are similar in size and behaviour, and they occurred in similar densities in the Matopos Study Area indicating a possible balance between the two. In the LSA, the higher density of African Hawk Eagles may exclude Wahlberg's Eagles from establishing territories. The favoured nesting habitat of these species is river courses (Steyn 1982). There is one main river course in the LSA, the Nyamasikana River, where a high eagle nesting density may have excluded this small species. *Acacia nigrescens* and *Lonchocarpus capasa*, favoured nest trees for Wahlberg's Eagles in the rest of the Lonestar Reserve, were not common in river courses in the LSA.

Although the CLSA had a lower overall density than the LSA, the densities for all eagles other than Black and Wahlberg's Eagles exceed those measured in the Matopos Study Area.

African Hawk and Black Eagles dominated the CLSA and Matopos Study Areas respectively There is perhaps a greater similarity between the Matopos and the CLSA; than between the LSA and the Matopos, especially as the former comparison is between granite outcrop areas.

Black and Crowned Eagles appear to be restricted to hill habitat (Table 6) with a few pairs of Black Eagles in Hwange National Park being restricted to atypical small cliffs along river courses (Howells & Hustler 1984). African Hawk Eagles occurred in lower densities in savanna habitat the hill areas. The difference between the African Hawk Eagle densities in the Lonestar hill and savanna habitat areas were notably large. The estimate of 0.31 pairs per 40 km$^2$ of this species in the Lonestar savanna area is probably an underestimate as adult African Hawk Eagles were seen in areas where no nests for them were known. Even at double the measured density, the Lonestar savanna African Hawk Eagles would be at almost half the density of those in the LSA. Other than Wahlberg's Eagles in the two South African savanna examples (both were part of the same uninterrupted habitat) which clearly dominated the eagle assemblage in terms of breeding density, there was no clear dominance by density of any other species of eagles. The high density of territories of Wahlberg's Eagles in the Sabi-Sands Study Area was similar to the level of African Hawk Eagle territory density in the LSA. It is probably significant that Wahlberg's Eagles are migratory, thus not using resources of food and space during the dry seasons when food availability decreases (Steyn 1982). African Hawk Eagles however are not migratory, which indicates that their high density in both study areas can be supported through seasonal fluctuations in food, and the density of breeding birds is not set by resource availability during periods of abundance.

Little Banded Goshawks were the commonest small diurnal raptor in all the hill areas compared, while African Goshawks were the commonest nesting accipiter seen in the Sabi Sands study area. Possibly their reliance on small reptiles makes Little Banded Goshawks suited to rock outcrop habitat (Steyn 1982) although in the LSA and CLSA they were more often seen taking birds. Their intermediate size may enable a wide size spectrum of reptile and bird prey to be exploited, while larger accipitrines cannot efficiently meet food needs on small reptiles.

Barn Owls appeared to be the most abundant raptor in the LSA, and in the CLSA along with Little Banded Goshawk. This is not surprising given the capacity of this species to reproduce, with clutches of eleven eggs recorded at two nests in the LSA (Davison 1996; Steyn 1982, P. Mundy - pers. comm.). Davison (1996) found this species had a wide, and seasonally variable diet in the LSA. Rodents were the commonest prey item, and of all the prey recorded in the LSA and CLSA, these show the greatest population fluctuations (pers obs.). Barn Owl clutch size is determined by energy availability, and populations should increase with increased food supply (P. Mundy - pers comm.; Steyn 1982). It is likely that Barn Owl populations are the least stable of the raptors in both of the study areas.

Barred Owls were also common in the LSA and CLSA, more so than the physically and ecologically similar Pearlspotted Owls. The reason for this is not clear, as the Pearlspotted Owl is apparently more common than the Barred Owl in the Matopos Study Area and the owl study area in the Rhodes Matopos National Park (S. & V. Tarr - pers. comm.). As with the Little Banded Goshawk population, larger size may allow a wider spectrum of prey sizes to be taken. Food and predation considerations for the Barred Owl will be discussed in Chapter 4.

### *3.4.3 Breeding and territories of eagles in LSA*

The number of pairs of raptors breeding usually does not equal the number of territory holders in any one season. The proportion of a population breeding, and the rate of young fledging should largely be an effect of resource availability (Gargett 1990; Gargett & Gargett 1993a; b; c). In this study, where food and nest resources were abundant, the high raptor density in the area may limit breeding, and the maximum carrying capacity of raptors may not equal the breeding capacity of the population.

A greater proportion of the Black Eagle population bred than any other eagle species in the LSA. Prey availability is the most important factor affecting breeding, which indicates that hyrax were readily available during the 1995 breeding season, despite high rainfall which increases vegetation cover and reduces visibility to the eagles and foraging distances of hyrax, and thus their susceptibility to predation (Gargett 1990). Black Eagles in the Matopos had a high rate of breeding attempts in seasons of below average rainfall, except when droughts reduced hyrax numbers (Gargett 1990). Breeding failure in one season increases the probability that a pair will attempt breeding in the next season, and low productivity in 1994 may have encouraged breeding attempts, although no breeding records were kept that year. Breeding attempts were reduced in 1996 after a 200mm greater than average rainfall period. Low productivity and high rainfall are factors which should affect reproductive efforts in opposite manners. The proximity of nest sites, territory boundary changes and new territories have negative effects on breeding attempts, although no nests were inter-visible, and areas of habitat not used in territories indicated that the Black Eagles were not crowded despite small territories (Gargett 1990). Neighbour effects and density are not thought to affect breeding attempts, as the nearest neighbour of a new pair bred in the year that a new territory was formed.

A lower proportion of African Hawk Eagles attempted breeding than Black Eagles in the LSA. Breeding attempts were made in 60% and 71% of the pairs in 1980 and 1981 in the Matopo study area, and 58% and 70% of the nesting attempts fledged chicks respectively in the two years (Archer 1981). The ten year average of fledging in Hwange National Park, between 1973 and 1984, 1977 and 1978 not included, was 59% (Hustler & Howells 1988). Data from Howells & Hustler (1984) suggests that 501 breeding attempts were recorded in 1250 pair years, or 40% in Hwange National Park between 1971 and 1982, [calculations assume that no data were collected in 1977 and 1978 (Hustler & Howells 1988)]. The proportion of the pairs attempting nesting in the LSA was comparatively low, although in 1995 almost all the nests reared chicks. This may indicate that the high nesting density of this species in the LSA may reduce nesting attempts, but high food availability increases the chances of fledging chicks. Most nesting failures in this, and all the eagle species in the LSA, were probably due to predation largely by other raptors, and this should increase with increased raptor density and diversity.

Crowned Eagles showed the lowest proportion of the population breeding in either season as some pairs had a biennial breeding cycle in the LSA while others bred in two consecutive years between 1994 and 1996. In 1996, two pairs nested simultaneously less than 1.5km apart, although it is not thought that either pair successfully fledged chicks. Density in this species is not thought to affect breeding attempts, and no instances of intraspecific aggression were seen.

# Chapter Four: Resource Utilization and Availability

## 4.1 Introduction

In providing a description of raptor assemblages at the habitat level which is ecologically meaningful, the components of the assemblages should be treated as functional units which interact with each other and with other components of the ecosystem. Resource utilization, and factors affecting it, are the functional processes of an ecological community. In raptor assemblages, space, food and nesting resources are often shared. Root (1967) defines guilds, which are treated as functional units of communities in this study, as sets of organisms which have large overlap in resource utilization and utilize resources in similar ways. These organisms often do not belong to one taxonomic class. Much debate has arisen as to how to define how much overlap of resource utilization should be used to categorise guilds, and what constitutes a "similar way", although food is commonly recognised as the main limiting factor in most communities (*e.g.* Adams 1985; Hawkins & MacMahon 1989; Jaksić 1981; Simberloff & Dayan 1991).

This chapter details resource utilization, overlap and partitioning, and interactions resulting from these in the raptor component of the vertebrate predator community in the two study areas. Feeding guilds are used to describe the functional role of raptors in the community mosaic. It was not within the scope of the study to investigate resource utilization amongst other vertebrate predators which probably shared feeding guilds with raptors in the study areas, but a description of their possible effects on raptors is given.

## 4.2 Materials and Methods

### *4.2.1 Nesting resources*

Nests were found during systematic ground searches. K. Wolhuter conducted a search for eagle nests in the whole of the Lonestar Reserve in November and December 1994. Thirteen nests which had not been found by Wolhuter were found in the LSA during my study.

Descriptions of habitat around each nest, the tree species for tree nest sites, and inter-visibility of other nests were made at each nest site. Slope of the ground at nest sites was estimated by measuring the interval between contour lines on 1:50 000 topographical maps, and dividing this by the height change.

The height of the nests above the ground was measured by one of two methods. A line was dropped from the nest to the ground and the distance measured. Nests in trees and on cliffs were reached using standard rock climbing equipment and fixed-aid techniques. The second method involved the principles of trigonometry and isometric triangles. A stick, measuring the exact height of the observers eye from his feet when standing, was used. The observer lay on his back with his feet flat against the stick and sighted the top of the stick on the nest so a straight line was described between his eye, the top of the stick and the nest. The ground distance between the position of the observers' eye and a point directly under the nest was measured and closely approximated the height of the nest above the ground. The principles of this method, and the mathematical derivation of nest height from the ground distance are given in Figure 5.

Error is incurred in this method when the ground around the nest trees is not flat, so the ground distance was always taken on the flattest ground and distances were measured to the nearest metre to allow for slight error.

### *4.2.2 Food resources*

#### *4.2.2i Predation*

Prey remains were identified using osteological and skin collections housed in the Mammals, Ornithology and Herpetology departments of the Bulawayo Natural History Museum, Zimbabwe. Prey remains were collected from nests after nesting periods, and from beneath nests when old prey remains fell out. This method is not an entirely accurate measure of predation as some eagles, *e.g.* Crowned Eagles, ingest bones, and more durable bones last longer at nests. When prey remains are collected frequently, these problems are minimised (Jarvis 1978). Prey were categorized into the number of individuals identifiable in each taxon from bones. The composition of prey remains from each eagle species was expressed as the percentage proportion of number of prey individuals per taxon to the total number of prey individuals collected.

The masses of prey individuals were estimated from mean or median adult masses reported in literature, except for hyrax. The masses of hyrax prey individuals were estimated from skull lengths using linear equations for *H. brucei* and *P. capensis* worked out for hyrax in the Matobo Hills by Barry & Barry (1996). More hyrax prey individuals were identified from various bones from each of the hyrax eating eagle species than the number of skulls collected. The average calculated mass of hyrax for each eagle species was multiplied by the number of hyrax counted in addition to the number of skulls collected to arrive at a estimate of total mass of hyrax prey collected. The composition of prey by mass for each eagle species was expressed as the percentage proportion of total estimated mass of individuals of each prey taxon to total estimated mass of prey individuals collected.

Fresh prey remains were also identified at eagle nests in the LSA observed during breeding periods. Skull length and femur length of fresh prey remains of hyrax, and tibia-tarsal lengths of francolin as well as spur lengths of male francolin, and masses of fresh, mostly unconsumed hyrax and francolin prey remains were measured. The same measurements were taken from freshly shot hyrax and Natal Francolin sampled from the LSA, (Natal Francolin used in the measurements were also shot near Bulawayo). The regression relationship between morphometric parameters allowed an extrapolation of the masses of the prey at the nests from bone remains.

Predation attempts were witnessed occasionally, and the behaviours of the raptors and the prey types were noted.

The feeding behaviour of Barn Owls in the LSA was the focus of another concurrent study, the results of which are quoted here (Davison 1996). This involved the monthly collection of regurgitated prey remains from seven Barn Owl roosts from April 1995 to October 1996. Methods of the study are presented in Davison (1996). A similar survey with the same methods of analysis was carried out in the CLSA. Prey species of rodents were compared to type specimens collected by A. Davison.

Prey remains were seldom collected from other small raptor nests, few of which were found. Hunting events seen augmented the prey spectrum quoted in literature.

### *4.2.2ii Prey distribution and availability.*

In the LSA, two transects of 7 and 4.6 km were walked between 06h00 and 08h00 and potential prey species of large raptors were enumerated. The transects were straight lines, although one followed an old fence line which changed direction once, less than 45°. Both transects ensured independent sampling as they had been laid along fence lines, placed along straight lines and not affected by habitat, or compass bearings. The transects were divided into quadrats each 200m long. The quadrats were measured either using 200m lengths of line, or a range-finder, calibrated each day before the measurements were taken.

The number of potential prey items on roughly 25m of either side of the transect line was counted. Notes were made of the sex and broad age category (adult, subadult or juvenile) of the prey individuals, the number of hyrax colonies as indicated by hyrax groups and latrines, and the relative size of these colonies. The average number of hyrax counted per quadrat per habitat over five repeated samples indicated habitat differences in hyrax densities.

The habitat types in the transects were subjectively differentiated by dominant vegetation type and proportion of cover, substrate type and slope.

The first two measures of transect one were conducted in the later part of 1995, and in the second quarter of 1996 (Table 7) The rest of the measures in both transects were conducted in October and November 1996 Although the sampling period was a short part of the study period, the aim of the transects was to obtain the distribution and relative densities of prey in different habitats, and the method was not capable of monitoring temporal changes in densities without many more repeats which would have been time consuming (each repeat took more than a day to complete) The repeats were usually conducted at least five months after hyrax parturition and Natal francolin hatching, and density figures obtained give an estimate of post winter survival

Five 1km x 1km areas which coincided with the $1km^2$ grids on the 1:50 000 topographical map of the LSA were chosen in four broadly different habitat areas in the LSA, and all the hyrax colonies were mapped The habitat differentiation of the quadrats was as follows;

1) Flat, sandy with low grass cover over large areas, uniform height *Brachystegia glaucescens*, rock outcrops scattered and low.

2) Sloping ground, rocky ribs, *B. glaucescens*, springs and dry water courses.

3) Incised rocky river courses, cliffs and steep slopes 10-15m high, Dense mature *Androstachys johnsonii*, tall rock outcrops 25-30m.

4) Flat open grassland, *Terminalia sericea*, isolated rock outcrops, 20m high, rock ridges of outcrop 50m high.

The number of hyrax visible in each of three colonies was counted on several occasions, once a day between 06h00 and 08h00 when the animals were mostly sunbathing, in September and November 1996 Hyrax were counted during one count each at 30 colonies during the same period up until 11h00

### *4.2.3 Space resources*

#### *4.2.3i Territories*

The areas used by pairs of raptors in the LSA were assumed to be defended territories, and no difference between territory and home range was assumed. Territory boundaries for pairs of Gymnogenes, Black, African Hawk, African Fish, and Crowned Eagles were ascertained by plotting flight paths on a 1:50 000 topographical map, and the farthest points where the birds were seen in flight joined on the map. Behaviours such as pendulum displays (described in Gargett 1990 and Steyn 1982), vocalising in flight, and chasing intruders gave good indications of where territory boundaries were. This method was suitable for Black and African Hawk Eagles which were often in flight and were strongly territorial, but was not as easy to apply for the other species which perched more; only one Crowned Eagle territory was delimited accurately. The mapped territories were overlaid on a grid on which the area represented by each square was known, and the number of squares covered by the mapped territory counted and converted to km$^2$.

Aggressive interactions were assumed to be related to defending breeding and food resources in space. All aggressive interactions, such as vocalization, tandem flight between non-paired raptors, attacks and chasing amongst all raptors in both study areas were noted.

#### *4.2.3ii Nest spacing*

The square of coefficient of variation of squared smallest between-nest-distances (S) and the ratio of the geometric mean to the arithmetic mean of squared nearest nest distances (G) were employed in order to tests statistically for regularity and randomness of large raptor nests in the LSA and the CLSA.

The formulae for these are:

$$S = \frac{\sum_{i=1}^{n} d_i^4 - \left(\sum_{i=1}^{n} d_i^2\right)^2 / n}{(n-1)\left(\frac{\sum_{i=1}^{n} d_i^2}{n}\right)^2}$$

$$G = \frac{\prod_{i=1}^{n} d_i^2 \,{}^{1/n}}{\left(\frac{\sum_{i=1}^{n} d_i^2}{n}\right)}$$

where the distance to the nearest nest from the $i$th nest in the sample of $n$ nests is $d_i$. These tests are described by Brown (1975) and Brown & Rothery (1978). These statistics have the advantage of identifying regular spacing even when points are clumped, which other tests are not capable of doing as they include the area and density of the points (Brown & Rothery 1978; Clark & Evans 1954). The nearest nest distances were measured to the nearest millimetre on 1:50 000 topographical maps. These tests were used to describe the degree of regularity in all large raptor nest sites, all nest sites in use during the study period, all nest sites of Black, Crowned and African Hawk Eagles, and all nest sites of these species in use during the study period.

### *4.2.4 Time*

#### *4.2.4i Daily time budget*

The times at which any raptors were seen in flight in the two study areas and a description of the flight behaviour were noted during excursions at frequent random intervals, usually between 07h00 and 17h00, during the study period. Gargett (1990) argues that the purposes of flights in Black Eagles were difficult to determine as predation occurred during different flight patterns in the Matopos study area. Davies (1994) and Brown (1988) describe flight behaviours in Black Eagles in other areas which usually resulted in attempted predation. In this study all flight behaviours of raptors, other than those directly involved in courtship, aggression, or territory defence and maintenance were assumed to be associated with prey capture.

The total numbers of large raptors in each species which were counted in each hourly period from 06h00 to 18h00 were compared. Repeated measures ANOVAs were used to test for significant differences and effects amongst the proportions, after arc-sine transformation, of species seen in flight in each time period. Paired t-tests were used to test whether there was any significant link in activity patterns between species.

#### *4.2.4ii Seasonal time budget - flight*

The sightings of large raptors, per species, seen in flight per day per month were calculated from the recorded daily flight sightings. The CLSA was not sampled every month and monthly sighting rates are thus not presented.

The rates of sightings were compared between the same months in 1995 and 1996 using paired t-tests. The pattern of sighting rates for each of the main eagle species in the LSA in 1995 and 1996 was compared using Multinomial tests. The monthly sighting rates in 1995 were converted to proportions of the sum of 1995 sighting rates and compared against monthly sighting rates for each main eagle species in 1996. Data from December 1995 and January 1996 were not comparable with any other months' data and were not used in any tests.

#### *4.2.4iii Seasonal time of breeding*

The approximate periods of the various breeding stages of Gymnogenes, Black, African Hawk, Crowned, African Fish, and Brown Snake Eagles in the LSA in 1995 and 1996 were estimated by aging chicks, and deducting the expected period since the start of incubation to estimate laying dates, or from the dates of hatching at monitored nests. Chick ages were estimated from the literature. In a few easily-observed Black Eagle nests the laying date was recorded to within a few days, although nests were usually not approached during expected early incubation to avoid disrupting breeding. Few breeding records were obtained in the CLSA. ANOVAs were used to test for significant differences between the dates of these events between species and between years within species.

## 4.3 Results

### ***4.3.1 Nesting resources***

#### *4.3.1i Nest sites*

Crowned Eagles were the most specific in choice of nest sites in both areas, using only baobabs, while African Hawk Eagles in the LSA were the most generalist in their choice of nest sites. All African Hawk Eagle nests in the CLSA were in baobabs which were the favoured nest trees in the LSA as well. Black Eagles rarely nest in trees, but one nest in a baobab in the LSA was used in both years; otherwise this raptor is one of the most specific nest site users in Africa

(Gargett 1990, Smith 1996).

Large raptors which nested well within the hill habitat use baobab nest sites (with the exception of Black Eagles) while those closer to the margin and in flat sandy valleys used other nest sites, as baobabs were not common in these areas. This was noticeable especially in African Hawk Eagles, which favoured *Termnalia sericea* when nesting in sandy or marshy valleys, and acacias when nesting on the margin of the hills and plains. Baobabs were the tallest indigenous tree species in the LSA and CLSA, and were common on sloping ground and rocky kopjes (Table 8). Several species nested in numbers too low for adequate discussion of their nest site choices.

Small diurnal raptors chose medium sized nest trees all of which had medium to dense foliage when the birds were nesting, and/or were protected by thorns. Only one Pearlspotted Owl nest was found in the CLSA, in a *Brachystegia glaucescens*.

Ten types of nest sites occurred in the LSA and three in the CLSA. Baobabs were at least three times more common than any other nest site type in the LSA, and 2.5 times as common as *Acacia nigrescens* nest sites in the CLSA. Cliffs, *Terminalia sericea*, *Acacia nigrescens* and *Brachystegia glaucescens* were used commonly in the LSA, in fairly equal proportions, although cliffs were used only by Black Eagles and *Brachystegia glaucescens* mainly by accipiters (Table 9). Other trees were infrequently used, and most of these were more typical of plains habitat and plains nesting raptors.

### *4.3.1n Ground aspect at nests nest trees*

The aspect angles of the slope at Black, Crowned and African Hawk and African Fish Eagle nest trees or nests (Black Eagles) in the LSA did not differ from equal distributions among the eight main compass directions (Multinomial test; Chi$^2$, $p>0.05$). Small samples of Black and Crowned Eagle nests meant that apparent patterns of aspect directions did not alter the test outcomes. Fifty percent of the Black Eagle nest sites were west facing (Fig. 6a). The slope aspects at LSA Crowned Eagle nest trees had a narrower range of directions (between west and north east) than at Black or African Hawk Eagle nest sites or nest trees. Many (nearly 40 %) of African Hawk Eagle nest trees were on flat ground which did not face in any particular direction, whereas all Crowned and Black Eagle nest trees or nests were on slopes. More nests or nest trees overall (40 %) were on west facing ground than on any other aspect (Fig. 6). There were too few nests of other eagle species in the LSA to include in the analyses.

There were too few nest sites per eagle species in the CLSA to compare slope aspects at nest trees within or between species. The aspect angles of the ground slope at all eagle and gymnogene nest trees in the CLSA did not differ from equal distributions amongst the eight main compass directions (Multinomial test; $\text{Chi}^2=8.64$, $P > 0.05$).

### *4.3.1iii Slope at nest trees sites*

Most nest trees/sites were on gentle slopes below 0.12:1 (figures are the change in vertical distance:horizontal distance). Six nest trees/sites were on flat ground (0:1) and eight (Black Eagle) nests were on vertical rock faces (1: about 0). African Hawk Eagles, Wahlbergs', Martial, Tawny, Gymnogenes, and Crowned Eagles nest trees were typically on gentle slopes or relatively flat ground. There are fewer nest trees on slopes between 0.2:1 and 0.8:1, with five nest sites of Crowned, African Hawk, and Black Eagles, occurring on 0.2:1 and 0.4:1 slopes each. The steepest nest site slope, of 0.8:1 was at an African Fish Eagle nest site (Fig. 7).

### *4.3.1iv Nest heights*

There were no significant differences in nest heights between raptor species and between nest tree species (ANOVA; F values $<0.6$, $P$ values $>0.1$) nor between raptor species in different nest trees (Two-way ANOVA, F=0.03, $P$=1). However, half of the African Hawk Eagle nests were between 20 and 22m high whereas nearly 80 % of Crowned Eagle nests were less than 20m high. More than half of the Black Eagle nests (about 60 %) were higher than 20 m - this species having the highest nest sites. The majority of all nests were between 14 and 22 metres high (Figs 8a-b).

*4.3.1v Nest spacing and distribution*

$S$-values of 0 indicate absolute regularity and higher values - increasing randomness of nest patterns, while $G$-values from 0 to 0.65 indicate randomness and above this to 1 - increasing regularity (Brown 1975, Brown & Rothery 1978; Nilsson *et al.* 1982). $S$ is sensitive to outliers especially when small samples are used, which explains the discrepancy between $S$ and $G$-values for Crowned Eagles in the LSA (Table 10). In these cases $G$ is the more robust statistic (Watson & Rothery 1986).

Regular nest patterns indicate a tendency towards maximum spacing between nests (Nilsson *et al.* 1982). In each of the study years and in both years combined, the pattern of all occupied large raptor nests was random, but for each of the three main species it was regular (Table 10). This indicates that the three eagles tended to maximise internest distances intraspecifically, but not interspecifically; the differences are statistically significant (Table 11).

Although African Hawk Eagle pairs nested relatively close to one another, they nested further from other raptors on average than the other main eagle species and all large raptors combined did (Table 11). Sixty percent of African Hawk Eagle pairs nested in outlying hills, broad valleys and the hill/savanna ecotone where few other raptors nested. Black Eagle nests were spread out, but were usually in areas where other species also commonly nested. Most (80%) of the Crowned Eagle pairs nested in the Nyamasikana River valley and its tributaries where an accumulation of other raptors nested, resulting in low inter- and intraspecific nearest-nest distances for this species (Table 11).

There were significant differences in the intraspecific nearest-nest distances between 1995 and 1996 for African Hawk Eagles (One-way ANOVA; $F=6.12$, $0.25<P<0.05$) and all large raptors (Kruskal-Wallis test; $t=6.06$, $0.01<P<0.02$) but not for Black Eagles (Kruskal-Wallis test; $t=2.94$, $P>0.05$). Interspecific nearest nest-distances did not differ significantly between 1995 and 1996 for any species or all large raptors (One-way ANOVAs and Kruskal-Wallis tests; $P>0.1$). Overall intra- and interspecific nearest nest-distances did not differ significantly amongst the three main species and all large raptors (intraspecific: Kruskal-Wallis test; $t=4.72$, $P>0.1$; interspecific: One-way ANOVA, $F=2.72$, $0.1>P>0.05$).

Breeding at nests <1km from other nest sites in use was typically successful, but most nests spaced farther apart had breeding failures (Table 12).

### *4.3.2 Prey resources*

#### *4.3.2i Predation*

African Hawk and Crowned Eagles had similar diversity of prey remains at nests, which was approximately double that found at Black Eagle nests (Fig. 9a). Despite this, the diets of all three species were dominated by one (Black Eagle) or two prey groups. Insufficient prey remains were collected from CLSA nests, where few breeding attempts were seen during the study period. Most CLSA eagle prey remains collected were hyrax, while a few giant plated lizard remains were found.

African Hawk and Crowned Eagles in the LSA had two main prey groups each, while Black Eagles preyed almost exclusively on hyrax, most commonly *H. brucei*. Hyrax made up 94

% of Black Eagle and 78.1 % of Crowned Eagle prey individuals collected in the LSA, but only 29 % of prey individuals collected at African Hawk Eagle nests. Natal Francolin were the commonest prey remains at African Hawk Eagle nests (48 % of prey individuals). Antelope, probably bushbuck *Tragelaphus scriptus*, were the other common prey group for Crowned Eagles. There were significant differences in the composition of prey by proportion of numbers, and by mass, amongst the three eagle species (Wilcoxon Matched Pairs tests; P>0.1).

Several differences in prey composition by numbers and mass occurred amongst the three eagle species (Fig. 9a & b). Antelope (probably bushbuck) formed a higher proportion of estimated prey mass (43 %) than prey numbers (17.4 %) at Crowned Eagle nests. An estimated average juvenile bushbuck weighing 10kg [birth mass = 3.5 to 4.5kg, and mature mass of approximately 40kg after 12 to 14 months (Skinner & Smithers 1990)] is four times heavier than adult *H. brucei*. The estimated mass proportions of antelope and hyrax prey were similar (hyrax = 54 % of total prey mass) despite differences in the numbers of prey individuals collected. The estimated proportional mass of hyrax (51.3 %) in African Hawk Eagle diets was greater than that of Natal Francolin (32.8 %), although the latter were the most numerous prey in any taxa (48 % of total prey individuals).

Most hyrax skull remains from LSA Black and Crowned Eagle nests were from individuals heavier than 2 kg. African Hawk Eagles appeared to prey proportionally more on *H. brucei* up to 2 kg and not on individuals heavier than 3 kg (Fig. 9c). However, the sample of *H. brucei* skull remains from African Hawk Eagle nests was small and comparisons should be made with caution. Too few intact *P. capensis* skulls (3) were collected from African Hawk Eagle nests for analysis and comparison. Hyrax prey masses were not evenly distributed for any eagle species (Multinomial tests; *P*=0) indicating that selection of certain prey sizes occurred.

Prey remains at African Fish Eagle nests in the LSA were mostly barbel *Clarias* sp. and Largemouth Bass *Micropterus salmoides* was the only other identified fish species. Hyrax remains were found in low numbers, but were frequent at a nest which was shared with Crowned Eagles.

Prey from a Little Banded Goshawk nest in the LSA included a head of a striped skink, and a few unidentified small passerine feathers. Unidentified passerine feathers were also collected from a Little Sparrowhawk nest in the LSA. Another Little Banded Goshawk nest had no prey remains in the nest despite having three chicks, indicating small prey which was eaten whole.

Barn Owls in the LSA had the most diverse prey of any raptor sampled in the LSA in terms of species (24) and taxa (7 orders, Fig. 10a-b). There was no significant randomness in the occurrence of prey species between prey collection sites (Wald-Wolfowitz runs test; Z=-2.514, P 0.05). The commonest prey by number were *Mastomys natalensis* (35% of total) while *Crocidura* spp., *Tatera leucogaster* and Solifugidae each made up more than 10% of prey individuals, and Orthoptera, *Steatomys pratensis* and *Quelea quelea* were each more than 4% of prey individuals (Table 13).

There were significant differences in the proportions of different Barn Owl prey species collected (ANOVA, F=61.4, P=0) but these differences were not significantly consistent between months (Two-way ANOVA, F=4.57, P=0). This was due in part to increases of Solifugae prey between November 1995 and January 1996 (wet months) to between 58.2 % (SD±26.3%) and 65.5% (SD±39 %) of prey individuals, and Orthoptera to 23.3% (SD±40.3%) of prey numbers in February 1996 and 12.2% (SD±24.4%) in April 1996. In the dry winter months between June and October 1996 these groups made up less than 1.5 % (SD±0 to 4.2%) of prey individuals. Concurrent to these decreases was an increase in the proportion by numbers and mass of *Mastomys natalensis* prey individuals which comprised between 37.1% and 81.1% (SD±14.4 -

34.6%) by numbers and between 51.8% and 90.9% (SD±8.2 - 35.7%) of mammal prey mass per month. Between September/October 1995 and January 1996 (end of dry to middle of wet season) this species comprised only between 10.3 % and 30.7 % (SD±14.4 - 22 %) of the prey individuals, but between 26.7 and 58.4 % (SD±18.1 - 31.2 %) of monthly mammal prey mass (Figs 11a-b).

Of the prey mammals, *M. natalensis* provided the greatest estimated prey mass in all collection months (between 26.7 and 90.9 % of total monthly mass) except in November 1995 when *T. leucogaster* made up a greater proportion of the prey mass. Musk shrews (*Crocidura* spp. were a relatively large part of Barn Owl diet mass between September/October 1995 and June 1996 between 4.6 and 22.3 % (SD±4.1 - 16.8%) but were less common after this (Fig. 11a-b). The contribution of each mammal species to monthly mammal prey mass did not significantly differ from their contributions to monthly prey numbers except for *M. natalensis* (Paired t-test; t=5.45; $P<0.001$) and *T. leucogaster* (Paired t-test; t=2.43, $P<0.05$) both of which contributed more to mammal prey mass than prey numbers in each month. No average prey masses were availible for other prey species (Davison 1996) although arthropod prey had lower masses than most mammal prey and were less important in the diet than indicated by their numbers.

Davison (1996) live trapped rodents for 293 trap nights between March and June 1996. The commonest rodents caught were *Aethomys* spp. and *Acomys spinosissimus* (8 and 5 of 19 individuals caught). Neither of these were prevalent in the diet of Barn Owls.

### *4.3.2ii Prey availability*

### *(Hyrax density per habitat - LSA)*

Thirteen and nine different habitat types were identified in transects 1 and 2 respectively (Table 14). Transect 1 passed mostly over relatively high hills with steep slopes and cliffs, and through large as well as incised valleys. Transect 2 ran near the southwest margin of the hills and the habitat was typically low rock outcrops giving way to small sandy drainage areas or vleis in places.

Only hyrax which were out of their crevice refuges could be counted in the transects. Most hyrax were probably outside crevices in the early mornings when they sunbathed, and when they were undisturbed. The highest of five counts of hyrax per quadrat was considered to be nearest to the actual number of hyrax per quadrat. This yielded an estimate of about 14800 hyrax in the LSA, a density of 3.7 hyrax per ha. (Table 15). To test the variability in the numbers of hyrax counted in relatively undisturbed colonies, hyrax in two colonies outside the transects were counted on at least five occasions when the hyrax showed little sign of disturbance. The same maximum numbers of hyrax (32 and 9 hyrax) were counted at least twice in both colonies indicating that all, or nearly all, individuals had been counted. The lowest counts were between 78 and 84 % of the maximum counts, indicating that at least 75 % of hyrax in quadrats were counted. The 25 % error in uncounted hyrax is lower than the estimated 38% change in the Matobos National Park hyrax population before and after peak parturition (Barry 1993) therefore any error in estimating the LSA hyrax population would probably be less than the temporal variation in the population.

The average maximum numbers of hyrax per quadrat differed significantly between habitats only at the 10 % level (Kruskal-Wallis test; t=24.2, $0.1>P>0.05$) although differences in hyrax densities between habitats were apparent (Table 15). Habitats with sandstone outcrops (*e.g.* habitats 2, 4, 5, 6, 8, 11, 14 and 17) were typically dense with hyrax, while habitats associated with drainage areas (habitats 9, 12, 13, 15) had few or no hyrax. The highest densities of hyrax were counted on top of cliffs (habitat 8) and on a sandstone ridge with *Androstachys johnsonii* coppices (habitat 17). Habitat 8 was typical along the escarpments of the Nyamasikana

River valley and its tributaries where African Hawk, Black and Crowned Eagles nested in relatively high numbers. Habitat 17 was less common and mostly limited to the south-west portion of the LSA. Habitats with high hyrax densities occurred in about 56 % of the quadrats and were assumed to make up the same proportion of the LSA area. These contained an estimated 81.2 % of hyrax in the LSA (extrapolated from hyrax densities in the transects) or about 12000 individuals in about 22 $km^2$ of "prime" habitat (or about 5.5 hyrax per ha.) and about 2800 in the remaining 18 $km^2$ (about 1.6 hyrax per ha.).

Only hyrax outside refuges are available as prey for raptors. The average number of hyrax seen per quadrat per sample gives an estimate of the density of predator-prone hyrax between 06h00 and 08h00, which was about 1.4 hyrax per ha. or about 5500 hyrax in the LSA (about 37% of the total estimated hyrax population).

*(Hyrax colony density - LSA and CLSA)*

Hyrax from an estimated 26 colonies were counted in the transects, but only 16 colonies were thought to be centred within the transect area (an extrapolated estimate of 27.6 colonies per $km^2$). The average number of colonies counted in three randomly chosen 1 $km^2$ area was 26.3 (SD±8.4) but only 8 colonies were counted in another 1 $km^2$ area which did not have typical LSA habitat. The average maximum number of hyrax counted at colonies (n=16 in transects + 5 randomly chosen) was 10.4 (SD±6.2, counts of <5 hyrax not included). The colonies had too few individuals to estimate colony sizes using the Robson - Whitlock technique (Fairall & Crawford 1983). The counts may have underestimated colony sizes (by 25 %) although Skinner & Smithers (1990) give *P. capensis* family group sizes as 4 - 6 on small isolated outcrops and maintain that *H. brucei* have similar habits. Both species occur together in colonies in the LSA, thus colony sizes may be between 8 and 12 according to the authors. Hyrax densities may therefore be between 2.7 (SD±1.6, estimated from colonies in 1 $km^2$ areas) and 2.9 (SD±1.7, estimated from colonies in transects) hyrax per ha., or between about 10900 (SD± about 6500) and 11500 (SD± about 6800) hyrax respectively in the LSA. The estimate gained from hyrax densities in the quadrats is higher than these, but within the upper limits of their error. It is probably more accurate as it is based on actual counts of hyrax densities and not estimates.

In the CLSA only 28 colonies were counted. Hyrax in the CLSA were easily disturbed and accurate counts of colony sizes were not made. If colonies were the same size on average as LSA colonies, there were only about 300 hyrax in the CLSA (0.04 hyrax per ha.). Colonies in the CLSA were probably larger as they occurred on larger rock outcrops, but at even three times the population estimate, the hyrax density in the CLSA probably did not exceed 10 % of that in the LSA.

(*Natal Francolin density per habitat - LSA*)

Natal Francolin had home-ranges which often extended over more than one transect quadrat. The same individuals were probably sometimes counted in different quadrats during repeated samples. Data from each quadrat could not be compared to data from other quadrats from other repeated samples without the risk of the same individuals being counted in both. During each sample individuals which moved from one quadrat to another after being counted were not recounted. Data from each quadrat were only independent when compared to other quadrats in the same repeated sample. The highest numbers of individuals counted per quadrat were not accurate estimates of densities because data from different samples were compared. The average numbers of individuals per quadrats were more accurate indicators of densities because all data, which were independent, were used in the calculations.

Natal Francolin were most commonly encountered in sandstone outcrop areas and on hill slopes, often where there were dense stands of shrubs or small trees (*e.g.* habitats 2, 7, 8, 11, 16, 17) and also in dense riverine vegetation (habitat 12, Table 15). About 3000 Natal Francolin were estimated to occupy the LSA (0.75 birds per ha.). On average 45 % of Natal Francolin in the transects were counted in these habitats which comprised about 31 % of the transect area. This extrapolates to about 1350 birds in about 12 km$^2$ of "prime" habitat (about 1.1 birds per ha.) in the LSA and about 1650 in the rest of the area (about 0.6 birds per ha.). As with hyrax, areas near cliffs (habitat 8) had the highest density of Natal Francolin which were usually found in the thick shrubs at the base of cliffs or in the *Androstachys johnsonii* stands above cliffs.

### *4.3.3 Space utilization*

#### *4.3.3i Territories*

Although African Hawk Eagles were the most numerous nesting eagles in the LSA, they had the largest territories on average (Table 16). This was because their territories often extended beyond the LSA whereas Black and Crowned Eagle territories usually did not (Fig 12a-c) and because territories 7 and 9 were atypically large (16.8 and 15.6 km$^2$ respectively, Fig 12). These two territories covered largely mopane (*Colophospermum mopane* and dense miombo woodland with scattered rock outcrops or savanna plains which appeared to have relatively low densities of francolin. The other territories which were measured were in more hyrax- and Natal Francolin-rich habitat along the Nyamasikana River valley and tributaries and in the southern portion of the hills, and averaged 8.4 km$^2$ which was slightly larger than the average Black and Crowned Eagles territories. There was no significant difference in territory sizes amongst these three species in the LSA (One-way ANOVA; F=0.69, $P>0.05$). Only one African Hawk Eagle territory was measured in the CLSA, but it is likely that all CLSA African Hawk Eagle territories were larger than those in the LSA as nests were farther apart in the CLSA

Black Eagle territories in the LSA had more space between them than Crowned and African Hawk Eagle territories (which appeared to be compressed) in the LSA (Fig. 12a-c). Although fewer Black Eagles nested in the LSA than the other two species, average territory sizes were similar for all three (if African Hawk Eagle territories 7 and 9 are considered atypical and ignored). Black and Crowned Eagles were seldom seen outside of habitats with rocky outcrops (and hyrax) in both study areas. They also had a large degree of territory overlap in the LSA while African Hawk Eagles usually had larger parts of their territories (usually those outside the hill areas) which did not overlap with either of these two species.

African Fish Eagles in the LSA spent most of their time near the Malilangwe and Ntabazinduna Dams but occasionally they were seen away from these areas, often flying above about 200 m and vocalising. Areas near the dams were defended by the adult birds, but it is not known whether the larger areas covered by the birds were defended territories or undefended home-ranges.

Territories of Wahlberg's and Tawny Eagles which nested near the margin of the LSA were not mapped, but apparently covered relatively small parts of the LSA and thus had little overlap with the three main eagle species. Only a Martial Eagle and a Tawny Eagle pair were seen frequently over the central part of the LSA and were often engaged in aggressive interactions with one of the three main LSA eagle species and also with African Fish Eagles. A Gymnogene pair held a territory which overlapped with at least four eagle territories near the Malilangwe Dam.

### *4.3.3ii Distribution of small diurnal raptors*

Of the five accipitrine species seen in the LSA, Little Banded and Gabar Goshawks and Ovambo Sparrowhawks were the most common (Fig. 3b-d). Little Banded Goshawks were most commonly seen in the south-western and north-eastern section of the hills which have a fairly diverse mosaic of habitats (Fig. 2). The distribution of independent sightings was not regular indicating that either this species was clumped in a preferred habitat (most sightings, about 52 %, were in valleys or low flat areas) or occurred randomly (Table 17). Sightings of Gabar Goshawks in the LSA were also not regularly distributed and most sightings (82%) were in valley or flat woodland habitat. Ovambo Sparrowhawks, which were seen more in the central and north-eastern sections of the hills and relatively more often in outcrop areas, had the most regular spacing of sightings of any of the small raptors in the LSA.

A Peregrine Falcon and a Bat Hawk (or a pair of each) were usually seen near the Malilangwe Dam (Fig. 3f-g). Peregrine Falcon sightings were often made in the evenings shortly before the time when Bat Hawk sightings were most commonly made (after 18h30).

Barred and Barn Owls were the most commonly seen and widespread small raptors in the LSA (Figs. 3h&j). Barred Owls were seen in all four of the main habitats but usually where there was dense vegetation especially *Androstachys johnsonii*. The distribution of sightings of this species was regular. Barn Owls, which were only seen at daytime roosts, were recorded only in hill and outcrop habitats, and the distribution of sightings was marginally regular. Pearlspotted Owls, although similar to Barred Owls, were seen in fewer areas, usually in valley habitats where sightings were clumped (Fig. 3i). Spotted Eagle Owls roosted in low outcrop areas with dense vegetation during the day and known roosts were regularly spaced (Fig. 3k).

### *4.3.4 Time Utilization*

#### *4.3.4i Timing of breeding - eagles*

In both years of the study there was no overlap in either egg laying or hatching dates between any of the three main nesting eagle species in the LSA (Fig. 13, ANOVA-laying dates, $F=106.7$, $P=0$, ANOVA-hatching dates, $F=65.4$, $P=0$). Although African Hawk Eagles laid eggs later than Black Eagles in both years, there was no significant overall difference in expected fledging dates (ANOVA, $F=2.02$, $P>0.1$). African Hawk, Black and African Fish Eagles started their breeding towards the middle of each year and had generally completed the nesting cycle (up to fledging of chicks) by November which was the start of the rains. Crowned Eagles laid in the latter half of the dry season (in September and October) and were expected to have completed the nesting cycle towards the end of the rainy season (in February and March) in the following year. There were no significant differences in the dates of breeding events in each of the three main species between years (ANOVA; F values = 0.01 - 0.6, $P$ values $>0.1$).

The other large raptors nesting within the LSA were a pair each of Brown Snake Eagles and Gymnogenes (another Gymnogene pair nested on the margin of the hills). Egg laying and hatching dates of Gymnogenes overlapped only with Crowned Eagles, although the nearest Crowned Eagle neighbours did not nest in the same year. The main breeding events of the Brown Snake Eagle pair would not have overlapped with the same events in any other eagle species had the pair bred successfully. Tawny and Martial Eagles which bred on the margins of the LSA had similar expected breeding periods to the three main eagle species breeding in the LSA. A Wahlberg's Eagle pair had overlapping breeding events with Crowned Eagles but did not nest near any Crowned Eagle nest.

### *4.3.4ii Aggression and timing of aggression*

Aggressive interactions involving eagles in the LSA were seen at a rate of about 0.2 per day, *i.e.* aggression was uncommon. African Hawk, Black, Crowned and African Fish Eagles accounted for about 0.16 of these interactions per day. Intraspecific aggression made up about 13 % of all aggression seen. In the CLSA aggressive interactions were seen at a rate of about 0.5 per day and intraspecific aggression was seen only once (between Brown Snake Eagles). Aggression was not seen often enough (n=14) in the CLSA for analysis.

African Hawk Eagles were the most commonly aggressive eagle species in the LSA (Table 18). Although they were most often aggressive towards Black Eagles, attacks against Crowned Eagles were more sustained and usually involved contact being made. Aggression towards other species was usually in the form of flying together or chasing without contact. Most aggression was seen in July and August in both years and in November in 1995 (Fig. 14) which overlapped with egg laying, hatching and fledging dates respectively (Fig. 13). The monthly pattern of aggression was not repeated between years (Multinomial test; $\text{Chi}^2=21.21$, $P<0.05$) although the monthly rates of aggression were not significantly different between years (Wilcoxon Signed Ranks test; $Z=1.01$, $P>0.1$). The first peak in aggression in July 1995 coincided with increases in Black and African Fish Eagle aggression. Black Eagles were more aggressive in July 1996 as well (during the egg laying period) but did not overlap with a peak in African Hawk Eagle aggression.

Other peaks in Black Eagle aggression occurred in March (prior to nesting but during the period of territory reinforcement, courtship and nest building) and December 1995, and between February and April 1996 (also prior to egg laying). Other than heightened aggression in July in both years, the monthly pattern of aggression was not repeated between years (Multinomial test; $\text{Chi}^2=161.30$, $P<0.001$) although monthly rates of aggression were not significantly different between years (Wilcoxon Signed Ranks test, $Z=2.50$, $P>0.1$). Black Eagles were most commonly aggressive towards Bateleur Eagles which more often flew closer to Black Eagle nests than other eagle species (Table 18).

African Fish and Tawny Eagles, although uncommon in the LSA, were the only other eagle species which were relatively frequently seen in aggressive interactions. An African Fish Eagle pair were most commonly aggressive towards Black Eagles and an Osprey when these were near the Malilangwe Dam. The pattern of monthly aggression sightings in African Fish Eagles was similar between years (Multinomial test: $Chi^2=0.63$, $P=0.99$). Peaks around July in both years and in February 1996 coincided with high Black Eagle aggression. The July peaks also coincided with the start of nesting of African Fish Eagles. A pair of Tawny Eagles which had part of their territory extending into the LSA were sometimes seen to be aggressive towards a Black Eagle pair. Aggressive interactions in other species, which were uncommon in the LSA, usually occurred near the LSA margin.

### *4.3.4iii Seasonal timing of flight - eagles*

Eagles in the LSA were more active in flight in March, April, July, August and October in 1995 (on av. 1.9-3.3 flight sightings per day; Fig. 15a). The average daily rates of sightings of eagles in flight per month in 1996 did not differ significantly from those in 1995 (Paired t-test; $t=2.04$, $0.1>P>0.05$, December 1995 and January 1996 not included in test). Higher daily rates of flight sightings in 1995 were caused by close monitoring of Black Eagle nests which resulted in more flight sightings of these birds.

The first peak period of flight activity of Black Eagles in 1995 (March -April) occurred when adults were in courtship, nest building and reinforcing territories. The latter peak (July - August) coincided with hatching of chicks and increased aggression. In 1996 the birds were active in flight between January and June (prior to egg laying, and coinciding with increased aggression) and to a lesser extent after September. Although they did not exhibit two clear peaks of flight activity in 1996, the highest peak in June was at a similar period to the highest peak in 1995, *i.e.* July. The differences in flight sighting rates between years was largely due to more time being spent observing nests in 1995 and fewer pairs breeding in 1996. Although there was no significant difference in sighting rates per month between years (Paired t-test, t=1.40, $P>0.1$, December 1995 and January 1996 not included) the 1995 flight activity pattern was significantly different to that in 1996 (Multinomial test; Chi$^2$=43.83, $P<0.001$, December 1995 and January 1996 data not included).

African Hawk Eagles however did show a significant repetition of the 1995 flight activity pattern in 1996 (Multinomial test; Chi$^2$=1.827, $P=0.99$, December 1995 and January 1996 data not included). Two periods of increased flight activity occurred in each year. The first occurred between March and May in 1995 and between January and March in 1996 (prior to egg laying), and the second between August and October in 1995 and between July and November in 1996 (when chicks were on nests and aggression was high). As with Black Eagles, most flights during these periods were fairly high cruising flights, often along territory boundaries. Slightly fewer birds were seen in flight per day in 1996 than 1995, although differences in the monthly sighting rates between years were not significant (Paired t-test; t=1.64, $P>0.1$, December 1995 and January 1996 data not included). The first peak in flight activity in each year coincided with peaks in Black and Crowned Eagle flight activity. The second peak in each year occurred a month after the largest peak in Black Eagle flight activity, but coincided with peaks in Crowned and African Fish Eagle flight activity.

Crowned Eagles were common in the LSA but were not often seen in flight. Two peaks in flight activity occurred in each year around the expected fledging (March - April 1995 and

February 1996) and laying (October 1995) or pre-laying (July 1996) periods. There was no significant repetition of flight activity patterns between years (Multinomial test; $Chi^2$=63.87, *P* 0.001, December 1995 and January 1996 not included). There was however, no significant difference in monthly flight sighting rates between years (Paired t-test, t=-0.123, *P* 0.1, December 1995 and January 1996 not included). Most (83 %, n=12) Crowned Eagle flight sightings at the beginning and end of each year were of adults cruising above about 100m and usually displaying and/or vocalising at about midday, while all the sightings in June and July 1996 were of birds flying low between perches, often in the early mornings or evenings. It is possible that changes in the times of observations affected the sighting rates.

Similarly, few Fish Eagle flight sightings were made as there were only two pairs which were localised near two dams. There was a significant repetition of flight activity patterns between years (Multinomial test; $Chi^2$= 13.22, $P < 0.1$) although significant differences in monthly flight sighting rates between years occurred (Paired t-test; t=2.32, $0.05 > P > 0.04$). The largest peak in flight activity in both years was around July (egg laying period) and another peak occurred in October 1995 (fledging period). The largest peaks in 1995 and 1996 coincided with peaks in Black and African Hawk Eagle flight activity respectively, and with aggression from both species in 1995 and African Hawk Eagles in 1996. The October peak coincided with Crowned Eagle flight activity.

### *4.3.4iv Daily eagle flight activity*

Black and African Fish Eagles in the LSA were most commonly seen in flight during mid-mornings (09h00-11h00) and mid- to late-afternoons (15h00-17h00, Fig. 16a). They were more active in flight in the afternoons than the mornings. African Hawk Eagles were most active in flight around midday and around 15h00. Crowned Eagles were also most active in flight around midday, but were also often seen flying between perches in the early mornings (before 07h00) and late afternoons and evenings (after 17h00). Nearly all (95%, n=20) Crowned Eagles which were seen flying between 11h30 and 13h30 in the LSA were higher than about 100 m and were often pendulum displaying, vocalising and sometimes engaged in inter- or intraspecific aggression. All the main eagle species in the LSA had reduced flight activity between 12h30 and 14h30, although African Hawk Eagles were still largely active in flight during this time. There were no significant differences between the hourly rates of flight sightings of African Hawk and Black Eagles (Paired t-test; $t=0.765$, $P>0.1$) and of Crowned and African Fish Eagles (Paired t-test; $t=1.75$, $P>0.1$). The first two species were commonly seen in flight while the latter two were less frequently seen in flight over the LSA.

African Hawk Eagles in the CLSA showed similar peaks in flight activity towards midday and in mid-afternoons (15h00) to conspecifics in the LSA, although a lower rate of flight sightings were made before 12h00 in the CLSA (Fig. 16b). The slight reduction in flight activity around 14h00 was also apparent in this species in the CLSA. African Hawk Eagles in both areas showed no significant difference in rates of flight activity (Paired t-test; $t=2.07$, $0.1>P>0.05$). Crowned Eagles in the CLSA were active in flight in the early mornings, as they were in the LSA, but were not so commonly seen in flight towards midday as they were in the LSA. Nonetheless, there was no significant difference between the hourly rates of flight sightings of this species in the two areas (Paired t-test; $t=0.742$, $P>0.1$). Brown Snake Eagles which were most active in flight at around 08h00 and 11h00 and Bateleur Eagles which were most active in flight around 09h00 and 10h00 did not have overlapping periods of peak flight activity. There was however no significant differences in the hourly rates of flight sightings between these two species (Paired t-test; $t=1.11$, $P>0.1$) nor between any other two eagle species in the CLSA (Paired t-tests; all t values $<2.00$, all $P$ values $>0.05$).

### *4.3.4v Weather effects on eagle flight activity*

African Hawk, African Fish and Black Eagles were more commonly seen in flight on clear, warm days, while Bateleur Eagles flew more on overcast or cool days in the LSA (Fig. 17a). Little difference existed in the number of days when no eagles were seen in flight in either weather condition in the LSA. African Hawk and Crowned Eagles were seen in flight at a greater rate on warm and clear days in the CLSA, while Bateleur and Brown Snake Eagles were sighted more frequently in flight on cool and/or overcast days (Fig. 17b).

### *4.3.4vi Monthly sightings of small diurnal raptors.*

Small diurnal raptors were seen at a greater rate in 1996 than 1995, with the exception of Peregrine Falcons and Ovambo Sparrowhawks - the latter being seen at similar rates in both years (Fig. 15b). Most species were sighted at a greater rate between March and September 1996. Although the monthly sighting rates of some species, *i.e.* Peregrine Falcons, Ovambo Sparrowhawks and Little Banded Goshawks, were not significantly different between years (Wilcoxon Signed Ranks tests; $Z$ values $< 1.0$, $P$ values $> 0.1$) the patterns of monthly sighting rates of all the species were significantly different between years (Multinomial tests; $Chi^2$ values $> 60$, $P$ values $= 0.00$).

Little Banded Goshawks were the commonest small diurnal raptor seen in the LSA (Fig. 15a). Other than high sighting rates near the beginning of both years, the patterns of monthly sighting rates showed no repetition between years. They were relatively infrequently seen for most of 1995 (March to October) and after July in 1996. The other commonly seen accipitrines were Gabar Goshawks and Ovambo Sparrowhawks which were seen about 16 % and 20 % as often as Little Banded Goshawks respectively. A single Peregrine Falcon was seen in April and May in both years and appeared to move in and out of the LSA at random at other times of the year. The bird probably had a large home range and occupied the LSA for short periods before moving to other areas.

Barred and Pearlspotted Owls were active often enough during the day to be considered diurnal as well as nocturnal. Hunting, courtship and interspecific aggression were seen during daylight hours. Although similar in size and behaviour, Pearlspotted Owls were seen only about 35 % as often as Barred Owls and only in 1996. Pearlspotted Owls were most often seen between March and July 1996 with a peak of sighting rates in May. Barred Owls appeared to be equally active in most months in 1996.

## 4.4 Discussion

### *4.4.1 Nesting resources*

#### *4.4.1i Nest sites*

About 28 % of known breeding attempts of eagles and gymnogenes in the LSA between 1994 and the end of 1996 were thought to have failed due to predation, and a further 14 % failed for unknown reasons, possibly predation (n = 37 breeding attempts). It is expected that nest sites were selected to reduce the risk to eggs and chicks from terrestrial (mostly mammalian and including semi-arboreal species) and avian predators. The selection of baobab *Adansonia digitata* nest sites supports this as the smooth waxy bark and high first branches makes these trees difficult for terrestrial predators to climb. A common potential mammalian predator, and adept tree climber, in both areas were smallspotted genets (*Genetta genetta* but which were never seen in tall baobabs. Along with *Kirkia acuminata*, baobabs were also generally the tallest indigenous trees in both study areas (some > 24 m high) and nests were therefore high above the ground. Baobabs tended to grow thinner and taller on rocky slopes than the more squat individuals on flat ground (no eagle nests were found in the latter type). It is uncertain whether large raptors nested in trees on slopes because of the morphology of the nest trees, or because of some property, such as effects on wind patterns, inherent in sloping ground. Suspected predation of chicks occurred in 11 % of breeding attempts in baobab nests (n=18) and in 33 % of breeding attempts in other tree species (n=12). Predation at baobab nests was probably from avian predators, while terrestrial predators were probably responsible for more breeding failures in other nest tree species. The success rates of breeding attempts were similar (64-66 %) in both nest types as some Crowned Eagle breeding attempts in baobab nests failed in the egg incubation stages (n=3). Baobab nests in other areas of lowveld have been reported for Crowned Eagles and Bat Hawks, but are not common nest trees in other parts of southern Africa (Friis 1985; Hall 1989; Hough 1949; Steyn 1982).

Tree nest sites may be selected differently if defence from avian predators is more of a criterion than defence from terrestrial predators. In this case behavioural options to nesting pairs would be, 1) to aggressively defend a nest site, 2) choose a camouflaged nest site, 3) nest away from areas where avian predators were common, or 4) nest at different times to when avian predators were common. The first and last options would not limit where nests could be selected, whereas the second and third would. Aggression in African Hawk, Black and African Fish Eagles in the LSA did increase during breeding periods, *i.e.* they exhibited the first behaviour. These species also nested close together (interspecifically) indicating that they generally did not follow the third behaviour, and nest site selection was not much affected by avian predation risk. African Hawk Eagles which nested in *Terminalia sericea* and Crowned Eagles nesting in baobabs during the rainy seasons had nests camouflaged from above by dense leaf canopies. Crowned Eagles were not aggressive towards other raptors and probably relied on camouflage to protect nests. This species was possibly limited by avian predation risks in their selection of nest sites. However, they also nested later in the year during the rains when prey availability for other raptors was probably high and the likelihood of predation on chicks was lower. Crowned Eagles nested lower in trees in the LSA than African Hawk Eagles which may have afforded the former more leaf canopy cover and the latter better vantages to watch for other raptors (African Hawk Eagles generally nested in the tallest tree in an area). However, the large nest structure of Crowned Eagles probably required the birds to build on the larger lower branches of baobabs, and baobabs may have been the only trees in the LSA large enough to support their nests.

Dominance of one nest tree species has been seldom reported in southern Africa. In Hwange National Park, four species of vultures were found to have preferred nesting sites (Whiteheaded Vultures *Trigonoceps occipitalis* preferring baobabs) while Tawny Eagles preferred *Acacia* spp. (Howells & Hustler 1984). Baobabs were used as nest trees for Wahlberg's and African Fish Eagles in the Siabuwa area, Zimbabwe, although *Acacia* spp. and others were commonly used as well (Hartley 1990). The two most comparable raptor community studies in southern Africa, in the Matopos Study Area and Sabi-Sands Reserve, do not give nest sites for most of the raptor species (Gargett 1990; Macdonald & Gargett 1984; Simmons 1994). The two study areas are unusual in that the dominant nest tree species is not the commonest tree species in the area. There appears to have been a strong selection for baobabs as nest trees as eagles generally appeared to nest in other trees only when there were no close baobabs. *Brachystegia glaucescens* was the commonest tree species in the LSA and large parts of the CLSA, but had no used eagle nests. It was used by Little Banded Goshawks and probably other small raptors for nesting. This tree is commonly used in the rest of Zimbabwe by eagles as a nest tree (pers. obs.; R. Hartley - pers. comm.) but in the LSA these trees were not tall as in other parts of the country.

Cliffs were not typically higher than 15 metres in the LSA, and most of those which were had Black Eagle nests on them. The presence of a nest in a baobab also indicated that cliff nest sites were limited (Gargett 1990). Most cliffs at nest sites were not vertical and all of the nests were easily accessed, especially by baboons. Two recently hatched chicks were almost certainly eaten by baboons (which were chased away from the nest but probably returned and ate the chicks after the observer left). The parent birds were not seen to defend the chicks actively, and similar incidents probably account for the disappearance of further five chicks out of nine chicks which hatched in nests on cliffs (another chick disappeared from the nest in a baobab). Only one chick in a nest on a cliff survived to fledging age, and another from the nest in a baobab fledged in 1996. The cliff nest was visited every 2-3 days and baboons were often chased away from the area. A road building crew near the nest may also have inadvertently kept baboons away from the nest. Black Eagle nests in the Matobo Hills are on granite outcrops which generally appear less accessible to terrestrial predators, especially primates, than the sandstone cliffs in the LSA (pers obs.). Breeding success (to fledging) in the Matopos Study Area has been reported in over 70% of the pairs which laid eggs between 1978 and 1988 (Gargett 1990). Most of the deaths of nestlings in the Matopos Study Area (1959-1984) were unexplained and were probably due to predation, less than 30 % of chick deaths or disappearances could be attributed to causes other than predation *e.g.* sickness. Rock pythons may have eaten several nestlings in the Matopos Study Area (Gargett 1990).

### *4.4.1n Aspect*

The aspect of the ground on which nest trees grow may affect the microhabitat of the nest, notably temperature and wind. The dominant wind directions in the LSA were from the south-east and north-west (the latter generally slower). Slopes at nest trees which face the wind may have updraughts associated with them which assist in flight, especially first flights by chicks. However, only Black and Crowned Eagles nests showed some pattern of slope aspect in the LSA. Crowned Eagles do not usually soar or glide, and with their powerful wings probably do not need wind to assist their take-offs (Steyn 1982). Black Eagle nest sites, as has been pointed out, were probably limited and the birds probably did not use aspect as a selection criterion. African Hawk Eagles, which most often do soar and glide did not select nest trees on any particular slope. The selection of nest sites based on ground slope aspect at the nest trees/sites to gain benefits from wind patterns probably did not occur in the main eagle species in the LSA. Any patterns in ground slope aspects at nest trees are probably more as a result of there being more nests in the Nyamasikana River valley which had predominantly north-east and south-west facing slopes.

Air temperatures at cliff nests which face the sun have a higher range than temperatures at tree nests which are not directly heated by the sun. Gargett (1990) found that the aspect was not important in the siting of Black Eagle nests in the Matopos Study Area, although there were no north-facing (most directly towards midday sun) cliff nest sites in the LSA. In both the Matopos Study Area and the LSA, Black Eagle chicks often appeared to suffer heat discomfort (panting and seeking shade) at nests which faced the sun. Gargett (1990) surmised that they were physiologically tolerant of heat, especially as all water needs were met from their food. Not enough chicks survived to fledging in the LSA to test the effects of thermal environments at nest sites on chick growth and mortality. The limited number of optimal nest sites for Black Eagles (based on height, ledge size and accessibility to terrestrial predators) probably meant that aspect was not an important criterion for nest site selection in the LSA. Maximum shade air temperatures in the LSA during the nestling periods (August to October) often exceed $35^0$C whereas temperatures in the Matobo Hills are usually lower. Temperature may have a greater effect on Black Eagle breeding performance in the LSA.

No known studies have indicated that African raptors select nest sites to optimise microclimates near nests, or that microclimates affect breeding success. Some raptor species in the Arctic show tendencies towards choosing nest sites which are not exposed to harsh (hot or cold) conditions which can cause breeding failure (Poole & Bromley 1988)

### *4.4.1m Slope*

Sloping ground at nest sites may cause updraughts of wind which assist take-offs from nests, which might be particularly significant for first flights of fledglings. Newly fledged young initially often land on the ground near nests where they are susceptible to predation. Sloping ground assists in running take-offs downhill. Also higher elevation of nests on slopes affords better vantage points.

However, the LSA nest trees were mostly on gentle slopes or flat ground, and there were no nest trees on slopes greater than 1 (45°). Most of the African Hawk Eagles built nests in trees on fairly flat ground. Although this species is also typically a plains savanna nesting bird, it tends to nest in trees on slopes, especially in valleys (pers. obs., R. Hartley - pers. comm.; Miller 1947; Steyn 1975, Tuer 1973, Wheeler 1970). Pairs may nest in trees on flat ground in the LSA because they have been excluded from nesting on slopes by conspecifics. The high density of African Hawk Eagles nesting in the LSA indicates that some pairs may spill over into less optimal nesting habitats, but that there are resources (probably food) abundant enough to support these.

Crowned Eagle nests were usually in trees on slopes in the LSA, and because tall nest trees were commonly used, height may be a criterion for nest siting. Steyn (1982) gives nest height ranges for this species of 12-30 metres. It has already been mentioned that baobabs on slopes tended to grow higher than those on flat ground, and that Crowned Eagles were specific to baobabs, while African Hawk Eagles in the LSA also nested in *Terminalia*s and *Acacia*s which only grew on flat ground. No other species nested commonly enough to draw conclusions concerning slope preferences for nest sites.

### *4.4.Iv Nest heights*

Possible relationships between height of nests above the ground and protection against predators have been discussed. African Hawk Eagle breeding attempts in nests higher than 15 m failed on about 17 % of occasions (n= 6 breeding attempts, 5 attempts in baobabs) while about 38 % of breeding attempts in trees lower than 15 m failed (n=8 breeding attempts, 2 breeding attempts in baobabs). Only one breeding failure was known to be due to an addled egg, the rest were disappearances of eggs or chicks probably due to predation. High nests tended to be in trees which had high first branches and tall trunks which were difficult to climb. Tall baobab nest trees of all eagle species tended to be found in prey rich areas, which meant that not only were nests secure, but the chicks had abundant food resources and good chances of survival. Eagle densities were high in these areas and the threat from avian predators was possibly greater in taller trees where nests may be more obvious.

African Hawk Eagles in the LSA tended to nest higher than is usual for this species in the rest of southern Africa where the usual range is 9 to 15 m. Most nests tend to be *Acacia* and other plains savanna species which typically do not grow high. Crowned Eagles in the LSA had lower nests than the 12 to 30 m range given for this species in the rest of southern Africa, although this species is better known for nesting in tall deciduous forest trees (Steyn 1982). The differences in nest heights of these two species have been discussed. There was possibly a significant partitioning of nest resources between these species whereby Crowned Eagles select baobabs which have large branches and nest relatively low in the trees, whereas African Hawk Eagles select taller, narrower baobabs with smaller branches. Competition between the two species for optimal baobabs was increased by high aggression between the two which meant they could not nest close together. African Hawk Eagles which could not compete for territories with optimal baobab nests were probably displaced to areas where they used less optimal tree species.

Black Eagles were the only diurnal raptors to occupy the cliff nesting niche in the LSA, and although nests were higher than other eagle species, nest height afforded little protection from predators especially at nests near the top of cliffs and accessible from above. Barn Owls were the only other rock nesting raptor, but usually used caves in small rock outcrops, although one Barn Owl nest was within 10 metres of a Black Eagle nest. Another Barn Owl pair nested in a house. In the Matopos study area: Augur Buzzards *Buteo augur*, Gymnogenes *Polyboroides typus*, Black Storks *Ciconia nigra*, Whitenecked Ravens *Corvus albicollis* (one nests is within a metre of a Black Eagle nest, pers. obs.), Peregrine Falcons, Rock Kestrels *Falco tinnunculus*, Barn Owls and Mackinder's Eagle Owls *Bubo capensis mackinderi*, and other smaller species also use cliff nest sites and potentially compete (Gargett 1990). Finer differences in nest site choice may partition cliff nest resources. Nesting resources in the LSA and CLSA are more tree based.

### *4.4.2 Prey resources*

#### *4.4.2i Predation*

Food is usually the most immediate need for raptors, upon which almost all activities depend (Brown & Amadon 1968; Newton 1979). The measure of fitness, in an evolutionary sense, for raptors is successful reproduction, and the primary requirement for this is adequate food. All raptor behaviours are directly or indirectly linked to the need to find food and reproduce (Table 19). The type of prey used by each raptor species in the LSA can be used to assign species to feeding guilds. As feeding guilds are descriptive of resource utilization, they can be used to describe how the components (*i.e.* species) of trophic level and habitat defined communities interact. The LSA had a diverse array of feeding guilds (Table 20). Hyrax were the dominant prey for Black, Crowned and African Hawk Eagles in the LSA, and also in the Matobo Hills (Auman 1995; Auman & Chiweshe 1995, Gargett 1990; Steyn 1973a; Tuer 1973). African

Hawk Eagles had the most general diet of the three in both areas, although their reliance on hyrax was greater in the Matobo Hills (55 - 59.4% of the diet by numbers) than in the LSA during the study period (29% by numbers). This species preyed more commonly on Natal Francolin, but hyrax made up a larger portion of the estimated mass of prey taken. The juvenile bushbuck preyed on by Crowned Eagles LSA were the largest prey items of eagles in the LSA. Bird, reptile and arthropod feeders were the most diverse groups, although the bird feeding guild had the most raptors not shared with any other group, and was dominated by accipitrines. Specialist feeding groups were fish and carrion feeders. African Fish Eagle prey were limited to available water bodies. Carrion feeders were limited by the low number of large mammalian predators which provided carrion. Leopards were common in the LSA but probably fed on small prey, thus leaving little carrion.

Black Eagles are hyrax specialists, these making up between 49 % and 99 % of their diet in various parts of Africa (Auman & Chiweshe 1995; Barry & Barry 1996; Boshoff *et al.* 1991; Boshoff & Palmer 1988, Brown & Amadon 1968; Brown *et al.* 1982; Davies 1994; Gargett 1990; Steyn 1982). Together with their propensity for nesting on cliffs, they are usually restricted to the hill habitats.

Crowned Eagles were also restricted within the LSA, although their prey was more diverse. Their preference for hyrax and bushbuck and for baobab nest trees probably restricted their distribution. Crowned Eagles appear to be specialists where abundance of one prey type occurs, for instance they are monkey specialists in forests (Skorupa 1989) although prey may be diverse where no one prey species is more availible than others (Boshoff *et al.* 1994; Jarvis *et al.* 1980; Vernon 1979a). Crowned Eagle diet, and other aspects of their biology, have not been well documented in Zimbabwe (Smith & Hartley 1996). However a nest in the same habitat and district as the LSA had a similar array of prey species, with the exception of impala which were not found at nests in the LSA (Friis 1985). Hyrax, *P. capensis* and *Dendrohyrax arboreus*, formed 25% and 53% of prey individuals in forest and savanna biome Crowned Eagle nests respectively, and mammalian prey formed 96% of the prey in the Cape, South Africa (Boshoff *et al.* 1994). In eastern Africa about 98% of the prey has been estimated to be mammalian, and more than half of the prey at two nests were antelope. Monkeys are common prey in east African forests, while in another area *D. arboreus* and suni *Nesotragus moschatus* were the staple prey species (Brown 1971, Brown & Amadon 1968). In the Kibale Forest, Uganda, primates constituted 87% of the prey individuals at four nests, and 89% of the prey killed away from nests. Colobus monkeys made up 58% of the prey (Skorupa 1989).

Skorupa (1989) equates the Crowned Eagle to the Philippine Monkey Eating Eagle *Pithecophaga jefferyi* and the Harpy Eagle *Harpia harpyja* as specialised primate predators, although other prey is taken outside forests as has been discussed. Primates were not common as prey in the LSA, as vervet monkeys *Cercopithecus aethiops* were not common there. Although baboons were common, the size of adults and their gregariousness may make predation difficult. A pair of Crowned Eagles often hunted hyrax at a tourist camp in the LSA, but were never seen to hunt the resident vervet monkey troop.

*H. brucei* were more common prey at Crowned Eagle nests than *P. capensis* in the LSA. The former were more abundant in the LSA. *Heterohyrax* feed more commonly in trees which may make them vulnerable to Crowned Eagles hunting from perches beneath the canopy. One hunting method of Crowned Eagles is to catch monkeys in trees from underneath, using the canopy for concealment, a method which may be modified to catch *Heterohyrax* (Steyn 1982). The larger *Procavia* would be energetically more economical to feed on as they are well within the size range of prey for Crowned Eagles (Daneel 1979; Brown 1971).

Bushbuck juveniles occurred less often as Crowned Eagle prey than hyrax, but were heavier. As bushbuck bones are more durable at the nest than hyrax bones, the proportion of bushbuck prey remains may be an overestimate of their contribution to the diet, as most bones were old. Peaks of bushbuck births are thought to occur in February/March and October/November in southern Africa, the later peak being synchronous with Crowned Eagle breeding in September and October in Zimbabwe, suggesting increased availability of young bushbuck as food (Skinner & Smithers 1990). Juvenile bushbuck are left in dense foliage for the first few days after birth, and may be vunerable to Crowned Eagles hunting beneath the canopy.

The prey spectrum of African Hawk Eagles is wider than the other main eagle species in the LSA. African Hawk Eagles are smaller, and smaller prey items, which are more widely available than Black and Crowned Eagle prey, are energetically economical as prey. Greater speed in horizontal flight and aggressive hunting probably results in a wider spectrum of prey being caught. Smaller prey are usually more abundant than larger prey, (because of lower food needs), which coupled with a lower food need in African Hawk Eagles possibly results in higher densities of this species in the LSA than larger eagles.

African Hawk Eagles may have switched to Natal Francolin due to increased gamebird breeding success in two above-average rainfall seasons during the study period. African Hawk Eagles were more catholic in their diet than the other main LSA eagles, and diet varied between nests, indicating their generalist feeding which allowed them to also inhabit plains and riverine vegetation. Their adaptability probably reduces the species' susceptibility to prey population fluctuation, unlike Black Eagles whose breeding and population dynamics mirror those of hyrax in the Matobo Hills (Chiweshe 1996; Gargett & Gargett 1993a-c). Elsewhere, African Hawk Eagles prey mainly on francolin-sized birds in savanna habitats, the proportion of birds in the diet varying from 74% to 86% (Brown 1952; 1955, - cited in Smeenk 1974; Steyn 1975; Smeenk 1974, Tarboton & Allan 1984). Mammals sometimes form 54% to 70% of the prey (68% in the

Matobo Hills; Kinahan 1975, Smeenk 1974, Tuer 1973). The proportion of birds in the LSA African Hawk Eagles diet was 60%, of which 48% was Natal Francolin, while mammals made up 36%, of which 29% were hyrax, and reptiles made up 2%. Dominance of prey species differed between nests, birds and small mammals being common at nests on the hill habitat margin.

Ospreys, African Fish and Brown Snake Eagles were probably the most specific feeders in the LSA. Hyrax remains were found at African Fish Eagle nests, which is an uncommon prey item for this species, and indicates an abundance of hyrax (Steyn 1982). Records of African Fish Eagles pirating from and preying on water birds are fairly common, and one incident when a pair of African Fish Eagles attacked a Grey *Ardea cinerea*, and then a Goliath Heron *A. goliath* at the Malilangwe Dam was witnessed (Fletcher 1955, Gahamadze 1981; Harwin 1956; Hines & Raats 1989, Howells 1982, Junor 1968; Steyn 1982). Fish were stocked in only two dams in the LSA, and Ospreys and African Fish Eagles were often inter-specifically aggressive indicating competition for limited space, although fish were abundant.

The diets for Tawny and Wahlberg's Eagles are reported to be fairly catholic, and were not investigated in the LSA, they probably took mainly game birds (Boshoff *et. al.* 1981; Osborne 1982, Smeenk 1974, Steyn 1973b; 1980; 1982; Vernon 1979b).

Davison (1996) suggests that seasonal variation in prey of Barn Owls in the LSA reflected seasonal shifts in availability, which considering the seasonal differences in rainfall, and the r-selected life history patterns of most of the recorded prey species, is probably valid. The proportion of the total prey numbers contributed by arthropods, mostly solifugids, increased markedly in December 1995 and January 1996, which was at the onset of the rains when these largely nocturnal arachnids were commonly seen. During this period rodents formed less than a third of the diet by numbers which was probably due to little rodent reproduction during this period when grasses and other plants had not yet seeded. Although arthropods are smaller than rodents and thus less energetically efficient to capture. emergences of armoured crickets and other arthropods resulted in high densities of these prey items which Barn Owls could easily pick up off the ground without energetic hunting.

They relied on rodents from February 1996 until the end of the study in October 1996. Higher than average rainfall during this time caused a growth of grass and grass seeds which lasted until the start of the rains in December 1996. A rodent population outbreak probably occurred in 1996 as they were commonly seen, and rodent outbreaks in other areas of Zimbabwe occurred in 1996 and at the start of 1997, (P. Mundy - pers. comm., pers obs.) Rodents formed more than 80% of the prey individuals of Barn Owls which is typical of results of other southern African Barn Owl studies (Davison 1996). Reproductive output of Barn Owls is variable for a raptor species, and indicates the level of energy intake of the female owls; two clutches of eleven eggs were found in the LSA in 1996.

The variability of the diet of Barn Owls in the LSA is contrary to the belief that they are rodent specialists. The prey size spectrum utilized by this species contains organisms which have life histories in the LSA characterised by seasonal outbreaks followed by population crashes, or in the case of quelea, seasonal aggregations and local movements into the LSA following mostly water resources at the end of the rainy season. The owls thus sustained themselves on prey which was abundant at the time. The birds' feeding guild classification changed on a seasonal basis. Food resource overlap of Barn Owls probably occurred with Barred and Pearl Spotted Owls which were probably largely arthropod feeders at night, and possibly reptile feeders during the day. Prey spectrum overlap possibly also occurred with Blackshouldered Kites if the two species preyed on rodents which were both nocturnal and diurnal. Temporal overlap in feeding between the two species did not occur as Barn Owls are not diurnal hunters (Steyn 1982) although several individuals were seen outside roosts and active during daylight. Only one Black Shouldered Kite hunted periodically in the LSA, so little potential competition for food occurred. Other kestrels and kites which were potential rodent feeders were rarely seen in the LSA. More potential competition and resource overlap may have occurred with the several species of snakes in the LSA, notably yellowbellied sand snakes *Psammophis subtaeniatus*, which were abundant in the LSA, as well as small pythons *Python sebae* and black mambas *Dendroaspis polylepis*. These species and Barn Owls could be considered as part of the same feeding guild as rodents probably form the bulk of all their diets during high rodent availability. Additionally snakes are active and probably hunt at night, and use stealth and surprise to capture prey in a similar manner to Barn Owls, thus not contradicting Root's (1967) definition of a feeding guild.

### *4.4.2ii Prey availability*

Prey availability and dynamics are commonly considered to be the main controlling factors in raptor populations. They are also considered to control the diversity and density of raptor communities, implying that communities are organized around some limiting or enabling factors (Marti *et al.* 1993a,b; Poole & Bromley 1988). Few African studies have examined the interrelationships between the population dynamics of raptors and prey, habitat distribution of prey, and behavioural adaptations of raptors to the dynamics and variables of the prey. Smeenk (1974) is an exception, and studies of hyrax, and hyrax utilization by Black Eagles in the Matopos study area have started recently after decreases in hyrax were suspected to have caused a decline in Black Eagle breeding numbers (Barry 1993; Barry & Barry 1996; Gargett & Gargett 1993a-c; P. Mundy - pers comm.)

Black, Crowned, and African Hawk Eagles and Barn Owls in the LSA provided the best opportunities to study prey utilization and availability, as their prey distribution and dynamics were affected by habitat-level factors. The dominance of hyrax and Natal Francolin in the diets of these eagle species provided correlations between predator and prey densities, and between these and habitat characteristics. It also gave some insights into interactions between predators which had common prey. The investigation of predation in Barn Owls, coupled with trapping of rodents by Davison (1996) demonstrated seasonal changes in prey utilization, compared with the available prey spectrum.

The estimated hyrax density in the Matobos National Park ranges from about 10.3 hyrax per ha. in general, to an upper estimate of about 1.9 hyrax per ha. in the 1990's when rainfall was below average (Barry 1993, Gargett 1990; Gargett *et al.* 1995). These estimates are up to 178 % greater and 49 % less than the estimate for the LSA. Gargett's estimate in the 1970's was based on reported hyrax densities in the Serengeti, Tanzania, where different rainfall patterns to the Matobo Hills would cause differences in food availability for hyrax and thus population densities between the two areas. As shown by the difference in Barry's (1993) estimate and that in this study, extrapolation of densities from one area to another, even within the same climatic zone will yield inaccurate results. Barry's estimate was thought to have been of a population after a dramatic decline due to droughts, which probably also caused the decline in the number of Black Eagle breeding territories by up to 70% (in communal farming lands) in the Matobo Hills (Chiweshe 1996; Gargett *et al.* 1995). The severe 1992 drought in the south-eastern Lowveld probably caused a hyrax population crash in the LSA. The abundance of hyrax at the start of the study in 1995 and the numerous old hyrax seen (age judged from size) and shot or occurring as prey (age judged from tooth wear and size) indicated that many hyrax survived the drought. The population recovered within three years to levels which could sustain eagle breeding. The average size of hyrax colonies in the LSA was similar to colonies in other parts of Zimbabwe, *e.g.* 13 in central Zimbabwe (Richards 1991) but was smaller than some colonies in the Matobo Hills and in a coastal area of South Africa (N. Chiweshe - pers. comm.; Fairall & Crawford 1983). The other main prey resource. Natal Francolins, can reproduce at an even greater rate than hyrax. Clutches of more than five chicks were commonly seen in the LSA, and one pair raised three clutches in 1996.

The average African Hawk Eagle territory in the LSA had an estimated 3100 hyrax, the average Crowned Eagle territory - 2900 and the average Black Eagle territory -2800. The average Black Eagle territory in the Matobos National Park would hold between 1200 - 1700 (Barry 1993) and 9100 hyrax (Gargett 1990). A breeding Black Eagle pair in the Matobos Hills feeds on an estimated 340 hyrax a year (Gargett 1990). In the early 1990's, this equated to an estimated 20 % of hyrax in an average Black Eagle territory in the Matobos National Park, but only about 3.7 % of hyrax per territory according to Gargett's estimate. In the LSA, each Black Eagle pairs preyed on an estimated 330 hyrax per year which was 11.8% of the hyrax population in an average sized Black Eagle territory, or 28 % of the hyrax estimated to be out of refuges at any time. The predation rate on hyrax by African Hawk and Crowned Eagles in the LSA was not known.

The main eagle species in the LSA, which nested more densely in the Nyamasikana River valley, had territories where prey were more dense. Food probably had a greater influence on preferred nesting habitat than any other factor. The eastern margin of the LSA hills was primarily sandstone outcrops with fewer deep fissures providing refuge for hyrax, and had fewer nesting eagle pairs.

Parturition of *P.capensis* and *H. brucei* in the Matobo Hills peaks in March and April, while *H. brucei* peaks in May and June in central Zimbabwe (Barry 1994; Wright 1973). Young of both species could be seen at any time of the year in the LSA and the Matopos study area (Gargett 1990). An abrupt emergence of juvenile *H. brucei* occurred in the LSA in June in both years, around the time of Black and African Hawk Eagle hatching. Chicks and juvenile hyrax in the LSA therefore grew in mass at the same time and there was a parallel growth in Black Eagle food need and food availability. Although it is not conclusively known whether many bird species in Africa time reproduction to coincide with peak food availability (Brown & Brown 1984) the timing of reproduction in many raptors in various parts of the world during peak food availability has been shown (Gargett 1990; Newton 1979; Poole & Bromley 1988). Some raptors may not synchronise breeding with peak food availability if food is usually abundant throughout the year (Hartley & Hustler 1993). The timing of reproduction of eagles in the LSA with peak food availability indicates that; 1) food availability was seasonally variable, or 2) the eagle species did not vary their breeding times if food was abundant throughout the year, or 3) that timing of breeding was controlled by factors other than food availability. The close synchronisation of breeding events within species in the LSA, the repeated pattern of breeding times between years, and the similarity in breeding dates of some species between the LSA and other areas of Zimbabwe, *e.g.* Black Eagles in the LSA and Matobo Hills, indicates that the onset of breeding was controlled by responses to one or more predictable environmental variable *e.g.* air temperature, vegetation cover, end of rainfall *etc.* (day-length varies by less than a 0.5 hour at this latitude and is probably not used as an environmental cue).

Crowned Eagles however did not utilize peak periods of hyrax availability, although hyrax were their main prey species by numbers. Breeding periods for this species may have been set during their evolution in different habitats, in response to different prey, possibly primates. Peak prey needs in raptors are near the time of fledging, which for Black, and African Hawk Eagles in the LSA is between August and October, and for Crowned Eagles between December and March. Crowned Eagles were probably more generalist feeders than Black and African Hawk Eagles in the LSA because hyrax were less available during their peak periods of food requirement. Crowned Eagle chicks had a longer post-fledging dependence period on their parents than the other two eagle species which became independent sooner (Brown & Amadon 1968; Gargett 1990; this study). More abundant food is probably needed for Black and African Hawk Eagle juveniles to learn hunting skills sooner. Prey of juvenile Black Eagles is probably limited to hyrax, while Crowned Eagle juveniles may be more generalist, also scavenging larger prey (antelope) from their parents.

Although African Hawk Eagles utilized hyrax, and while their breeding was synchronous with peak hyrax availability, breeding was probably geared more to the availability of Natal Francolin in the LSA. The estimated number of Natal Francolin in an average African Hawk Eagle territory within the LSA was 630 birds, and a higher number was expected during breeding. Observations at an African Hawk Eagle nest over two breeding seasons indicated a maximum prey delivery rate of about once in two days, even when the chick was large. Approximately 66 prey items may have been delivered to the nest in the approximately 112 day breeding cycle, 32 of these being Natal Francolin on average. This is equivalent to 5.1 % of the estimated number of Natal Francolin in an average-sized territory.

Raptors position nests in territories where food is abundant (Newton 1979). It would therefore appear that the high nesting density in the Nyamasikana River and associated valleys was as a result of the high density of prey in the cliffs on the escarpments above the valleys (hyrax and Natal Francolin) and in the valleys (Natal Francolin and bushbuck).

Food is often the primary factor affecting raptor communities (Marti *et al.* 1993a;b; Smith & Murphy 1979; Poole & Bromley 1988; Steenhof & Kochert 1988), and the processes of interest in this study are those which give rise to dense communities, especially in hill habitat. Authors differ on the formation of communities, and whether communities are organized or random (Marti *et al.* 1993a). Two scenarios exist; 1) communities with diverse, non-habitat specific and sparse resources, where the raptor species are likewise diverse, non-specialised in feeding or nesting requirements, and sparsely distributed, 2) communities such as those in the LSA and probably the Matobo Hills which have specific and dense food and nesting resources, and raptor assemblages which are dominated by a few specialised feeding or nesting species. It is possible that in some habitats, such as hills or forests, changing resources can move the community from one category to the other. For instance, as food resources increase due to factors such as disturbance, or lack of it, change in climate, or succession, the raptor assemblage becomes less diverse as species utilizing the dominant food resource become more abundant and monopolise nesting and space resources which individuals of other species then cannot use. In the LSA, protection of the habitat from destructive human activities and high rainfall prior to and during the study period were probably instrumental in increasing hyrax, Natal Francolin and bushbuck numbers and protecting baobab nest sites. This would promote/reinforce the second community type characteristics. Increasing food resources initially allows reduction of territories to sizes more easily defended, allowing increased densities of raptors. As raptor densities increase, competition for space may increase to the extent that territories decrease to below optimal sizes. Resource driven density increases are then limited through aggression and competition, even if food is super-abundant. In the LSA, this scenario probably existed as food appeared to be abundant despite a probable setback in the 1992 drought. The smaller raptors were dominated by the small passerine and reptile feeding guild (Little Banded Goshawks), the nocturnal and diurnal arthropod and small reptile feeding guild (Barred Owls) and the nocturnal rodent feeding guild (Barn Owls). The small raptor assemblage in the Lonestar plains areas was more diverse, and had a wider range of feeding groups, including more owls which were probably not prey specific, and kestrels which were largely insectivorous. In the CLSA the other scenario probably existed. Few eagle species were typically specific feeders. Their breeding diversity was higher and breeding density lower than in the LSA. No eagle prey species were noticeably dominant, and the array of potential prey included viverrids, antelope, hyrax, large reptiles, game birds, domestic livestock and poultry, and fish. There is no reason to suppose that a raptor community will always move towards being a specialist-dominated, dense community, especially if prey species are held in check by some non-dynamic environmental variable such as the geology and pedology of an area. It is likely that specialised, dense communities often can change to the first type of community, especially due to human alteration of the landscape and resources. If the prior conditions returned, the community might change back again. This may happen when hill areas recover from drought or human land-use, or when forests regrow in cleared areas (and primate and small bird feeding guilds return). However, communities which are sparsely scattered and generalist in their feeding in natural undisturbed habitats probably seldom change to the other scenario except through human influences, such as turning savanna areas over to cultivation where rodent and small bird feeding guilds become dominant.

### *4.4.3 Space*

Black Eagle territories measured in the LSA are the smallest for this species recorded in the southern African subregion, along with the Matopos study area, where territory sizes were 8.9km$^2$ on average (n=11). The smallest LSA and Matopos territory was 5.9km$^2$ (Gargett 1990). Both study areas had empty spaces between territories indicating that small territories were not a result of crowding. The Matobo Hills are more rugged and undulating than the Malilangwe Hills, and have a greater proportion of exposed rock outcrops than LSA (pers. obs.) which are larger areas of hyrax habitat, and larger surface areas of Black Eagle territory.

Black Eagle densities and territory sizes are not available from other habitats comparable to the Matobo Hills and LSA, although there are populations along the granite shield of Zimbabwe, and in sandstone outcrop areas in the Limpopo valley, Zimbabwe. Elsewhere in the southern African subregion, Black Eagles utilize linear, sometimes high, cliffs. Territories and home ranges in these areas were estimated at 60.9km$^2$ in the Natal Drakensberg (39% of each of eight home ranges was suitable hyrax habitat), 35km$^2$ in the Magaliesberg, 14.2km$^2$, 24km$^2$ and about 64km$^2$ in the sedimentary and basalt cliffs of the karoo (Allan 1988, Boshoff & Palmer 1988, Brown 1988, Davies 1994, Siegfried 1968).

No studies to date have measured territory sizes of African Hawk Eagles. This study is probably the first to use mapped sightings to draw territory boundaries. The nesting density of this species is one pair to 22km$^2$ in the Matobo Hills, one pair to 51.5km$^2$ to 110km$^2$ in the Transvaal (Steyn 1982, Tarboton & Allan 1984). Data from internest distances in Hwange National Park in basaltic and sand substrate areas (half of the mean internest distance are assumed to be the mean radius of hypothetically circular territories) give territory size estimates of 17.7km$^2$ and 58.8km$^2$ on the two substrates respectively (Hustler & Howells 1988). The territories in the LSA (excluding two large territories which extended over the plains) are amongst the smallest recorded for any eagle species in the subregion and for one population, other than Crowned Eagles in the LSA. The nesting density of Wahlberg's Eagles in the Sabi-Sands Reserve was 23 per 100km$^2$, or one pair per 4.35km$^2$ (Simmons 1994a&b). This species is migratory and thus makes temporally limited use of prey resources. The African Hawk Eagles make use of prey resources similar to those of the Wahlberg's Eagles - largely game birds, small mammals and reptiles, year round, which attests to the availability of prey resources in the LSA. Wahlberg's Eagles are not common in the LSA, possibly due to competitive exclusion by African Hawk Eagles. Wahlberg's appear to be as common, or more common than African Hawk Eagles in the Matobo Hills where space resources are greater, and territories are larger and more spread out, *i.e.* competition should be less intense (pers. obs.; Macdonald & Gargett 1984).

Crowned Eagle territories were more difficult to map from sightings of this largely non-soaring bird, although one territory of 5.5km$^2$ was accurately mapped. Brown and Amadon (1968) give home range sizes of Crowned Eagles in forests as between 10.24 and 25.6km$^2$. R. Hartley (pers. comm.) reports that these eagles can nest close together in Zimbabwe, and the closest internest distance between two current nests of different pairs in the LSA was 1.65km.

The importance of knowing the territories of eagles is to indicate the area in which sufficient food resources and adequate protected nest sites can be maintained, and the interspecific effects of space utilization, *i.e.* are territory boundaries within a species fixed by the borders of conspecifics only, or other species as well. Newton (1979) describes three types of nesting dispersion in raptor populations: territorial, loosely communal and strongly communal. The breeding raptor species in this study were all territorial and areas of foraging overlapped between species. At the community level, however, partitioning of territories did not occur between eagle species, although regular spacing of nest sites within species did occur in the study areas. Time of foraging showed more separation between species and may have indicated active avoidance of competition and aggression, or incidentally resulted in lower aggression. Brown (1988) reported overlap of Black Eagle territories in montane habitat where up to 60% of the habitat was not suitable for prey, while in the Matopos study area and the LSA where habitat is more homogeneous, territory overlap within a species was not seen in any of the main nesting eagle species.

Despite size and feeding differences in the main eagle species in the LSA, territory sizes were remarkably similar. Although more numerous than other eagle species, African hawk Eagles in the LSA were able to have slightly larger territories by incorporating plains areas in their territories. Black Eagle territories were similar in size to those in the Matopos Study Area. This may indicate that territory sizes are not set by food availability when food is abundant, but have a minimum size set by the need to protect nest sites.

Nest spacing patterns have often been used to indicate space resource utilization and partitioning in various species of birds, especially when nests are assumed to be the centres of nesting territories (Brown 1975, Brown & Rothery 1978, Clark & Evans 1954, Poole & Bromley 1988). Black Eagles in the Matopos Study Area, and the main nesting eagle species did not always nest in the middle of their territories, nor were most of the territories roughly circular. The centres of territories are thus not equi-distant from all points on the territory boundary (Gargett 1990). The interpretation of nest spacing patterns in this study therefore must deal with inter- and intraspecific interactions in choosing nest sites, and not with territory formation around a nest as a marker. Intraspecific nest spacing in African Hawk, Black and Crowned Eagles in the LSA was regular, Black Eagles tending towards very regular, whereas the nest site pattern of all these species together was random, and apparently clumped in the Nyamasikana River valley. The siting of nests thus appeared to be influenced by the proximity of conspecific nest sites, but not of other eagle species despite interspecific aggression. The staggered start of breeding periods of the LSA eagle species probably meant that interspecific aggression at the start of the breeding season did not disrupt nesting. Black Eagles and Cape Vultures (*Gyps coprotheres* nesting near each other in the southwestern Cape, South Africa and which were interspecifically aggressive, also had staggered starts to breeding. None-the-less, breeding success for the Black Eagles was low (Robertson 1986).

The higher proportion of nest failures at nests which were more than a kilometre from the nearest conspecific nest in use in the LSA indicates that interspecific aggression, which should be higher at higher densities, had no detrimental effect on reproductive performance. Close nesting between species occurred more frequently in the Nyamasikana River valley which, as has been pointed out earlier, is richer in food resources than other parts of the LSA and thus benefits breeding. Higher densities of breeding eagles probably deter predators, especially avian ones, due to more vigilance. African Hawk, Black and African Fish Eagles were all seen to respond aggressively towards a Martial Eagle at the same time over the Nyamasikana River valley, whereas this behaviour was never observed near the hill margins. Mainly African Hawk Eagles nested on the outlying areas of the LSA and were usually more than one kilometre from the nearest non-conspecific nest site. These outlying areas were frequently overflown by Bateleur, Tawny, Steppe and Lesser Spotted Eagles which were less commonly seen flying over the more central parts of the LSA. At least four nest failures in African Hawk and Brown Snake Eagles in these areas were probably due to predation by other raptors, baboons or snakes. Predation probably resulted in most, if not all nest failures after hatching as weather and human effects were negligible and food was abundant. Competition effects on reproductive success were therefore probably not direct, and where food availability and raptor/predator densities were high, high densities of breeding raptors probably had a deterrent effect on predators.

Regular nest spacing indicates an abundance of nest sites (Newton 1979). Black Eagle nest sites were however probably limited resulting in a large variation in nearest internest distances. The low number of nesting pairs of this species with relatively large internest distances resulted in a high *G* statistic which was less affected by variation than larger samples. Low internest distances are usually correlated with high food abundance (Newton 1979). The food resources of the three main LSA nesting eagle species have been shown to have been abundant during the study period.

Where there is a dense community of territorial raptors, the question is whether high density is a cause, or an effect, of small territories. Empty areas between Black Eagle territories in the Matopos study area and LSA indicate that territories were not limited by crowding, and high densities resulted from small territories being held. No empty areas would be expected if high densities were compressing territories. African Hawk Eagle territories in the LSA had fewer empty areas, and the birds were more aggressive intraspecifically than Black Eagles. While their generalist diets increased food availability in the LSA, territory size may have been restricted by density. The small territory sizes of this species may have influenced nesting success; Wahlberg's Eagles had reduced breeding performance when nesting densities were high, perhaps because more time was spent in territorial defence at the expense of nesting activities (Simmons 1994b) and territories may have been below the optimal size. The regular spacing of nests in this species also indicates that habitat preference of territories within the LSA did not exist, territories being placed according to available space. Crowned Eagles were mostly restricted to valleys and baobabs, indicating that territories were chosen on habitat criteria, and small territories then allowed more birds to nest.

### *4.4.4 Time Utilization*

#### *4.4.4i Time sharing*

The period during which hunting, territory defence and courtship occurs in flight determines the potential for conflict with other raptor species. Black Eagles spend two to three hours in flight in the Matobo Hills, and 24% of daylight hours in flight in the Karoo National Park, South Africa, more than half of which was engaged in territorial defence (Davies 1994; Gargett 1990). This typically soaring species is highly visible in flight and evokes aggressive responses when territory boundaries of conspecifics or others are crossed during the breeding period.

The other common soaring raptors in the LSA were African Hawk Eagles, and conflict between the two was often seen. African Hawk Eagles were aggressive and regularly attacked other large raptors in flight such as Martial, Bateleur, Crowned, and Tawny Eagles, and various vulture species, all of which occasionally soared over the LSA. The CLSA had more soaring raptor species including Brown and Blackbreasted Snake Eagles, African Hawk Eagles, Martial, Tawny and Bateleur Eagles. There was sharing of air space between species, and differences in time periods budgeted for flight probably effected partitioning of activities and resource utilization. The alternatives for each raptor species are: to fly when fewer other potentially aggressive species are in flight, to fly in different areas to other raptors, or to tolerate sharing of air space.

Competition and interspecific aggression is evident in the Matobo Hills raptor community (Gargett 1990). Aggression was usually not evident between non-paired eagles when one flew close to the other, even during breeding periods. Aggression was also most commonly expressed as paired flying or chasing, and physical contact between birds was rare. This indicated a high level of tolerance in the LSA. There was extensive overlap of periods of flight activity amongst the eagle species in both study areas, although differences in peak periods of flight occurred in some species. Flight activities were probably not affected by the need to reduce competition, but by species-specific requirements for territory defence and hunting. The activity patterns of prey, and hunting strategies of the raptors probably dictated the timing of flights.

Crowned and African Fish Eagles tend to fly in the early mornings and late evenings, and midday and late evenings respectively (Steyn 1982; this study). This is possibly because flight for these birds with large broad wings is easier in calm conditions. High wing loading birds make better use of winds, and African Hawk and Black Eagles possibly fly in the midmorning when winds are stronger and thermals form, and are reluctant to fly when there is no wind. African Fish Eagles may use thermals over land next to water bodies at midday to gain height for more perpendicular views into the water. Mid-morning and afternoon breezes could obscure views of fish below the surface of the water.

The different periods of flight may also relate to prey availability. Crowned Eagles hunting in the early morning from perches use camouflage from the canopy and possibly the low angled sun to catch hyrax sunbathing in the early morning and feeding, as they cannot use the technique of soaring rapidly along a slope and capturing exposed hyrax as has been seen in African Hawk Eagles and Black Eagles (Gargett 1990). The morning sunbathing period of hyrax is apparently not exploited by Black and African Hawk Eagles, probably because there is no breeze in the mornings.

### *4.4.4n Monthly seasonal time utilization*

The importance of flight in hunting, protecting territory and performing courtship is greater during the breeding period of raptors, when flight activities are expected to increase. Flight activity peaked in the first half of the reproductive cycle from nest building to hatching, in the commonest nesting eagles in the LSA.

In the small diurnal raptors, increased sightings of birds before breeding were not evident. Little Banded Goshawks were seen more often between the two breeding periods in the LSA, possibly when the attachment to nest sites is less.

The breeding periods in the LSA resulted in partitioning of activities related to breeding (territory formation and protection), and space, food and, in some cases, nesting resource use. The onset of breeding is when most aggression occurs in raptors (Hammond & Pearson 1993). Overlap of these periods between species increases the time spent in territory defence against conspecifics and other raptors. In the LSA, the onset of breeding periods of the commonest eagles in 1995 did not overlap. The latter parts of African Hawk and Black Eagles breeding overlapped, and coincided with peaks in emergences of juvenile hyrax and Natal Francolin chicks. The laying dates of African Hawk Eagles were later than Black Eagles, and peaks of aggression in the two species did not overlap. The onset of Crowned Eagle breeding started near the end of the breeding periods of these two species. Other eagles which had overlapping breeding periods with African Hawk and Black Eagles were scarce, and their nesting territories were usually away from these species

# Chapter Five: Human Impacts and Conservation Issues

## 5.1 Introduction

Thirty of the 82 resident and migratory raptor species in the southern African subregion are listed as vulnerable, rare, threatened or endangered in all or part of their range (Maclean 1993). In South Africa, raptors make up more than 16% of the threatened birds listed in the *South African Red Data Book*, but make up only about 8% of the breeding population of all South African bird species (Tarboton & Allan 1984). Raptors in Zimbabwe are generally not as threatened as South African raptors, probably because of less intense land pressure in commercial farming and conservation areas (Hartley *et al.* 1996; Zimbabwe Department of National Parks & Wildlife Management 1991). Species under threat at the population level in Zimbabwe usually have naturally low densities, such as the Ayres's Hawk Eagle and Taita Falcon, or are specialized in diet and thus susceptible to poisoning (Hartley & Douthwaite 1994, Hartley *et al.* 1995; 1996). However, raptor assemblages in traditional farming areas in Zimbabwe and other parts of Africa have been altered by the effects of human land-use on their resources (Brandl *et al.* 1985; Sorley & Anderson 1994). Generalist feeding or scavenging raptors may benefit from high agricultural land-pressure while conserved areas maintain the resources for rare and/or specialist raptors. The high human growth rate and overpopulated communal/traditional farming areas in Zimbabwe, making up 30% of the land area, threaten raptor assemblages at the population level, although conservation management in CAMPFIRE areas and game ranching conservancies benefit raptor populations (Hartley *et al.* 1996; Whitlow 1980). Few studies besides this one have looked at the effect of habitat alteration and different land-uses on raptor assemblages/communities (Brandl *et al.* 1985; Gargett 1990; Hartley *et. al.* 1996; Simmons 1994a; Sorley & Anderson 1994).

## 5.2 Methods

The land management regimes of the two study areas were ascertained by talking to members of the land management structures in the two areas, namely the Malilangwe Conservation Trust in the LSA, and members of the Ndowoyo CAMPFIRE (Communal Areas Management Programme for Indigenous Resources) committee.

The human impact in the two areas was ascertained largely subjectively by looking for signs of wood cutting, hunting, trapping, and erosion. I looked especially for signs of direct persecution of raptors. In the LSA the possible impacts of man-made structures, and tourist activities were evaluated qualitatively.

## 5.3 Results and discussion.

The habitat in the LSA was mostly unaffected by human activities, although constructions were more common than in the CLSA where environmental alteration because of human land use was more noticeable. The LSA contained roads, tourist camps, residences, workshops, one large and four small dams. Roads have the greatest potential negative effect on raptors in the LSA, as Spotted Eagle Owls and Grass Owls in the plains perch in roads at night. The construction of roads can disturb nesting raptors and destroys potential nesting trees. In one case, explosives were used within 100 metres of a Black Eagle nest. The chick was fairly mature, but had the blasting taken place during the incubation or nest building phases the nest might have been abandoned, or later the chick might have left the nest. Gargett (1990) reports that Black Eagle chicks are little affected by loud noises, although disturbance of adults at the beginning of the nesting cycle can cause nest abandonment. Roads used for tourism went close to one Black Eagle nest which reared chicks to the early nestling period in both years of the study period. In both years of the study the chicks at this nests were probably eaten by baboons. A hide near the nest and the observers' frequent presence at the nest may have drawn the attention of the baboons to the nest, although the nest was not particularly well hidden, and it is likely that baboons could have found it without assistance

The risk to nesting raptors from human disturbance is real; Black Eagle nests have been abandoned in the Matobo Hills after they were visited by tour operators (W Goodwin - pers comm ) Nesting eagles were not a tourist attraction in the LSA, other than to a few specialised interest groups, and attempts were made in each case to reduce the affect on the nesting birds by taking people to nests where the adults had been habituated to having their nests watched. The visits were brief and the tourists did not approach too closely

The building of tourist lodges and residences in the hills will potentially affect raptors by displacing small raptors from nest sites, and disrupting hyrax and Natal Francolin groups. At the end of the study period, three tourist camps and six houses with gardens existed in the LSA, one camp being under construction. It is likely that the negative effect of construction on hyrax numbers will be short term, as in both of the completed camps and at one house, irrigation of lawns and trees appeared to enhance hyrax numbers, and the animals became habituated to humans fairly quickly A pair of Crowned Eagles often hunted hyrax at one of the camps, and Tawny and Black Eagles hunted near the camp as well. A Little Sparrowhawk pair nested near the camp and hunted within the gardens. All of the tourist camps have been built with the aim of protecting natural fauna and flora in the vicinity of the camp.

The stocking of two dams with exotic and indigenous fish for sport fishing has had a beneficial effect on African Fish Eagles and Ospreys, while the perennial seep from the dams maintains thick riverine vegetation downstream of the dams which is used by bushbuck and hyrax as habitat and food I saw Crowned Eagles do much of their hunting in thick riverine shrubs. A Peregrine Falcon and Little Banded Goshawks were seen hunting quelea flocks which drink at the dams in the evenings. The smaller dams attract antelope which drink at the water source. Leopards, which are very common in the LSA and also present in the CLSA, have been seen hunting in the vicinity of these and other water sources, and the remains of the prey are possibly scavenged by Bateleur and Tawny Eagles. An immature Bateleur was once seen feeding on the remains of a baboon killed by a leopard.

Gardens in the LSA were all well irrigated and contained large exotic and indigenous trees which possibly supported at least one pair of Little Sparrowhawk and probably other small accipiters and small owls. A pair of Barn Owls nested under the eves of a house and preyed on rodents living in the building.

Overall the direct human activities in the LSA had small and localized negative and positive effects, except for dams which had a larger positive influence. The potential exists for future impacts on raptors in the light of a planned increase in tourism and road building. Road planning did not take raptor nest sites into account, although knowledge of nest site locations was poor. Plans should be put into place not to disturb nests during early breeding periods, and some ordered approach to visiting nest sites used if it is ever decided to use raptor nests as tourist attractions. The attitude of the land managers towards protecting raptor nest sites has been healthy, and no plans have been made to turn raptor nest sites into tourist attractions.

For many years the LSA has been protected from over-utilization of trees and animals for food, and a limitation on construction, which has ultimately resulted in protection of raptors and raptor resources. Simmons (1990) points out that areas of high raptor densities, especially dominated by one species, may reduce reproductive performance as more time is spent protecting resources and less time in the care of chicks. In the LSA, production of Black Eagle chicks was low, while African Hawk Eagle's production was about average, and Crowned Eagles produced a high number of chicks for this slow-breeding species. Plans have been mooted to attempt to bolster the existing population of raptors by releasing captive-bred birds such as Peregrine Falcons or eagles, and hand rearing and later releasing Abel chicks in the LSA. These should be approached cautiously as increases in avian population pressure on raptors would have a negative effect on breeding performance and other behaviour in the raptor assemblage. Captive bred raptors have successfully repopulated areas in North America, but where natural raptor densities are much lower than in the LSA (Snelling 1975).

The CLSA suffered to a greater degree from habitat alteration due to tree cutting. Mining has also occurred in the CLSA hills in the past, and a mine may be reopened in the area, but the environmental effects of this appear to have been weakly negative in the immediate vicinity of the mines. At this stage, wood cutting has affected the surrounding plains to a greater degree than the hills where access for transport is more difficult. Much of the plains is covered in mopane scrub stands, which coppice after cutting and grow fairly quickly. These are also drought resistant and provide slow burning, efficient firewood, and these areas are used more extensively for firewood and building wood. A large number of mature *Brachystegia glaucescens* in the CLSA hills were dead, presumably from the 1992 drought. These dead trees are not used by raptors for nesting, nor by their prey, and the utilization of this resource for human needs would not affect raptors.

Limited trapping and hunting with dogs was witnessed. Hyrax numbers were low compared to the LSA, which may be a result of less habitat and hunting pressure. Cracks and crevices were not as common in the CLSA as in the LSA, with rock outcrops often low and flat gneissic granite. Harassment by dogs and humans possibly makes hyrax more nervous and alert, reducing their susceptibility to raptor predation. Hyrax were less approachable than those in the LSA, where in some areas they probably had never seen humans and could be approached to within four or five metres.

At present, the Save River gorge part of the CLSA is under CAMPFIRE principles management, although in the rest of the CLSA there is uncontrolled communal use of resources. Interviews with local inhabitants and CAMPFIRE managers indicate a willingness to conserve areas which could be used for tourist activities. Commercial hunting occurs in the south eastern part of the CLSA, and this area has had villages moved from it and is uninhabited. The Save gorge has a relatively high number of raptors, and is conserved, although resource utilization is still practised in a low but presumably uncontrolled fashion. Direct persecution of raptors is non-existent according to local inhabitants, and knowledge of raptors and nest sites is low.

South of the CLSA, two luxury tourist camps exist, and both use raptors in their advertising, presumably profiting from the raptor assemblages of the area. The conservation of raptors would therefore benefit these commercial ventures, and because they are part of the CAMPFIRE scheme and return a portion of their earnings to the local populace, local people would also benefit. Areas near the CLSA are used for birding safaris (D. Solomon pers comm.) in which eagles are potentially important, and direct protection of nest sites could benefit tourism.

A potential threat to the raptor assemblages of both study areas is the planned introduction or increase of large herbivore populations (CAMPFIRE personnel and J. Anderson pers comm.). Gargett (1990) has pointed out that the increase of large herbivores in the Rhodes Matopos National Park may have effects on the vegetation which reduce the habitat and food availability for prey species. This is pertinent in both areas of this study, especially the LSA where increases in elephant numbers are likely. Elephants in the LSA have been observed to feed on and damage *B. glaucescens* which are fed on commonly by *H. brucei*. The potential damage to trees by elephants has been well documented, yet in Hwange National Park only one Tawny Eagle nest tree was pushed over in 12 years despite the high population of elephants (Hustler & Howells 1986). Preferred nest tree species were not the most common in the LSA and could be seriously affected by elephants, especially baobabs which are eaten by elephants during droughts.

# Chapter Six: Conclusions

## 6.1 Conclusions

The LSA has a high density of raptors, higher than that expected from the usual relationship between area and density in sub-Saharan Africa, and this has been attributed to the abundant resources, mainly food. The hill habitat is thought to be richer in food resources than most plain savanna and riverine areas in southern Africa, but limited in nesting and space resources. The high density results in resource overlap and partitioning of food and breeding times resulting in temporal separation of peak food needs. The diversity of raptors may exclude certain species such as Wahlberg's Eagles and Martial Eagles which competed for food with the existing raptor species. Hill habitats probably withstand the negative effects of droughts better since the gutter effect of rock outcrops increases the effective precipitation.

The CLSA has a slightly lower density of eagles than would be expected from an area of its size, but still compares favourably with conserved areas in Africa, despite sharing its resources with humans. The CLSA is under more threat than the LSA unless conservation measures are put in place. The difference between the raptor assemblages and densities in the CLSA and the LSA is probably due to differences in prey availability. The lower densities of hyrax and Natal Francolin, the two principle food resources in both areas, are probably due to differences in topography which provide different amounts of crevice habitat. Food possibly affects the differences in the hyrax populations as the differences in geology and drainage between the two areas may affect vegetation.

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**Appendix 1.** Location sites and breeding attempts at eagle and gymnogene nests in the LSA (del = delapidated nest, a n = alternate nest)

| Species | Nest No. | Location | Nest Site | Breeding attempts |
|---|---|---|---|---|
| **African Hawk Eagle** | 6 | 21° 00′ 27″S<br>31° 56′ 59″E | *Kirkia acuminata* | 1995 |
| | 14 | 20° 59′ 23″S<br>31° 57′ 10″E | *Acacia nigrescens* | 1996? |
| | 19 | 21° 03′ 33″S<br>31° 51′ 49″E | *Adansonia digitata* | 1995<br>1996 |
| | 26 | 21° 03′ 13″S<br>31° 53′ 37″E | *Acacia nigrescens* | 1995<br>1996 |
| | 27 | 21° 03′ 21″S<br>31° 52′ 58″E | *Adansonia digitata* | del. |
| | 53 | 21° 03′ 06″S<br>31° 52′ 54″E | *Terminalia sericea* | a.n. |
| | 58 | 21° 00′ 32″S<br>31° 54′ 11″E | *Adandonia digitata* | 1996? |
| | 59 | 21° 00′ 30″S<br>31° 54′ 03″E | *Adansonia digitata* | a.n. |
| | 62 | 21° 01′ 02″S<br>31° 53′ 22″E | *Adansonia digitata* | del. |
| | 64 | 21° 02′ 12″S<br>31° 55′ 02″E | *Terminalia sericea* | del. |
| | 65 | 21° 02′ 06″S<br>31° 54′ 55″E | *Terminalia sericea* | 1996 |
| | 101 | 21° 02′ 18″S<br>31° 49′ 52″E | *Adansonia digitata* | 1995<br>1996 |
| | 105 | 21° 02′ 30″S<br>31° 52′ 12″E | *Adansonia digitata* | 1996 |

| | | | | |
|---|---|---|---|---|
| | 108 | 21° 01′ 55″S<br>31° 53′ 40″E | *Adansonia digitata* | 1995<br>1996 |
| | 110 | 21° 01′ 25″S<br>31° 51′ 15″E | *Adansonia digitata* | del. |
| | 111 | 21° 01′ 55″S<br>31° 55′ 33″E | *Terminalia sericea* | 1995 |
| | 113 | 20° 59′ 29″S<br>31° 59′ 20″E | *Acacia nigrescens* | 1996 |
| **Black Eagle** | 1 | 21° 00′ 36″S<br>31° 55′ 22″E | Cliff | 1995<br>1996 |
| | 2 | 20° 59′ 31″S<br>31° 59′ 23″E | Cliff | 1996 |
| | 21a | 21° 02′ 41″S<br>31° 51′ 34″E | Cliff | 1996 |
| | 21b | 21° 02′ 39″S<br>31° 51′ 35″E | Cliff | alt. |
| | 25 | 21° 02′ 46″S<br>31° 52′ 37″E | Cliff | 1995 |
| | 54 | 21° 02′ 20″S<br>31° 53′ 23″E | Cliff | del. |
| | 56 | 21° 01′ 08″S<br>31° 52′ 20″E | *Adansonia digitata* | 1995<br>1996 |
| | 106 | 21° 01′ 25″S<br>31° 56′ 48″E | Cliff | 1995 |
| **Crowned Eagle** | 17 | 21° 03′ 12″S<br>31° 52′ 06″E | *Adansonia digitata* | 1994<br>1995<br>1996 |
| | 22 | 21° 02′ 17″S<br>31° 51′ 52″E | *Adansonia digitata* | 1996 |
| | 34 | 21° 01′ 53″S<br>31° 54′ 06″E | *Adansonia digitata* | 1994<br>1995 |

| | | | | |
|---|---|---|---|---|
| | 38 | 21° 01′ 24″S<br>31° 56′ 24″E | *Adansonia digitata* | 1994 |
| | 60 | 21° 01′ 22″S<br>31° 53′ 18″E | *Adansonia digitata* | a.n. |
| | 61 | 21° 01′ 25″S<br>31° 53′ 08″E | *Adansonia digitata* | a.n. |
| | 63 | 21° 01′ 29″S<br>31° 52′ 59″E | *Adansonia digitata* | 1994<br>1996 |
| | 67 | 20° 59′ 49″S<br>31° 54′ 55″E | *Adansonia digitata* | del. |
| | 112 | 21° 01′ 08″S<br>31° 52′ 27″E | *Adansonia digitata* | ? |
| | 117a | 21° 01′ 56″S<br>31° 51′ 17″E | *Adansonia digitata* | none |
| | 117b | 21° 01′ 56″S<br>31° 51′ 17″E | *Adansonia digitata* | a.n. |
| **African Fish Eagle** | 16 | 21° 03′ 13″S<br>31° 52′ 14″E | *Adansonia digitata* | del. |
| | 23 | 21° 02′ 14″S<br>31° 52′ 30″E | *Acacia nigrescens* | 1996 |
| | 24 | 21° 02′ 14″S<br>31° 52′ 36″E | *Adansonia digitata* | del. |
| | 34b | 21° 02′ 21″S<br>31° 52′ 55″E | *Adansonia digitata* | 1995 |
| | 38 | 21° 01′ 24″S<br>31° 56′ 24″E | *Adansonia digitata* | 1995<br>1996 |
| **Tawny Eagle** | 3 | 21° 01′ 55″S<br>31° 56′ 59″E | *Acacia nigrescens* | 1995 |
| | 5 | 21° 02′ 18″S<br>31° 56′ 22″E | *Acacia nigrescens* | ? |

|  |  |  |  |  |
|---|---|---|---|---|
|  | 12 | 21° 02′ 18″S<br>31°57′25″E | *Acacia nigrescens* | a n |
| **Wahlberg's Eagle** | 109 | 20° 03′ 45″S<br>31° 52′ 38″E | *Lonchocarpus capassa* | 1995<br>1996 |
| **Martial Eagle** | 107 | 21° 02′ 45″S<br>31° 55′ 05″E | *Afzelia quanzensis* | 1995 |
| **Gymnogene** | 33a | 21° 02′ 21″S<br>31° 52′ 55″E | *Adansonia digitata* | 1995 |
|  | 114 | 21° 01′ 27″S<br>31° 57′ 27″E | *Acacian nigrescens* | 1995 |

## **Appendix 2.** Abreviations of words used in Figures 1-17

| | |
|---|---|
| Ac - | *Aethomys chrysophilus* |
| AFE & FE - | African Fish Eagle |
| AHE - | African Hawk Eagle |
| An - | *Aethomys namaquensis* |
| An - | Antelope/ bushbuck |
| A/P - | Acrididae/Pamphagidae |
| As - | *Acomys spinosissimus* |
| BA - | Bathyergidae |
| Barr - | Barred Owl |
| Bat - | Bateleur Eagle |
| Bb - | baboon |
| Bd - | misc. bird spp. |
| BE - | Black Eagle |
| Bo - | Barn Owl |
| BSE - | Brown Snake Eagle |
| CLSA - | Communal Land Study Area |
| CO - | Coleoptera |
| CR - | *Crocidura* spp |
| Gab - | Gabar Goshawk |
| Gym - | Gymnogene |
| Hb - | *H. brucei* |
| Hr - | hare |
| Lr - | *Lemniscomys rosalia* |
| LSA - | Lonestar Study Area |
| ME - | Martial Eagle |
| Mg - | mongoose |
| MI - | Michrochiroptera |
| Mn - | *Mastomys natalensis coucha* |
| Nf - | Natal Francolin |
| OR - | Orthoptera |
| Ovam - | Ovambo Sparrowhawk |
| PA - | passerines |
| Pereg - | Peregrine Falcon |
| Pc - | *P. capensis* |
| PSO - | Pearlspotted Owl |
| Rl - | Giant plated lizard |
| Sc - | *Saccostomus campestris* |
| SO - | Solipugidae |
| Sp - | *Steatomys pratensis* |
| Sq - | tree sqirrel |
| TE - | Tawny Eagle |
| Tl - | *Tatera leucogaster* |
| Tp - | *Thallomys paedulcus* |
| Uh - | unidentified hyrax |
| Un - | unidentified |

**Table 1.** Raptors in and around the LSA and CLSA and their status. (**BI** - breeds inside or on the margin of the study area and therefore uses space and food resources; **BO** - probably breeds outside; **I+** - uses space/food resources, breeds elsewhere; **I-** - intrudes does not use resources; NBM - non breeding migrant)

| **Species** | **LSA** | **CLSA** |
|---|---|---|
| ***Eagles & eagle sized*** | | |
| Steppe Eagle<br>*Aquila nipalensis* | NBM | -- |
| Lesser Spotted Eagle<br>*Aquila pomarina* | NBM | -- |
| Tawny Eagle<br>*Aquila rapax* | BI | BI? |
| Black Eagle<br>*Aquila verreauxii* | BI | BI? |
| Wahlberg's Eagle<br>*Aquila wahlbergi* | BI | BI |
| Brown Snake Eagle<br>*Circaetus cinereus* | BI | BI |
| Blackbreasted Snake Eagle<br>*Circaetus pectoralis* | BO, I- | BI? |
| African Fish Eagle<br>*Haliaeetus vocifer* | BI | BI? |
| African Hawk Eagle<br>*Hieraaetus spilogaster* | BI | BI |
| Martial Eagle<br>*Polemaetus bellicosus* | BI | BI |
| Crowned Eagle<br>*Stephanoaetus coronatus* | BI | BI |
| Bateleur Eagle<br>*Terathopius ecaudatus* | BO,I+ | BI |
| Osprey<br>*Pandion haliaetus* | NBM, I+ | -- |
| Gymnogene<br>*Polyboroides typus* | BI | BI |
| ***Vultures*** | | |
| Hooded Vulture<br>*Necrosyrtes monachus* | I- | I- |
| Lappet-faced Vulture<br>*Torgos tracheliotus* | I- | I- |
| White-backed Vulture<br>*Gyps africanus* | I- | I- |
| White-headed Vulture<br>*Trigonoceps occipitalis* | I- | I- |

| | | |
|---|---|---|
| ***Small Diurnal*** | | |
| Little Banded Goshawk<br>*Accipiter badius* | BI | BI |
| Black Sparrowhawk<br>*Accipiter melanoleucus* | -- | BI? |
| Little Sparrowhawk<br>*Accipiter minullus* | BI | BI? |
| Ovambo Sparrowhawk<br>*Accipiter ovampensis* | BI? | BI? |
| African Goshawk<br>*Accipiter tachiro* | BI? | BI? |
| Gabar Goshawk<br>*Micronisus gabar* | BI? | BI? |
| Dark Chanting Goshawk<br>*Melierax metabates* | BO, I+ | -- |
| Bat Hawk<br>*Macheiramphus alcinus* | BI? | -- |
| Dickinson's Kestrel<br>*Falco dickinsoni* | -- | BO?, I+ |
| Peregrine Falcon<br>*Falco peregrinus* | BO, I+ | I+ |
| European Hobby Falcon<br>*Falco subbuteo* | I+ | -- |
| Rock Kestrel<br>*Falco tinnunculus* | -- | BI? |
| Blackshouldered Kite<br>*Elanus caeruleus* | BO?,I+ | BO?,I+ |
| Yellowbilled Kite<br>*Milvus migrans parasitus* | I+ | I+ |
| ***Owls*** | | |
| Barn Owl<br>*Tyto alba* | BI | BI |
| Grass Owl<br>*Tyto capensis* | BO I+ | -- |
| Marsh Owl<br>*Asio capensis* | -- | BO? |
| Spotted Eagle Owl<br>*Bubo africanus* | BI | BI |
| Giant Eagle Owl<br>*Bubo lacteus* | BO? I+ | BI? |
| Barred Owl<br>*Glaucidium capense* | BI | BI |
| Pearlspotted Owl<br>*Glaucidium perlatum* | BI | BI |
| African Scops Owl<br>*Otus senegalensis* | BO | -- |
| Pel's Fishing Owl<br>*Scotopelia peli* | BI? | -- |
| Wood Owl<br>*Strix woodfordii* | BI | -- |

**Table 2** Number of nesting pairs of eagles and Gymnogenes in the LSA and CLSA in 1995 and 1996

| **Eagle species** | **No. nesting pairs**<br>**LSA** | <br>**CLSA** |
|---|---|---|
| ***Nests inside the hills*** | | |
| Black Eagle | 5 | 1? |
| Crowned Eagle | 5 | 2 |
| African Hawk Eagle | 5 | 5 |
| African Fish Eagle | 2 | 1? |
| Brown Snake Eagle | 1 | 2? |
| Martial Eagle | -- | 1 |
| Gymnogene | 1 | 1(+1?) |
| **Total** | **19** | **9 (+5?)** |
| ***Nests on hill margin*** | | |
| Crowned Eagle | 2 | -- |
| African Hawk Eagle | 5 | -- |
| Tawny Eagle | 2 | -- |
| Wahlbergs' Eagle | 1 | 1 |
| Martial Eagle | 1 | -- |
| Blackbreasted Snake Eagle | -- | 1? |
| Bateleur Eagle | -- | 1 |
| Gymnogene | 1 | -- |
| **Total** | **12** | **2 (+1?)** |
| **Total - all nests** | **31** | **11 (+6?)** |

**Table 3** Numbers of breeding pairs of eagles and Gymnogenes in the LSA in 1995 and 1996, and the number of territories per species in each year estimated from nests and repeated sightings of adults

| Species | Year | No. nesting pairs | No. chicks fledged | No. territories |
|---|---|---|---|---|
| Black Eagle | 1995 | 4 | 1 | 5 |
| | 1996 | 3 | 1 | 4* |
| Crowned Eagle | 1994/95 | 4** | 3 | 6 (+1?)*** |
| | 1995/96 | 2 | 1 | 6 (+1?) |
| | 1996/97 | 3 | ? | 6 (+1?) |
| African Hawk Eagle | 1995 | 6(+3?) | 5 | 10 |
| | 1996 | 6(+3?) | 3 | 10 |
| African Fish Eagle | 1995 | 2 | 3 | 2 |
| | 1996 | 2 | 1 | 2 |
| Brown Snake Eagle | 1995 | 0 | 0 | 2 |
| | 1996 | 1 | 0 | 2 |
| Tawny Eagle | 1995 | 2 | ? | 2 |
| | 1996 | 2 | ? | 2 |
| Wahlberg's Eagle | 1995 | 1 | 1 | 1 |
| | 1996 | 1 | 0? | 1 |
| Gymnogene | 1995 | 2 | 2 | 2 |
| | 1996 | 0 | 0 | 2 |
| **Total** | **1995** | **18 (+3?)** | **13** | **30 (+1?)** |
| | **1996** | **18 (+3?)** | **5** | **29 (+1?)** |

* One adult killed, partner not seen to be enforcing territory.

** Data from reports from K. Wolhuter & J. Anderson, and from assumed nesting when juveniles seen near nests and nest trees covered in mutes, and recent prey at nest.

*** Assumption is made that territories in 1995 and 1996 same as 1994 as no new nests built, nor empty territories (with disused nests) found.

**** 1995/96 Crowned Eagle data included in calculations.

***** 1996/97 Crowned Eagle data included in calculations.

**Table 4.** Estimated number of territories of small diurnal raptors and owls in the LSA in 1995 and 1996, based on sightings. The total count of territories per species over two years did not include territories recounted in 1996. The averages of territories per species per year were calculated from yearly totals, and included territories recounted in 1996.

| Species | Estimated number of territories | | Total no. territories counted | Av. no. territories counted per yr |
|---|---|---|---|---|
| | 1995 | 1996 | | |
| *Small diurnal* | | | | |
| Little Sparrowhawk | 2 | 1 | 3 | 2 |
| Little Banded Goshawk | 16 | 15 | 27 | 16 |
| Gabar Goshawk | 4 | 5 | 8 | 5 |
| Ovambo Sparrowhawk | 2 | 7 | 9 | 5 |
| African Goshawk | 2 | 1 | 2 | 2 |
| Peregrine Falcon | 1 | 1 | 1 | 1 |
| Blackshouldered Kite | 0 | 1 | 1 | 1 |
| Bat Hawk | 1 | 1 | 1 | 1 |
| **Total** | **28** | **32** | **52** | **33** |
| *Owls* | | | | |
| Barred Owl | 10 | 12 | 21 | 11 |
| Pearlspotted Owl | 4 | 6 | 7 | 5 |
| Barn Owl | 18 | 19 | 30 | 19 |
| Spotted Eagle Owl | 5 | 1 | 5 | 3 |
| Pel's Fishing Owl | 1 | 0 | 1 | 1 |
| **Total** | **38** | **38** | **64** | **39** |

**Table 5** Percentage contribution to total area raptor diversity of eagle, small diurnal raptors, owls, vultures and others species in four areas of Zimbabwe and one area of South Africa. Three hill areas, one gorge system (analogous to hill and riverine habitat), and two savanna ecosystem raptor assemblages are included (n = number of species)

| **Area** | **Eagles** | | **Small diurnaln** | | **Owls** | | **Vultures** | | **Others** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **%** | **n** | **%** | **n** | **%** | **n** | **%** | **n** | **%** | **n** |
| ***Hill habitat*** | | | | | | | | | | |
| LSA[1] | 42.9 | 9 | 28.6 | 6 | 28.6 | 6 | -- | | -- | -- |
| CLSA[1] | 47.9 | 11 | 30.5 | 7 | 21.7 | 5 | -- | | -- | -- |
| Matopos Study Area, Zimbabwe[2] | 34.4 | 11 | 43.8 | 14 | 18.8 | 6 | -- | | 3.1 | 1 |
| ***Gorge*** | | | | | | | | | | |
| Botoko Gorge, Zambezi River[3] | 29.4 | 5 | 47.1 | 8 | 23.5 | 4 | -- | | -- | |
| ***Savanna*** | | | | | | | | | | |
| Lone Star Reserve, Zimbabwe[1] | 26.7 | 8 | 30.0 | 9 | 26.7 | 8 | 13.3 | 4 | 3.3 | 1 |
| Siabuwa Communal Lands, Zimbabwe[1] | 33.3 | 6 | 44.4 | 8 | 22.2 | 4 | -- | | -- | |
| Sabi Sands/ Timbavati- Klaserie, South Africa[5] | 28.1 | 9 | 31.3 | 10 | 25 | 8 | 12.5 | 4 | 3.1 | 1 |

References:
[1] This study
[2] Macdonald & Gargett, 1984
[3] Hartley, 1993
[4] Hartley, 1990
[5] Simmons, 1994a

**Table 6.** Comparisons of the counted or estimated breeding densities of raptors in pairs per 40km$^2$ (the largest area which would not result in extrapolation of densities) in seven areas in Zimbabwe and South Africa The Zimbabwean study areas are the LSA, CLSA, Lonestar Reserve (LSR, K Wolhuter, unpubl data; this study) Matopos Study Area (Matop., Macdonald & Gargett 1984) and Hwange National Park (HNP, Howells & Hustler 1984), and the South African results are from Sabi-Sands Study Area (Simmons 1994a), and the Timbavati-Kleserie study area (Tarboton & Allan 1984) Complete owl and small diurnal raptor censuses were not conducted in the South African, Hwange and Lonestar savanna examples.

| **Species** | **Breeding densities (pairs per 40km$^2$)** | | | | | | |
|---|---|---|---|---|---|---|---|
| | **Hill** | | | **Savanna** | | | |
| | **LSA** | **CLSA** | **Matop.** | **LSR** | **Sabi-Sands** | **Timb.-Klaseri** | **HNP** |
| ***Eagles & eagle sized*** | | | | | | | |
| Black Eagle | 5 | 0.5 | 3.6 | -- | -- | -- | 0.01 |
| African Hawk Eagle | 10 | 2.5 | 2.2 | 0.3 | 1.3 | 0.7 | 0.4 |
| Crowned Eagle | 7 | 1 | 0.3 | -- | -- | -- | -- |
| Tawny Eagle | 2 | -- | 0.1 | 1.4 | 0.3 | 0.6 | 0.5 |
| Wahlberg's Eagle | 1 | 0.5 | 1.6 | 1.5 | 9.2 | 4.7 | 0.1 |
| Martial Eagle | 1 | 0.5 | 0.1 | 0.2 | 0.3 | 0.3 | 0.1 |
| Brown Snake Eagle | 1 | 1 | 0.5 | -- | 0.3 | -- | pres. |
| Blackbreasted Snake Eagle | -- | ? | 0.1 | 0.2 | 0.3 | 0.1 | pres. |
| Bateleur Eagle | -- | 0.5 | -- | 0.2 | 1.3 | 0.9 | pres. |
| African Fish Eagle | 2 | 0.5 | 0.1 | -- | 0.3 | -- | 0.04 |
| Gymnogene | 2 | 1 | 0.6 | | 1.3 | 0.1 | -- |
| | | | | pres. | | | |
| **Total** | **31** | **8.5** | **9.3** | **3.7$^1$**<br>**3.8$^2$** | **14.6** | **7.8** | **1.2** |
| ***Small diurnal*** | | | | | | | |
| Ovambo Sparrowhawk | 9 | 0.5 | 0.3 | | -- | -- | |
| Little Sparrowhawk | 3 | 0.5 | 0.3 | pres. | 0.3 | -- | |
| Little Banded Goshawk | 27 | 5.5 | 0.3 | -- | 0.6 | -- | |
| African Goshawk | 2 | 0.5 | 0.4 | -- | 0.8 | -- | |
| Black Sparrowhawk | -- | 0.5 | 0.5 | -- | 2.8 | -- | |
| Gabar Goshawk | 8 | 1 | 0.1 | | -- | 0.1 | |
| Bathawk | 1 | -- | -- | pres. | -- | -- | |
| **Total** | **50** | **8.5** | **3.0$^1$**<br>**7.2$^2$** | pres.<br>-- | **4.4$^1$**<br>**6.1$^2$** | **0.1$^1$**<br>**0.5$^2$** | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Owls* | | | | | | |
| Barn Owl | 30 | 5.5 | 0.6 | pres | 0.3 | -- |
| Grass Owl | pres. | -- | -- | many | pres | -- |
| African Scops Owl | pres. | -- | -- | pres. | many | -- |
| Pearlspotted Owl | 7 | 2? | 0.9 | pres | many | -- |
| Barred Owl | 21 | 4? | -- | pres | several | -- |
| Spotted Eagle Owl | 5 | 1? | 0.6 | many | several | -- |
| Giant Eagle Owl | 1 | 0.5 | 0.1 | -- | 0.8 | 0.7 |
| Pel's Fishing Owl | 1 | -- | -- | -- | several | -- |
| Wood Owl | pres. | -- | -- | pres | -- | -- |
| **Total** | **65** | **13** | **2.4**$^1$<br>**3.0**$^2$ | | **1.1** | **0.7** |
| **Area Totals** | **146** | **25.9** | **14.6**$^1$<br>**21.9**$^2$ | | **19.7**$^1$<br>**22.6**$^2$ | **8.4** |

**Table 7** Dates of repeat measures conducted on transects one and two in the LSA

| Repeats | Period<br>T1 | T2 |
|---|---|---|
| 1 | 3 Nov - 6 Dec. 95 | 19 Oct. - 21 Oct. 96 |
| 2 | 24 Apr. - 7 May 96 | 23 Oct. - 27 Oct. 96 |
| 3 | 1 Nov - 5 Nov 96 | 28 Oct. - 1 Nov 96 |
| 4 | 7 Nov. - 8 Nov 96 | 14 Nov. - 15 Nov. 96 |
| 5 | 12 Nov. - 13 Nov. 96 | 19 Nov. - 22 Nov. 96 |

**Table 8** Nest sites of raptors in the LSA and CLSA in 1995 and 1996, and the number of nest sites found, some of which became dilapidated or fell down during the study

| **Species** | **LSA** | | **CLSA** | |
|---|---|---|---|---|
| | **Site** | **No.** | **Site** | **No.** |
| Black Eagle | cliff | 7 | -- | -- |
| | *Adansonia digitata* | 1 | | |
| Crowned Eagle | *Adansonia digitata* | 11[1] | *Adansonia digitata* | 2 |
| African Hawk Eagle | *Adansonia digitata* | 9 | *Adansonia digitata* | 5 |
| | *Terminalia sericea* | 4 | | |
| | *Acacia nigrescens* | 2 | | |
| | *Acacia tortilis* | 1 | | |
| | *Kirkia acuminata* | 1 | | |
| African Fish Eagle | *Adansonia digitata* | 4 | -- | -- |
| | *Acacia nigrescens* | 1 | | |
| Tawny Eagle | *Acacia nigrescens* | 3 | -- | -- |
| Wahlberg's Eagle | *Lonchocarpus capasa* | 1 | *Acacia nigrescens* | 1 |
| Brown Snake Eagle | *Terminalia sericea* | 1[1] | -- | -- |
| Martial Eagle | *Afzelia quanzensis* | 1 | *Adansonia digitata*[2] | 1 |
| Bateleur Eagle | -- | -- | *Acacia nigrescens* | 1[2] |
| Gymnogene | *Adansonia digitata* | 1 | *Adansonia digitata* | 2 |
| | *Acacia nigrescens* | 1 | | |
| Unidentified nests (eagle) | *Brachystegia glaucescens* | 1 | | |
| | *Adansonia digitata* | 1 | | |
| | *Terminalia sericea* | 1 | | |
| | *Acacia nigrescens* | 1 | | |
| Little Banded Goshawk | *Brachystegia glaucescens* | 4 | *Kirkia acuminata* | 1 |
| | *Terminalia sericea* | 1 | | |
| Little Sparrowhawk | *Acacia* sp. | 2 | | |
| unidentified nest (accipiter) | *Brachystegia glaucescens* | 1 | *Acacia nigrescens* | 1 |

[1] Nest shared with another raptor species.

[2] Reported

**Table 9** Proportion of total of each nest site type in the LSA and CLSA in 1995 and 1996

| **Nest site** | **LSA** | | **CLSA** | |
|---|---|---|---|---|
| | **No.** | **%** | **No.** | **%** |
| cliff | 7 | 11.9 | -- | -- |
| | | | | |
| *Adansonia digitata* | 26 | 44.1 | 10 | 66.7 |
| *Terminalia sericea* | 6 | 10.2 | -- | -- |
| *Acacia nigrescens* | 8 | 13.6 | 4 | 26.7 |
| *Acacia tortilis* | 1 | 1.7 | -- | -- |
| *Acacia* sp. | 2 | 3.4 | -- | -- |
| *Brachystegia glaucescens* | 6 | 10.2 | -- | -- |
| *Kirkia acuminata* | 1 | 1.7 | 1 | 6.7 |
| *Lonchocarpus capassa* | 1 | 1.7 | -- | -- |
| *Afzelia quanzensis* | 1 | 1.7 | -- | -- |

**Table 10.** Results of G and S statistics testing for regularity and randomness in large nest spacing in the LSA. The tests were for all nest sites, all nest sites used in the study period, for three most common nesting eagle species nest sites, and these species' nest sites in use during the study period.

| **Test assumptions** | **S** | **G** | **n** |
|---|---|---|---|
| *All nests in use* | | | |
| 1995 | 2.27 | 0.44 | 21 |
| 1996 | 0.79 | 0.58 | 19 |
| **All used nests** | **1.07** | **0.56** | **29** |
| *Consp. nests in use* | | | |
| **African Hawk Eagle** | | | |
| 1995 | 0.08 | 0.97 | 7 |
| 1996 | 0.31 | 0.90 | 9 |
| **All used nests** | **0.26** | **0.89** | **11**[*] |
| **Black Eagle** | | | |
| 1995 | 0.48 | 0.87 | 5 |
| 1996 | 0.65 | 0.81 | 4 |
| **All used nests** | **0.28** | **0.89** | **6**[*] |
| **Crowned Eagle** | | | |
| **All used nests** | **1.10** | **0.73** | **5** |

[*] Two nests in one territory used in different years, both included in analysis.

**Table 11.** Mean intra- and interspecific nearest used-nest distances of African Hawk, Black and Crowned Eagles, and all large raptors in the LSA in 1995 and 1996. Crowned Eagles did not breed in annual cycles, thus yearly breeding figures are not included. P values are for: 1) Paired t-tests, and 2) Wilcoxon Matched Pairs Test testing for significant differences in nearest internest distances between inter- and intraspecific pairs.

| **Species** | **Mean nearest internest distance in km (±SD)** | | | |
|---|---|---|---|---|
| | **Intraspecific** | **Interspecific** | **n** | **P (test)** |
| **African Hawk Eagle** | | | | |
| 1995 | 3.14 (±0.45) | 1.83 (±1.02) | 7 | <0.005 (1) |
| 1996 | 2.45 (±0.63) | 1.67 (±0.95) | 9 | <0.025 (1) |
| **Combined** | **2.6 (±0.66)** | **1.61 (±0.88)** | **11*** | **<0.005 (1)** |
| **Black Eagle** | | | | |
| 1995 | 3.54 (±1.1) | 1.02 (±0.93) | 5 | <0.05 (2) |
| 1996 | 4.83 (±1.9) | 1.29 (±0.9) | 4 | =0.02 (1) |
| **Combined** | **3.54 (±1.1)** | **1.02 (±0.93)** | **5** | **<0.05 (2)** |
| **Crowned Eagle** | | | | |
| **All used nests** | **2.28 (±1.09)** | **0.83 (±0.3)** | **5** | **<0.05 (2)** |
| **All large raptors** | | | | |
| 1995 | 4.27 (±1.90) | 1.50 (±1.18) | 17 | <0.001 (2) |
| 1996 | 3.14 (±1.93) | 1.21 (±0.69) | 18 | <0.001 (2) |
| **Combined** | **3.38 (±1.79)** | **1.03 (±0.59)** | **26** | **=0.000 (2)** |

*Two nests in one territory included.

**Table 12.** Number of breeding successes and failures at eagle and Gymnogene nests in the LSA at nests less than. and further than 1km from nearest non-conspecific nest site in use during the study period in the LSA Only breeding attempts where the out was known were included

| Internest dist.<1km | | Internest dist.>1km | |
|---|---|---|---|
| **No. successes** | **No. failures** | **No. successes** | **No. failures** |
| 12 | 4 | 9 | 12 |
| **% of total attempts** | | | |
| 32.4 | 10.8 | 24.3 | 32.4 |

**Table 13.** Number of individuals, and percentage of total number of prey individuals made up by each prey category from Barn Owl diets in the LSA (from Davison 1996)

| Species | No. of Individuals Collected | % of Total Prey Individuals |
|---|---|---|
| **Mammals** | | |
| *Tatera leucogaster* | 339 | 12.0 |
| *Steatomys pratensis* | 140 | 5.0 |
| *Saccostomus campestris* | 59 | 2.1 |
| *Mastomys natalensis coucha* | 994 | 35.0 |
| *Aethomys namaquensis* | 35 | 1.2 |
| *Aethomys chrysophilus* | 3 | 0.1 |
| *Thallomys paedulcus* | 12 | 0.4 |
| *Acomys spinosissimus* | 1 | >0.1 |
| *Lemniscomys rosalia* | 3 | 0.1 |
| Bathyergidae | 2 | >0.1 |
| Crocidura spp | 421 | 14.9 |
| Michrochiroptera | 3 | 0.1 |
| **Sub-total** | **2012** | **71.0** |
| **Birds** | | |
| *Quelea quelea* | 116 | 4.1 |
| Ploceinae | 6 | 0.2 |
| Estrildinae | 3 | 0.1 |
| Viduinae | 1 | >0.1 |
| Laniidae | 1 | >0.1 |
| **Sub-total** | **127** | **4.5** |
| **Invertebrates** | | |
| Solipugidae | 463 | 16.3 |
| Orthoptera | 209 | 7.4 |
| Acrididae | 5 | 0.2 |
| Pamphagidae | 9 | 0.3 |
| Scarabaeidae | 7 | 0.3 |
| Tenebrionidae | 2 | >0.1 |
| Cerambycidae | 1 | >0.1 |
| **Sub-total** | **696** | **24.5** |
| **Total** | **2835** | **100.0** |

**Table 14** Habitat types identified in the prey Transects 1 and 2 in the LSA.

| Habitat type | Transect | Description |
|---|---|---|
| 1 | 1 | Steeply sloping, grass, small trees/shrubs, few boulders. |
| 2 | 1 | Rocky slope, dense shrubs/understorey, few large trees. |
| 3 | 1 | Cliff (5-10m high, cracks and crevices). |
| 4 | 1-2 | Dense grass, scattered large boulders, flat, scattered shrubs. |
| 5 | 1-2 | Low, long, bare sandstone rock outcrops, gulleys with dense *Androstachys johnsonii*. |
| 6 | 1-2 | Flat, open, sandy usually, mature trees (usually *Brachystegia glaucescens*) forming fairly to very open canopy, sometimes scattered rocks. |
| 7 | 2 | Flat, sandy, scattered boulders or low sandstone outcrops, dense shrubs and small to medium trees. |
| 8 | 1 | Flat rock, deep cracks/crevices, little vegetation, some *Androstachys johnsonii* shrubs, *Brachystegia glaucescens*. |
| 9 | 1 | Flat to gently sloping, *Colophospermum mopane*, *Adansonia digitata*, *Combretum* spp., little or no grass cover, dense and scattered stands of shrubs, basaltic soils and rocks. |
| 10 | 1+2 | Slope, grass dense, scattered trees, *Adansonia digitata*, *Kirkia acuminata*, *Combretum* spp., no *Brachystegia glaucescens* or *Androstchys johnsonii*. |
| 11 | 1+2 | Flat to undulating, low outcrops of sandstone rocks up to 5m high, *Brachystegia glaucescens* cover only, medium to dense. |
| 12 | 1 | Dense riverine. |

| | | |
|---|---|---|
| 13 | 1 | Incised small valley, thick grass, small drainage lines, rock outcrops, some large, often dense, mature tree stands |
| 14 | 1 | Scree slope of large koppie, large *Brachystegia glaucescens*, scattered boulders, some large |
| 15 | 2 | Small river valley, flat, dense grass cover, mostly *Terminalia sericea*, sandy substrate, scattered low sandstone outcrops |
| 16 | 2 | Sloping, stony ground or jumbled rocks, little grass cover, dense shrubs, often *Androstachys johnsonii* |
| 17 | 2 | Sandstone ridge, dense medium trees, often *Androstachys johnsonii* |

**Table 15** Average and average maximum numbers of hyrax (*H. brucei* and *P. capensis*) and Natal Francolin *F. natalensis* counted per quadrat (over 5 repetitions) per habitat class in transects 1 and 2 in the LSA.

| **Habitat class** | **Est. % area of LSA** | **Hyrax** | | **Natal Francolin** | |
|---|---|---|---|---|---|
| | | **Av. max . no. hyrax per quad.** | **Est. no. hyrax per habitat in LSA** | **Av. no. francolin per quad.** | **Est. no. N.Francolin per habitat in LSA** |
| 1 | 8.47 | 2.2 | **745** | 0.6 | **203** |
| 2 | 5.09 | 4.3 | **876** | 0.6 | **122** |
| 3 | 5.09 | 2.7 | **550** | 0.9 | **189** |
| 4 | 8.47 | 6.6 | **2236** | 0.5 | **169** |
| 5 | 10.17 | 6.2 | **2510** | 0.4 | **163** |
| 6 | 6.78 | 3.8 | **1017** | 0.3 | **68** |
| 7 | 11.86 | 2.7 | **1286** | 1.1 | **522** |
| 8 | 8.48 | 6.6 | **2239** | 1.3 | **434** |
| 9 | 10.17 | 0.0 | **0** | 0.2 | **69** |
| 10 | 1.70 | 0.0 | **0** | 0.0 | **0** |
| 11 | 13.56 | 4.0 | **2170** | 1.1 | **618** |
| 12 | 1.70 | 0.0 | **0** | 1.2 | **82** |
| 13 | 1.70 | 1.0 | **68** | 0.8 | **54** |
| 14 | 1.70 | 6.0 | **408** | 0.8 | **54** |
| 15 | 1.70 | 0.0 | **0** | 0.6 | **41** |
| 16 | 1.70 | 2.0 | **136** | 1.7 | **116** |
| 17 | 1.70 | 8.0 | **544** | 1.0 | **68** |
| **Total** | | | **14785** | | **2972** |

Av. no. individuals per quad; hyrax = 3.76 (SD±2.67)
Natal Francolin = 0.74 (SD±0.92)

**Table 16** Mean estimated territory sizes of eagles in the LSA and CLSA.

| Species | Locality | n | Mean (km$^2$) | ±SD (km$^2$) | Range (km$^2$) |
|---|---|---|---|---|---|
| African Hawk Eagle | LSA | 7 | 10.7 (8.4)* | 3.5 | 5.8 - 16.8 |
| | CLSA | 1 | 23.0 | -- | -- |
| Crowned Eagle | LSA | 3 | 7.8 | 1.4 | 5.8 - 9.6 |
| Black Eagle | LSA | 4 | 7.7 | 1.0 | 5.9 - 8.8 |
| African Fish Eagle | LSA | 2 | 33.8 | 1.0 | 32.8 - 34.8 |

* Average territory size with territories 7 and 9 excluded

**Table 17.** Results of *S* and *G* statistics which test for regularity of the spacing of sightings of small raptors in the LSA in 1995 and 1996 Where more than one sighting of a bird or a pair was thought to have been made, measurements to the nearest conspecific sighting were made from the central area of the sightings

| **Species** | ***S*** | ***G*** |
|---|---|---|
| Little Banded Goshawk | 1.048 | 0.596 |
| Gabar Goshawk | 0.988 | 0.488 |
| Ovambo Sparrowhawk | 0.341 | 0.839 |
| | | |
| Barred Owl | 0.523 | 0.804 |
| Pearlspotted Owl | 2.128 | 0.192 |
| Barn Owl | 1.038 | 0.677 |
| Spotted Eagle Owl | 0.766 | 0.652 |

**Table 19** Activities of raptors in the continuum of survival requirements from meeting energy requirements to reproduction, and the activities and requirements involved in each stage. Highlighted factors indicate direct reliance on food.

| Function | Activities involved | Requirements |
|---|---|---|
| 1) Energy provision | Hunting, recognition of prey, capture, ingestion, digestion. | Hunting skills, morphological adaptations to hunting. |
| 2) Securing resources | Territory formation & maintenance. | Aggressive defence of prey territory, **physical condition.** |
| 3) Procurement of mate | Courtship, assessment of territorial resources and mate fitness, defensive aggression. | Territory maintenance, **sexual maturity**, aggression. |
| 4) Reproduction | Courtship, nest building, incubation. | Nest site, **gamete and egg production**, instinctive response to environmental variables. |
| 5) Chick rearing | Incubation, **feeding**, fledging, **juvenile independence**. | **Energy, food procurement**, pair bonding, **feather development**, learning of flight and **hunting skills**. |

**Table 20** Feeding guilds of raptors in the LSA. Species are assigned to guilds based on the dominant prey overall. Parentheses indicate that the guild prey designation occurred often in the species' diet, but was not dominant overall. Question marks indicate the category was based on predation attempts seen, and/or from the literature records. Species in more than one guild, without parentheses or question marks, indicate equal proportions of more than one prey type in the diet.

| **Guild description** | **Raptor species** |
|---|---|
| Hyrax feeders; | |
| | Black Eagle |
| | Crowned Eagle |
| | (African Hawk Eagle) |
| Antelope feeders, | Crowned Eagle |
| Bird feeders, | |
| - francolin | African Hawk Eagle |
| | Tawny Eagles? |
| - small (mainly Passerine) birds | Little Sparrowhawk |
| | Little Banded Goshawk |
| | Ovambo Sparrowhawk |
| | Gabar Goshawk |
| | African Goshawk |
| | Peregrine Falcon |
| Reptile feeders, | |
| - snakes, | Brown Snake Eagle |
| - large reptiles | Brown Snake Eagle |
| | (Crowned Eagle) |
| | (African Hawk Eagle) |
| | (Tawny Eagle?) |
| | (Wahlberg's Eagle?) |
| | (Bateleur Eagle?) |
| - small reptiles | Little Banded Goshawk |
| | Barred Owl? |
| | Pearlspotted Owl? |
| Fish feeders; | Osprey |
| | African Fish Eagle |
| | Pel's Fishing Owl |
| Rodent/small mammal feeders; | Barn Owl |
| | Blackshouldered Kite |

| | |
|---|---|
| | Grass Owl? |
| Arthropod feeders, | Barred Owl?<br>Pearlspotted Owl?<br>Barn Owl<br>Wood Owl?<br>European Hobby<br>Spotted Eagle Owl |
| Generalists;<br>(no/variable prey preferences); | Wahlberg's Eagle |
| Carrion feeders; | Bateleur Eagle<br>Tawny Eagle |

## List of Figures.

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**Figure 4b** Raptor breeding diversities versus log. area in three latitudinal zones in Africa (data from Macdonald & Gargett 1984). Regression line and 955 and 99.9% fudicial limits are given.

**Figure 5** Triangulation method of estimating nest heights.

**Figure 6a-b** Aspects of ground at nest trees or sites in the LSA (a) and CLSA (b).

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**Figure 9b** Proportion of total mass of eagle prey remains made up by different prey species.

**Figure 9c.** Proportion of hyrax sizes in eagle diets in the LSA.

**Figure 10a-b** Proportion of total prey (by number) of each prey species of Barn Owls in the LSA (after Davison 1996)

**Figure 11a-b** Proportion of total prey mass made up by each Barn Owl prey species in the LSA (after Davison 1996).

**Figure 12a-e**. Mapped estimated territory boundaries (broken lines) of eagles in the LSA and CLSA (triangles =used and circles = disused nest sites).

**Figure 13**. Breeding chronology of eagles in the LSA from 1995 to April 1997 (lit.=from literature *i.e.* Maclean 1993; Steyn 1982).

**Figure 14**. Mean daily rates of aggression sightings per month of eagles in the LSA.

**Figure 15a**. Mean daily sighting rates of eagles in flight per month in the LSA.

**Figure 15b**. Mean daily sighting rates of small raptors per month in the LSA.

**Figure 16a-b**. Mean hourly flight sighting rates of eagles in the LSA (a) and CLSA (b).

**Figure 17a**. Mean daily rates of sightings of eagles in different weather conditions in the LSA (12a) and the CLSA (17b).

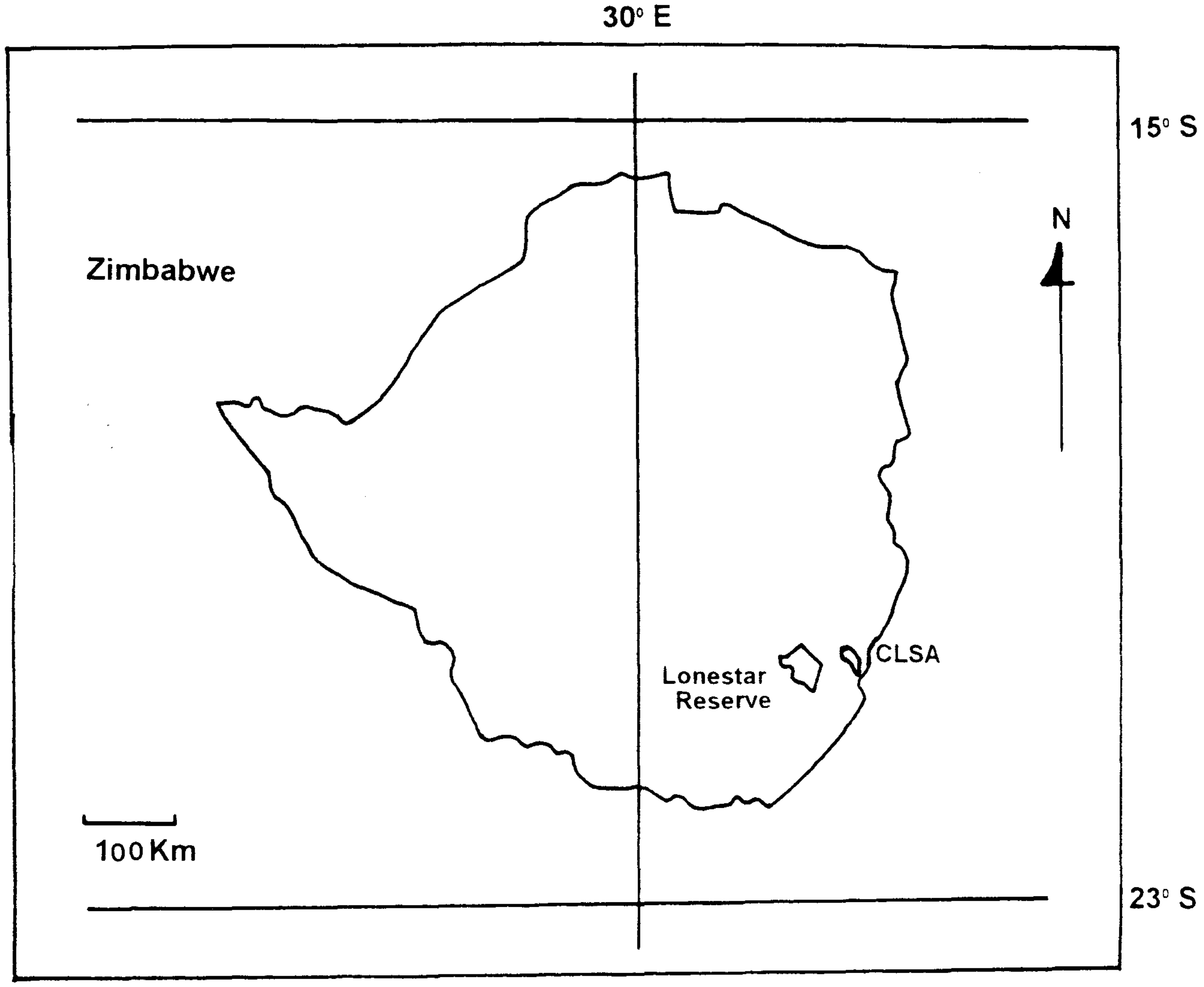


Figure 1a.

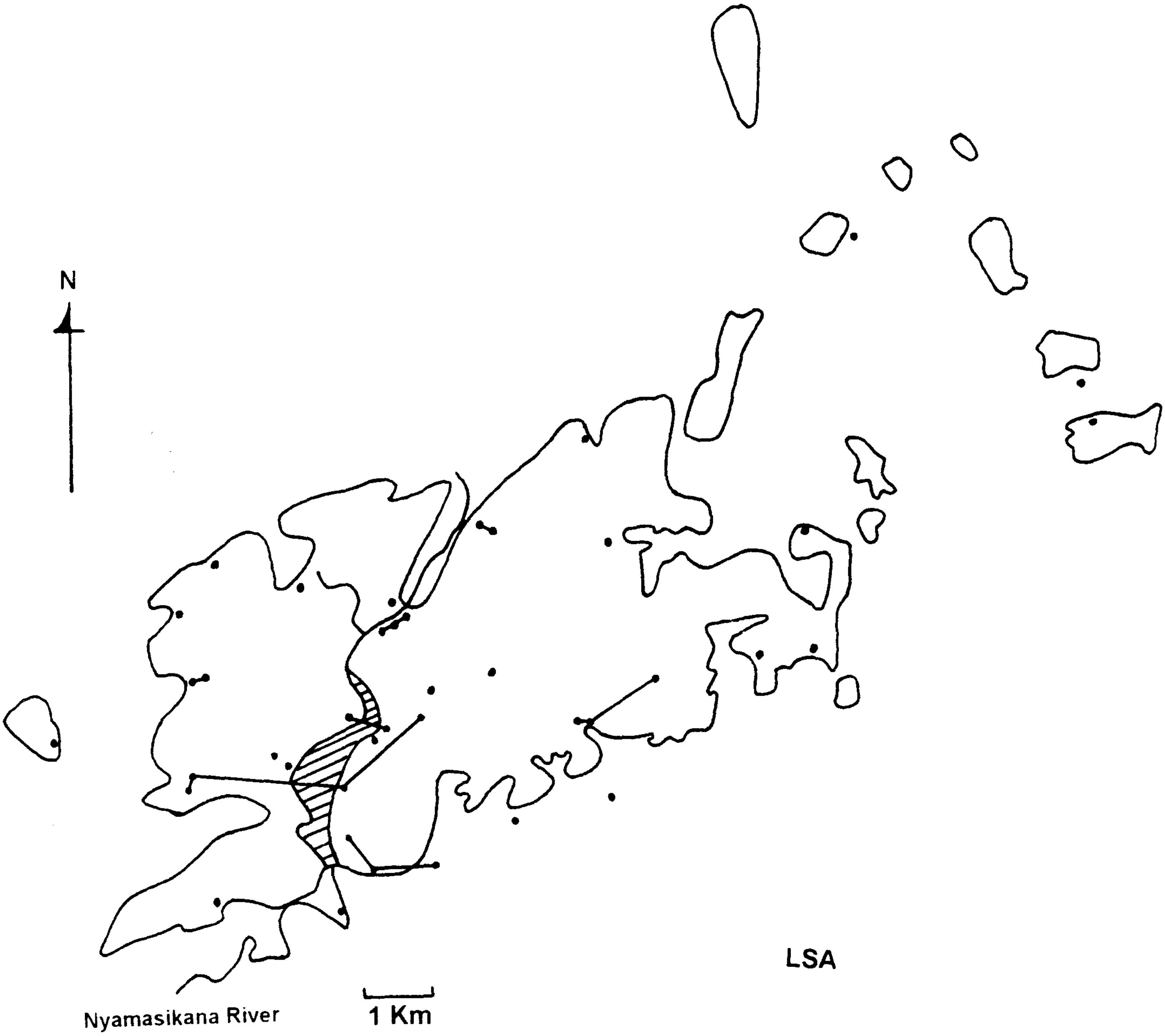


Figure 1b

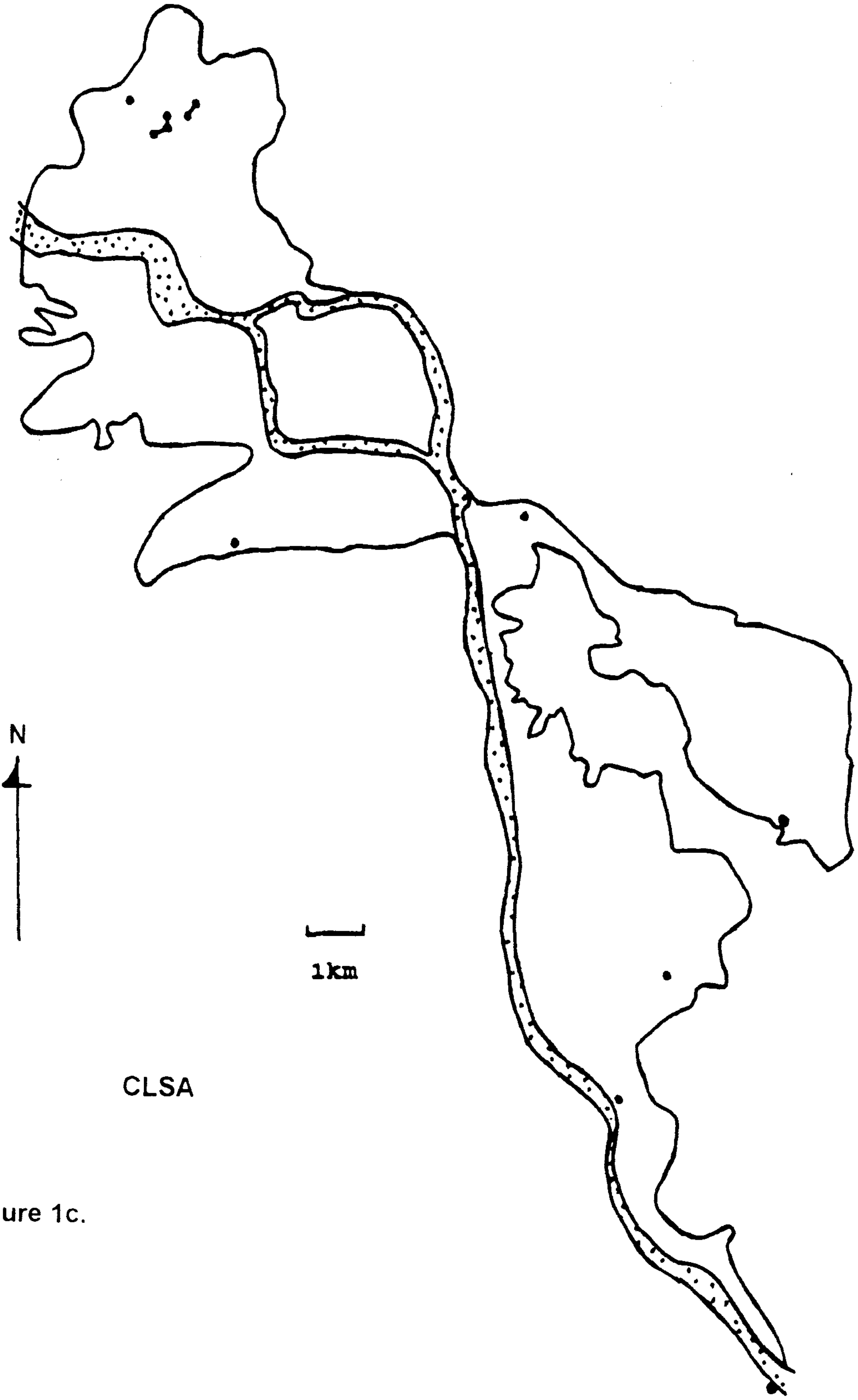


Figure 1c.

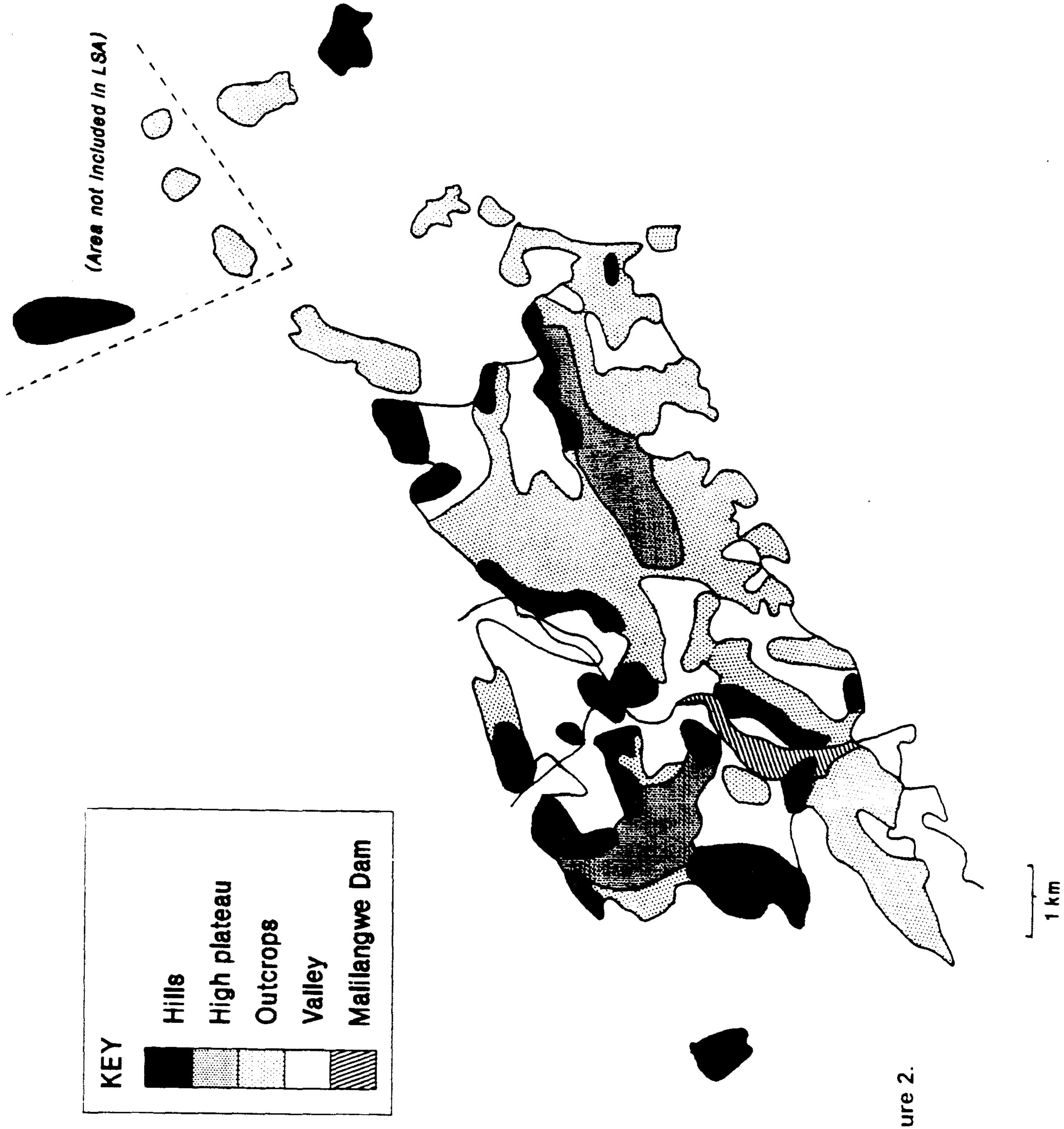
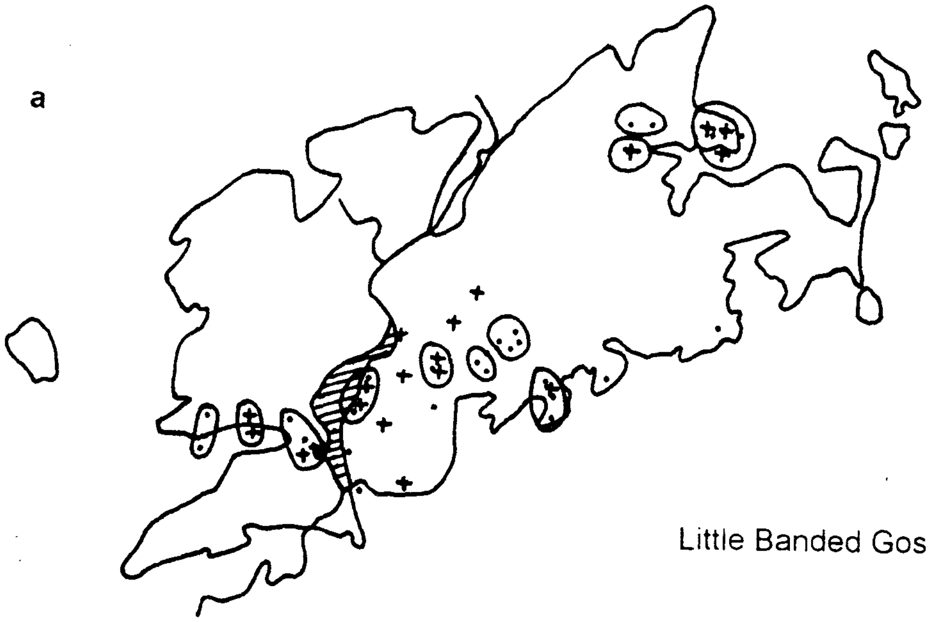

(Area not Included in LSA)
KEY
Hills
High plateau
Outcrops
Valley
Malilangwe Dam
1 km

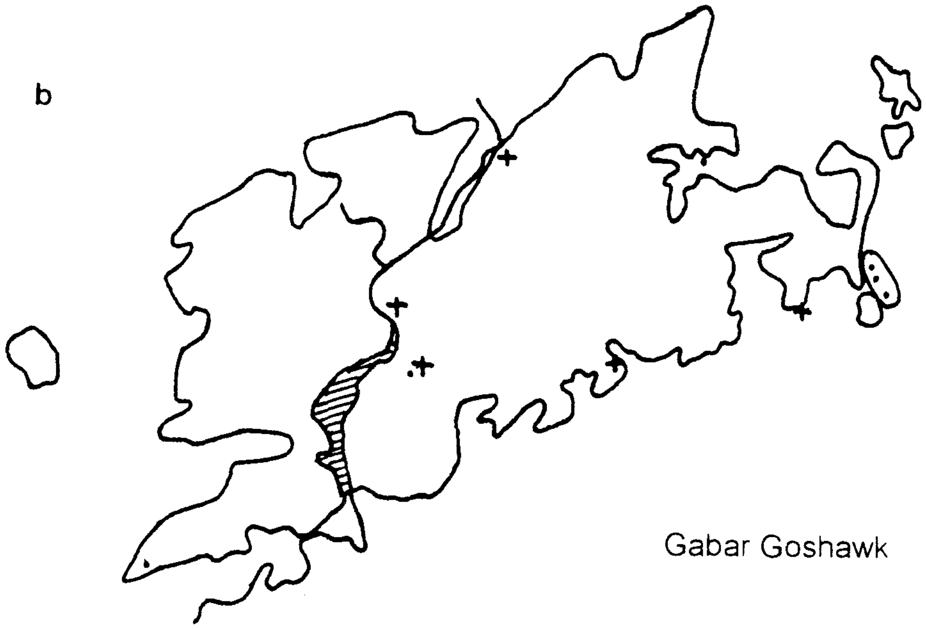
Figure 2.

a



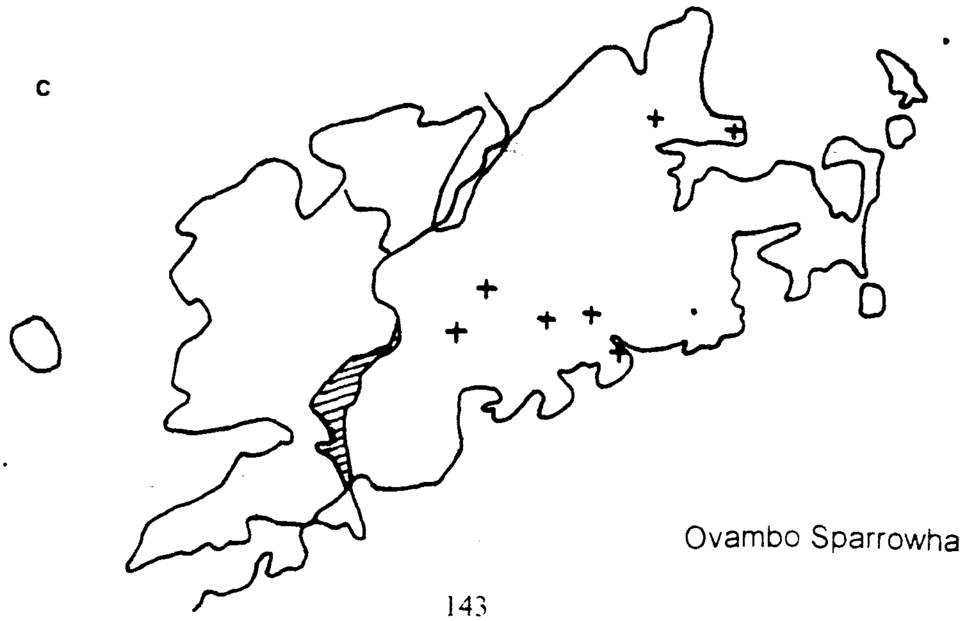
Little Banded Goshawk

b



Gabar Goshawk

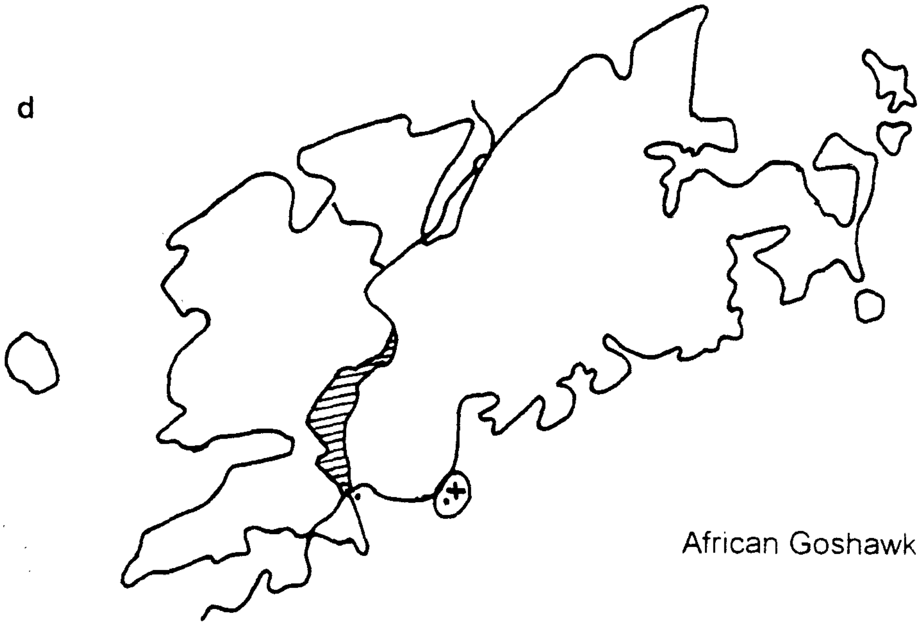
c



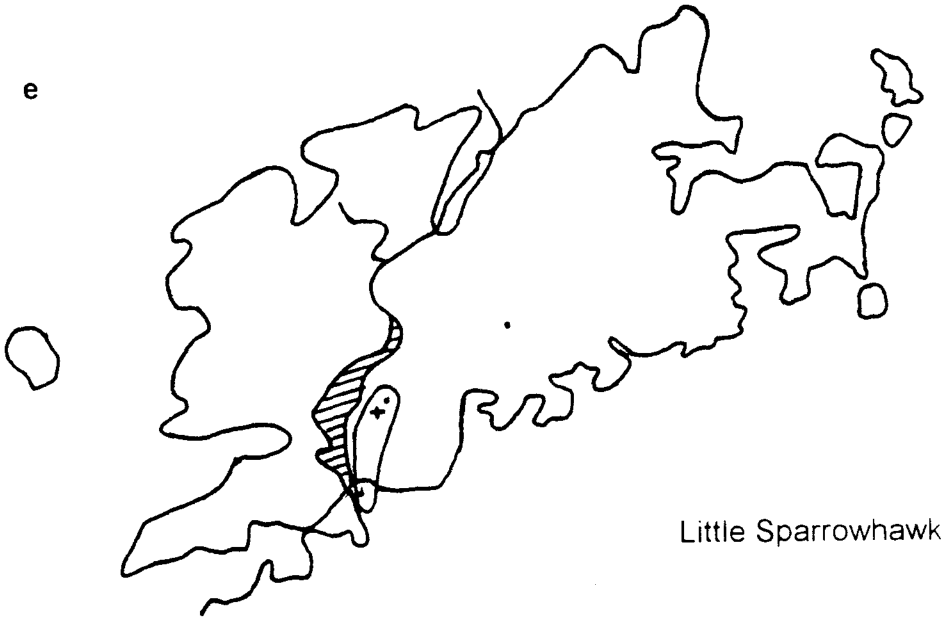
Ovambo Sparrowhawk

Figure 3.

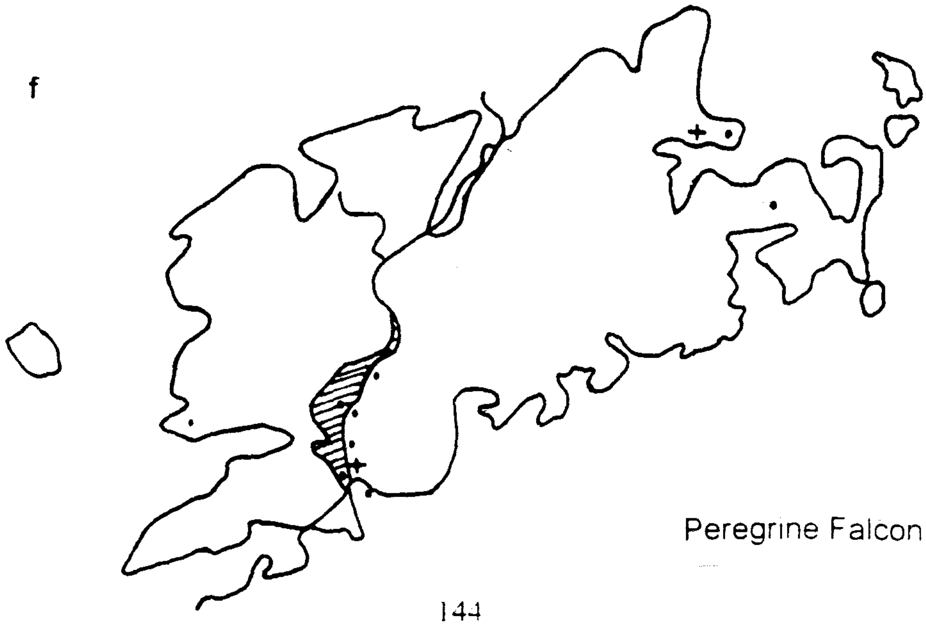
d



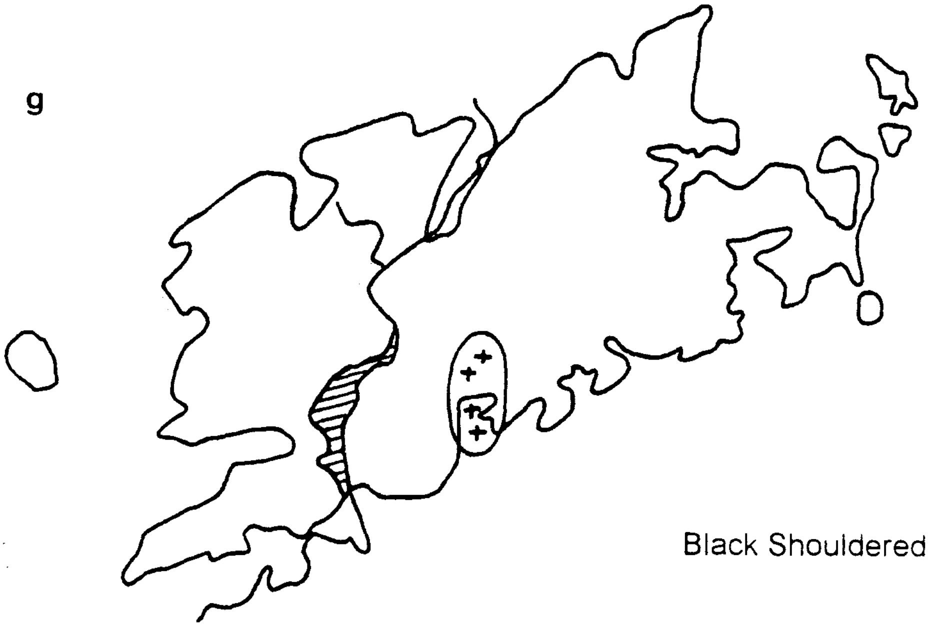
e



f

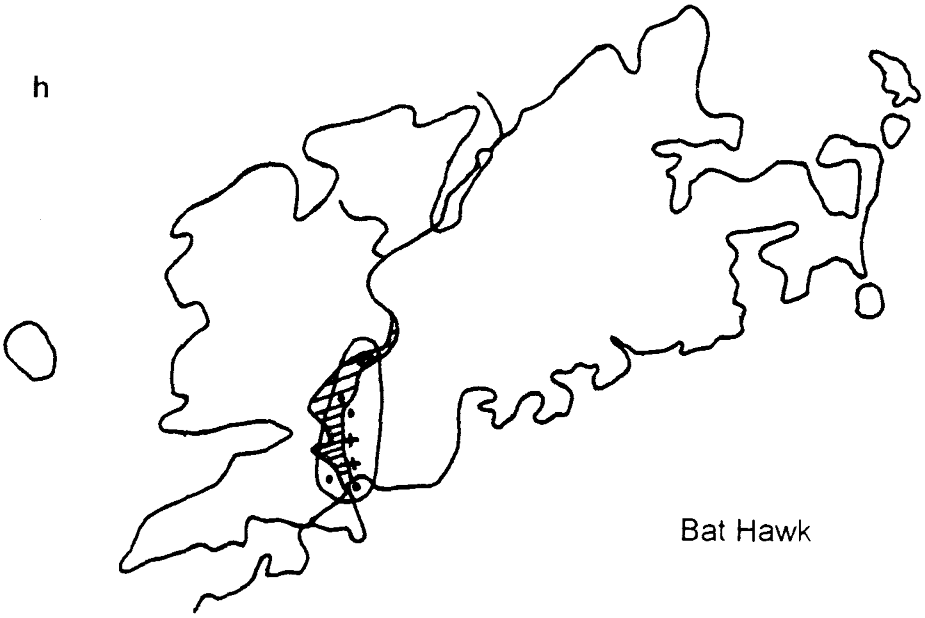


g



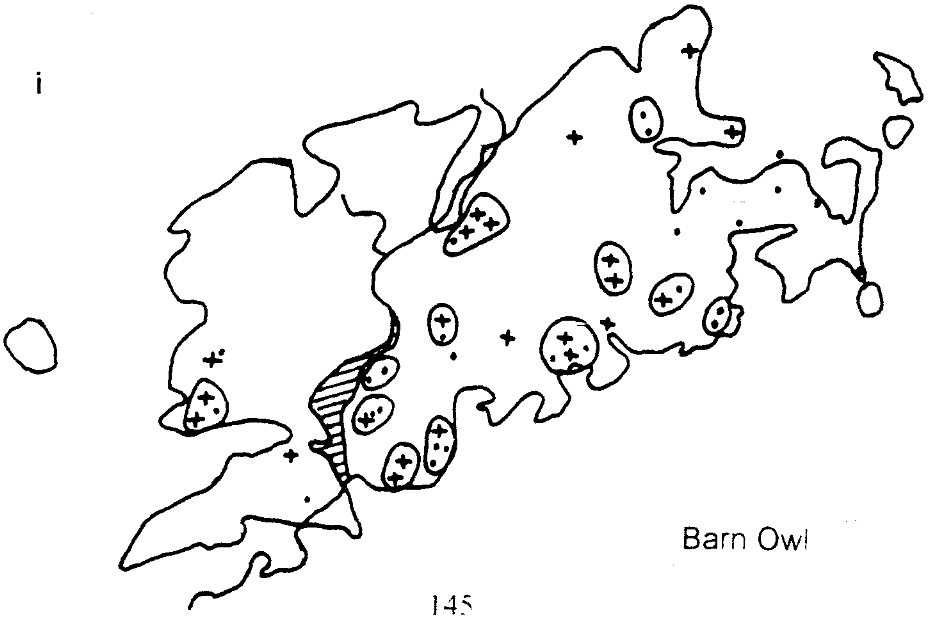
Black Shouldered Kite

h



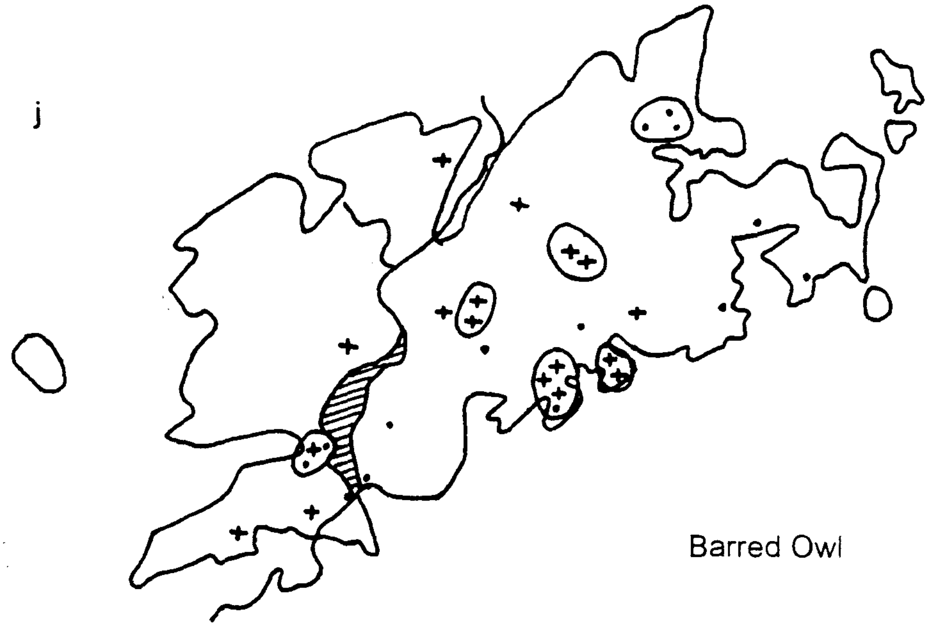
Bat Hawk

i

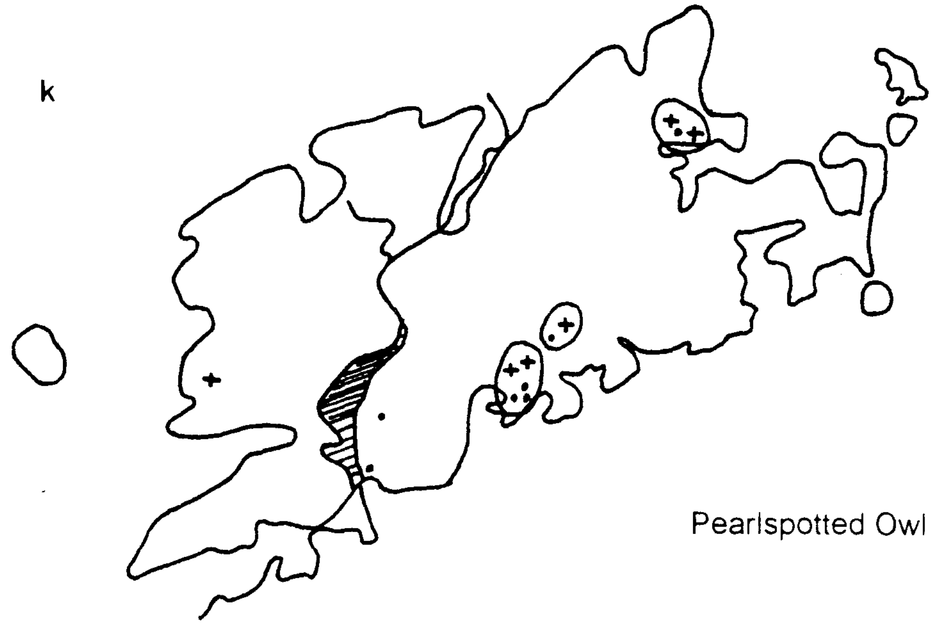


Barn Owl

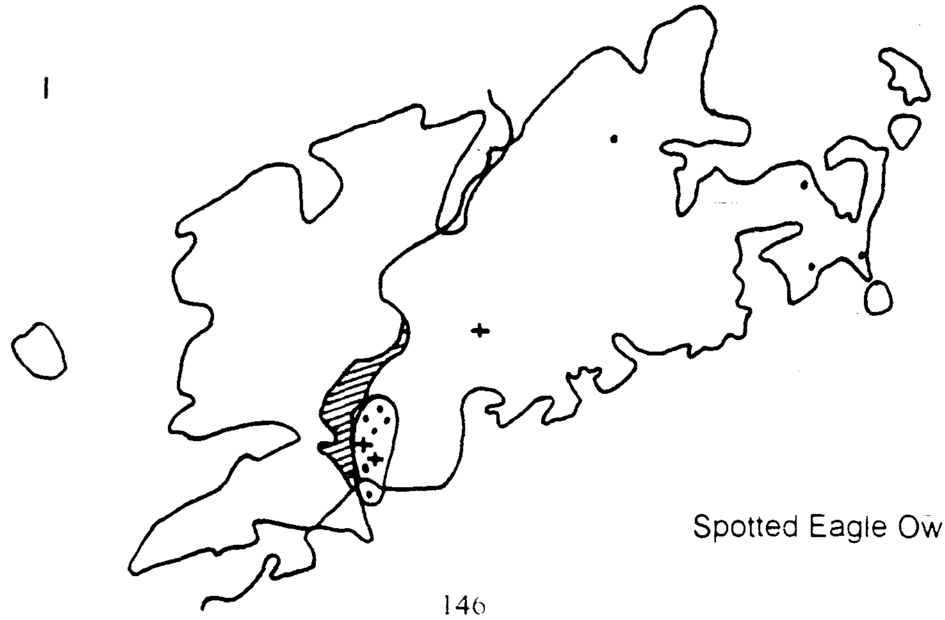
j


Barred Owl

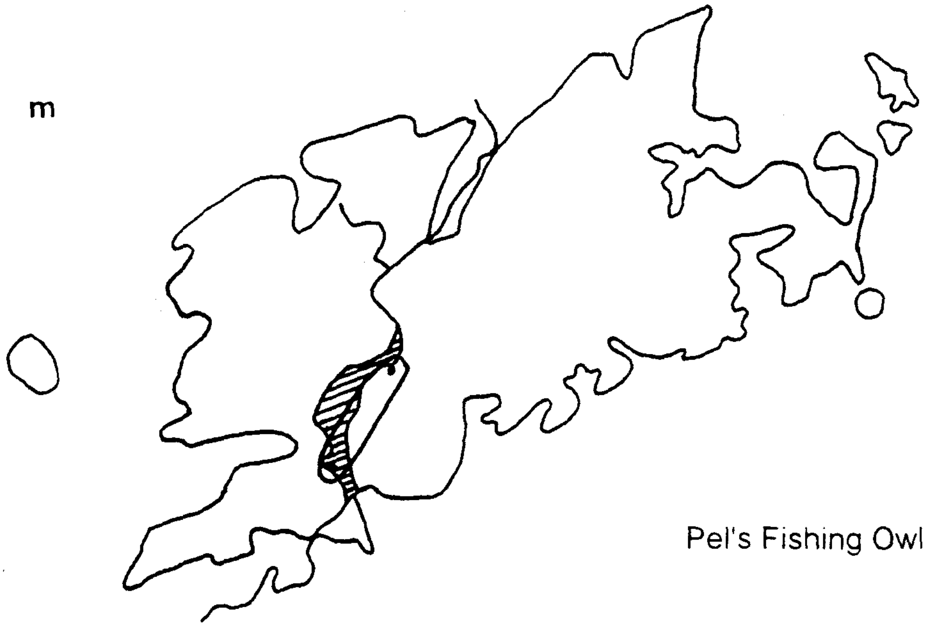
k


Pearlspotted Owl

l


Spotted Eagle Owl

m



Pel's Fishing Owl

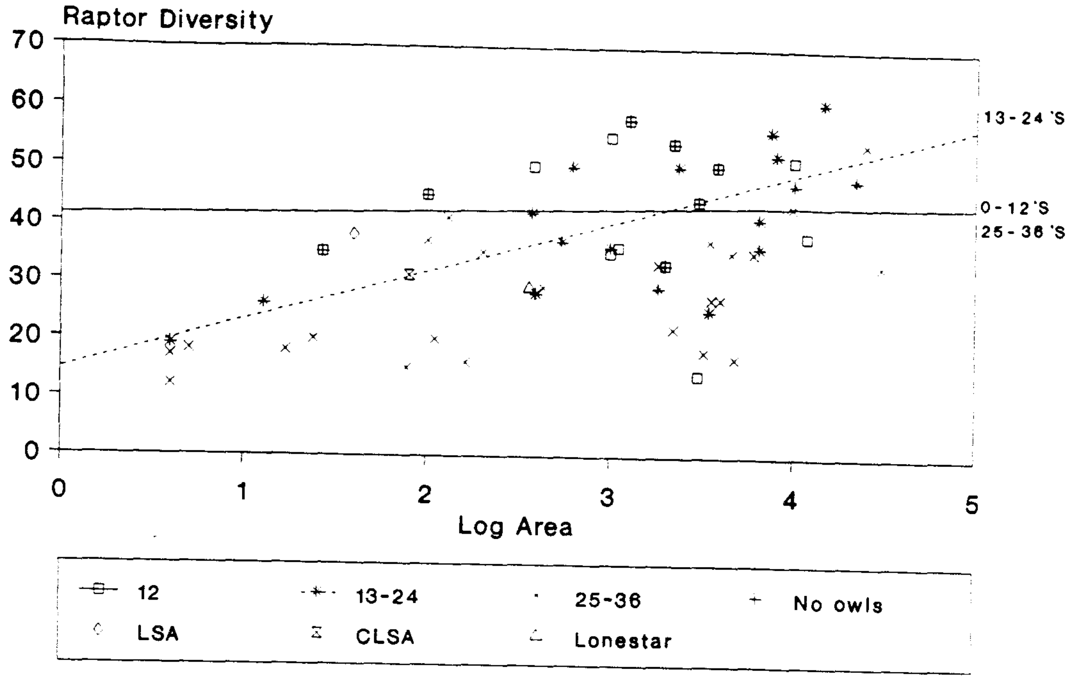

Raptor Diversity
70
60
50
40
30
20
10
0
0
1
2
3
4
5
Log Area
13-24'S
0-12'S
25-36'S
12
13-24
25-36
No owls
LSA
CLSA
Lonestar

Figure 4a.

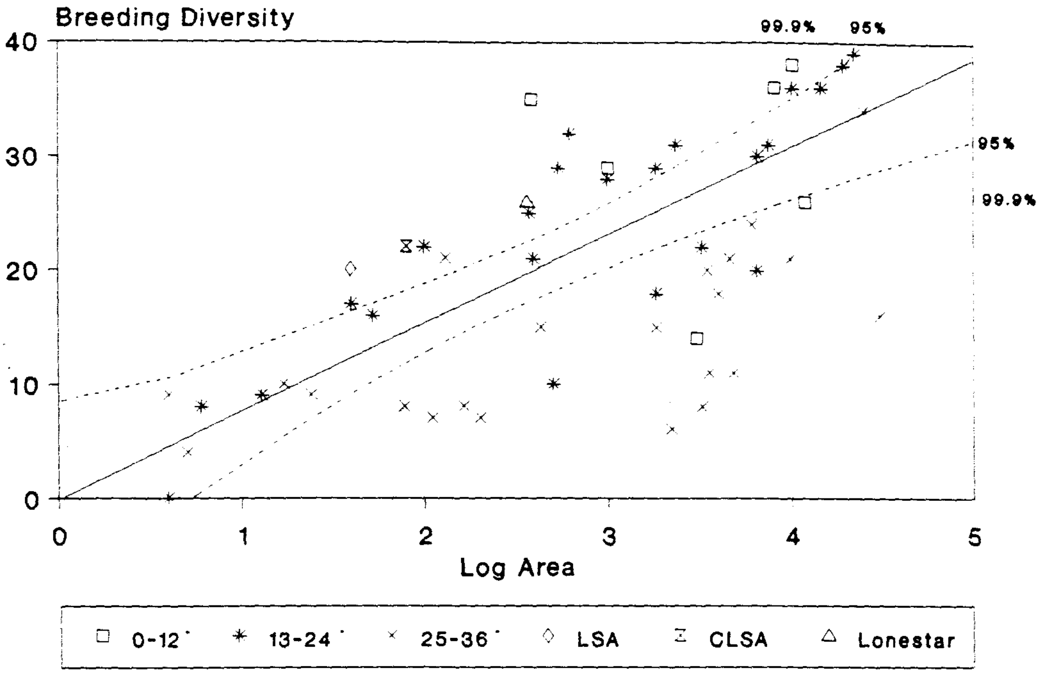

Breeding Diversity
40
30
20
10
0
0
1
2
3
4
5
Log Area
99.9%
95%
95%
99.9%
0-12'
13-24'
25-36'
LSA
CLSA
Lonestar

Figure 4b.

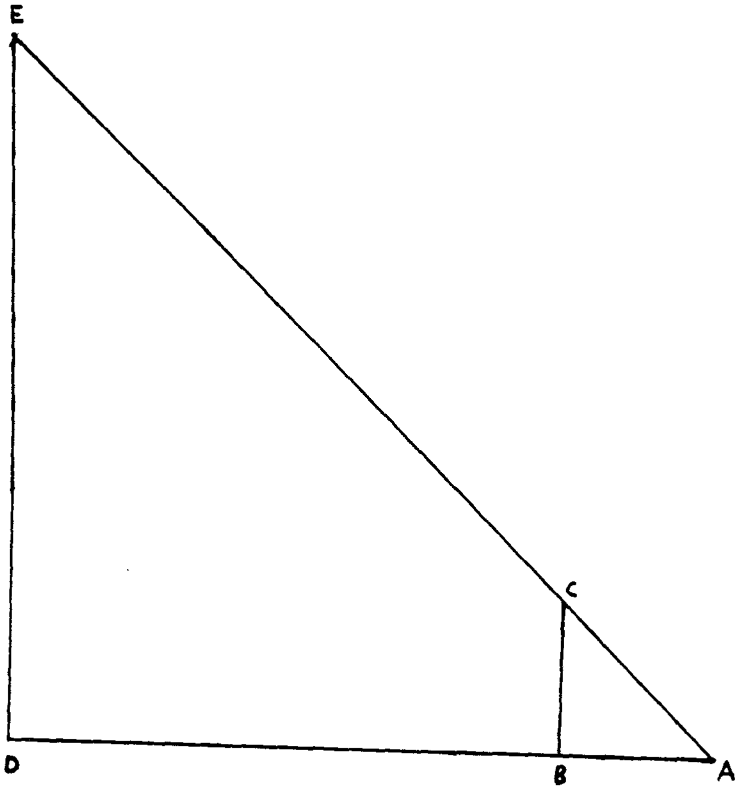


Figure 5.

A = Observor point
B = Base of sighting rod
C = Top of sighting rod
E = Nest
DE = Nest height from ground

AB = BC
Angle ABC = $90^0$
Therefore angles BCA & CAB = $45^0$
Angle ADE = $90^0$
Therefore angle DEA = $45^0$ (internal angles of a triangle = $180^0$)
Therefore AD = DE (two internal angles equal)

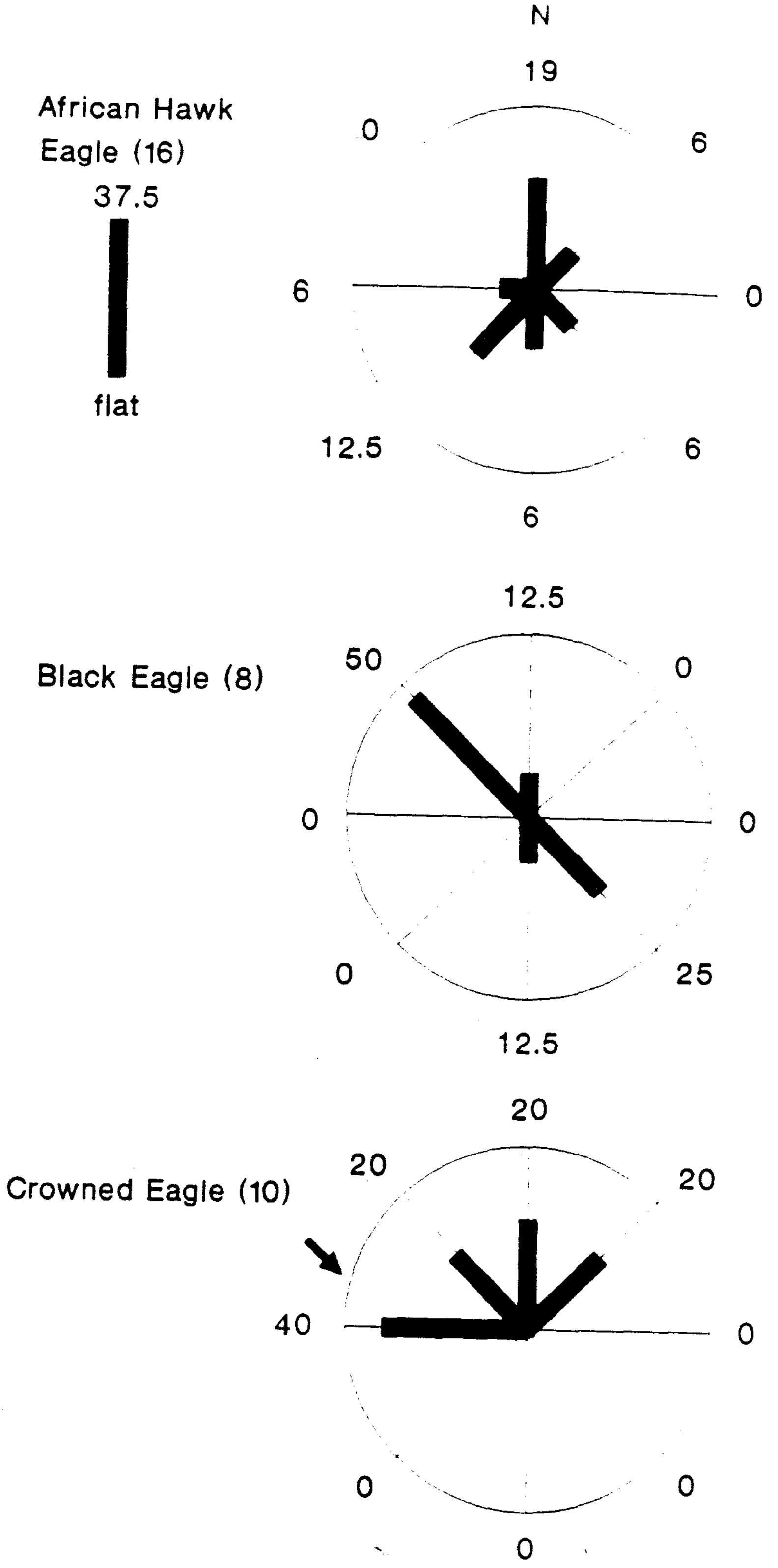


Figure 6a.

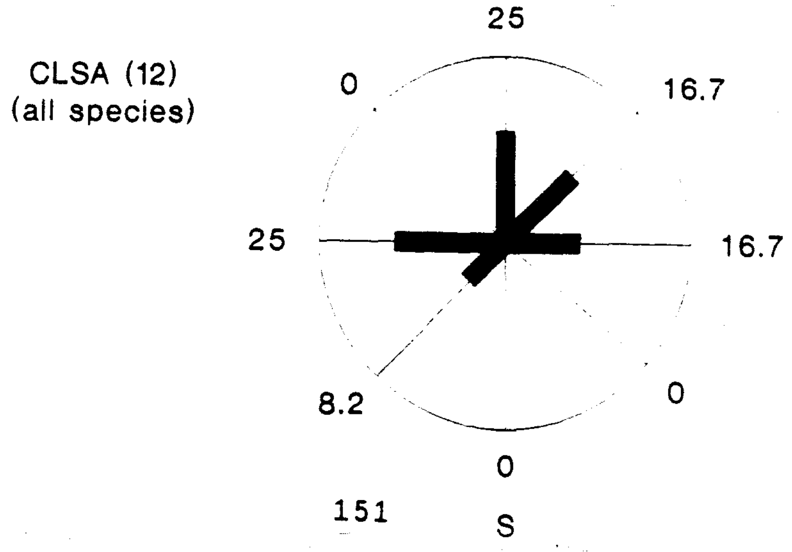


Figure 6b.

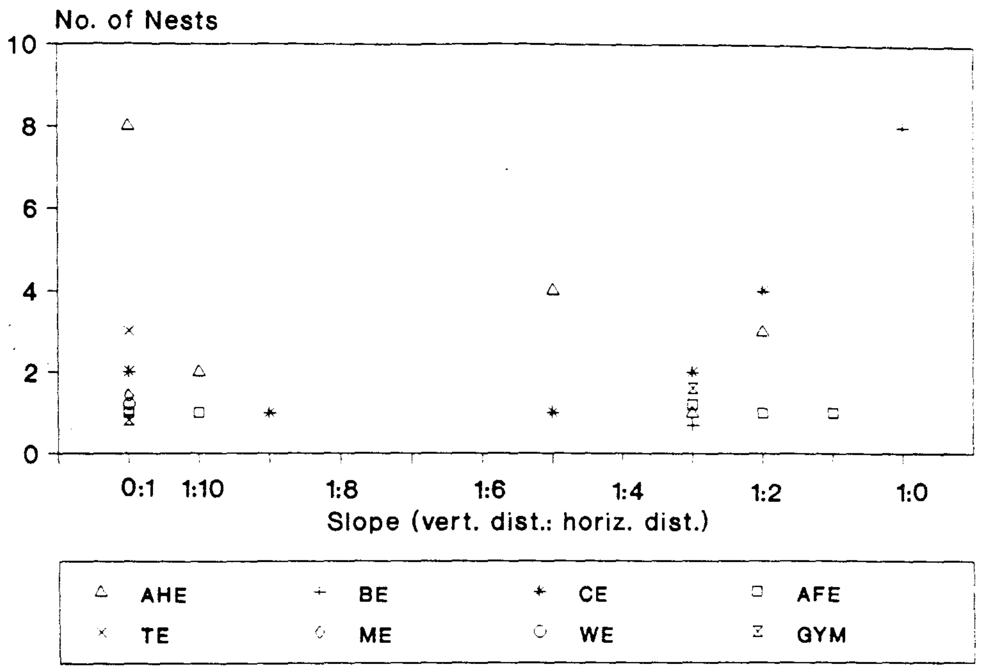

No. of Nests
10
8
6
4
2
0
0:1
1:10
1:8
1:6
1:4
1:2
1:0
Slope (vert. dist.: horiz. dist.)
AHE
BE
CE
AFE
TE
ME
WE
GYM

Figure 7.

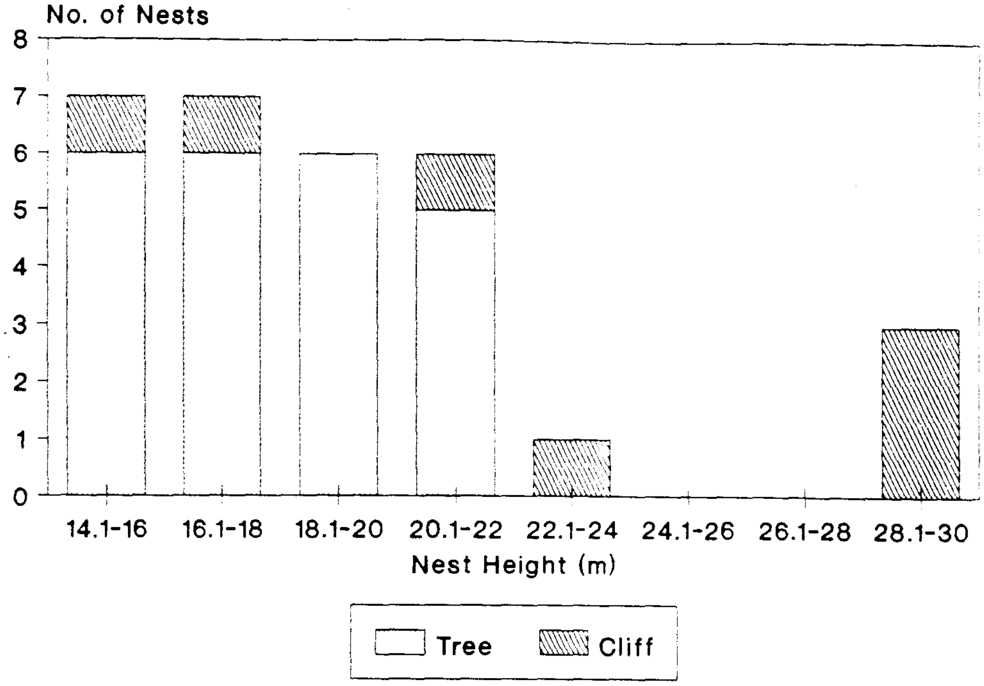

No. of Nests
8
7
6
5
4
3
2
1
0
14.1-16
16.1-18
18.1-20
20.1-22
22.1-24
24.1-26
26.1-28
28.1-30
Nest Height (m)
Tree
Cliff

Figure 8a.

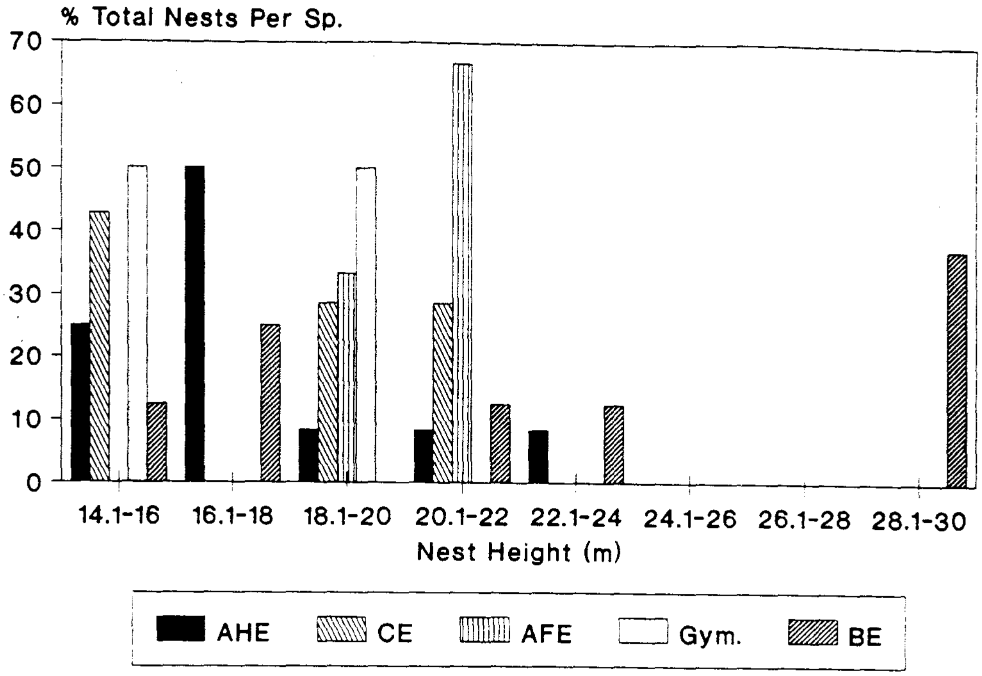

% Total Nests Per Sp.
70
60
50
40
30
20
10
0
14.1-16
16.1-18
18.1-20
20.1-22
22.1-24
24.1-26
26.1-28
28.1-30
Nest Height (m)
AHE
CE
AFE
Gym.
BE

Figure 8b.

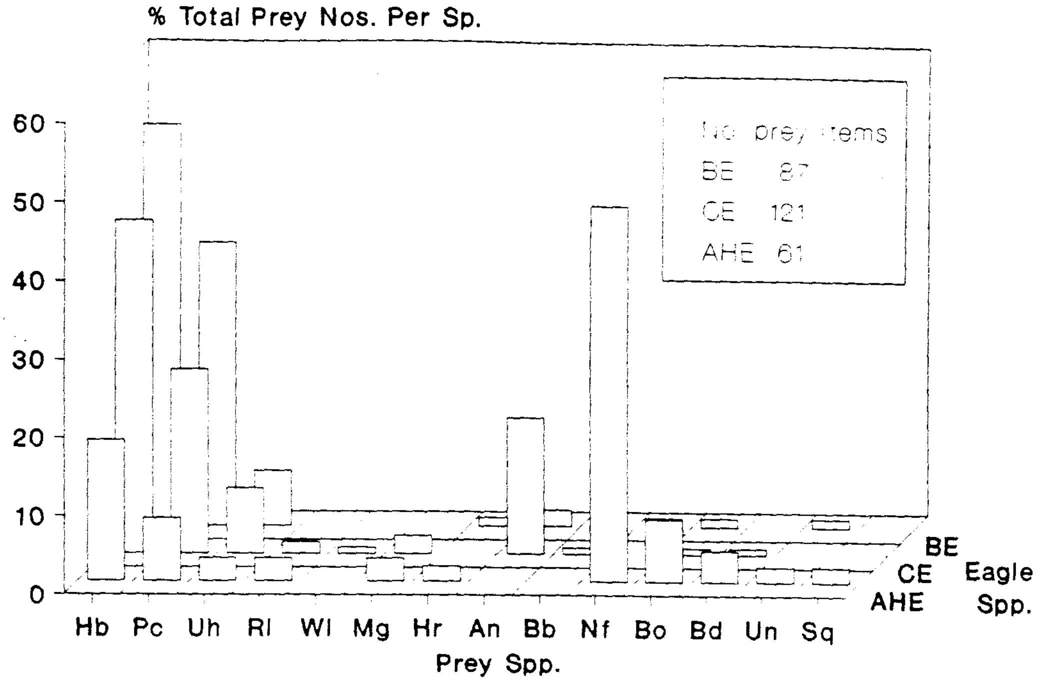
% Total Prey Nos. Per Sp.
60
50
40
30
20
10
0
No. prey items
BE 87
CE 121
AHE 61
Hb
Pc
Uh
Rl
Wl
Mg
Hr
An
Bb
Nf
Bo
Bd
Un
Sq
Prey Spp.
BE
CE
AHE
Eagle Spp.

Figure 9a.

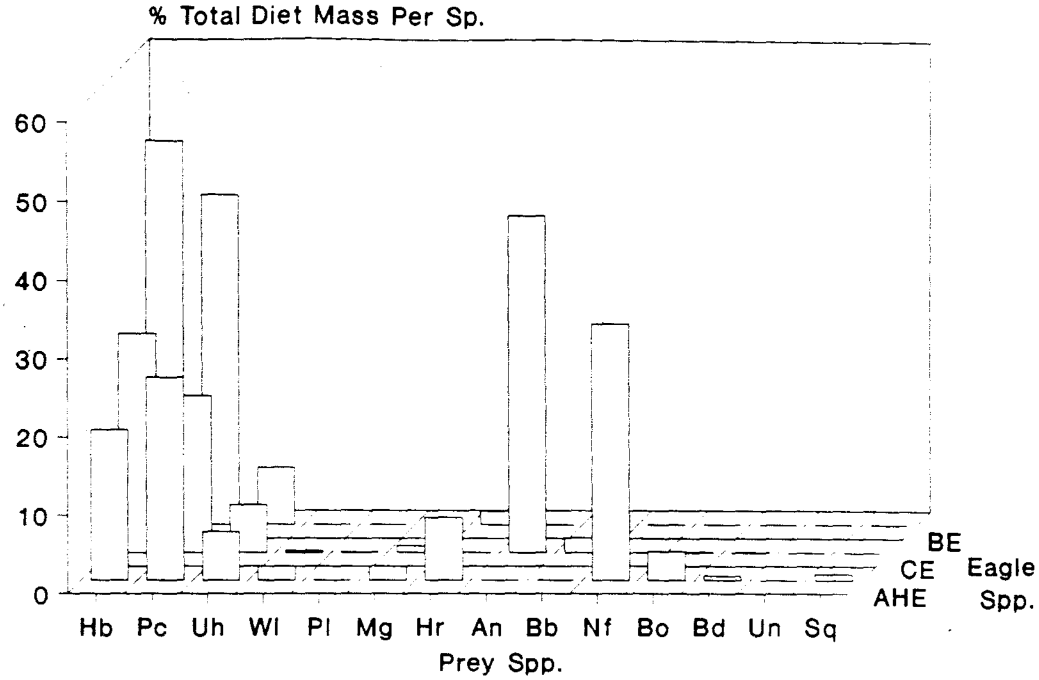

% Total Diet Mass Per Sp.
60
50
40
30
20
10
0
Hb
Pc
Uh
Wl
Pl
Mg
Hr
An
Bb
Nf
Bo
Bd
Un
Sq
Prey Spp.
BE
CE
AHE
Eagle Spp.

Figure 9b.

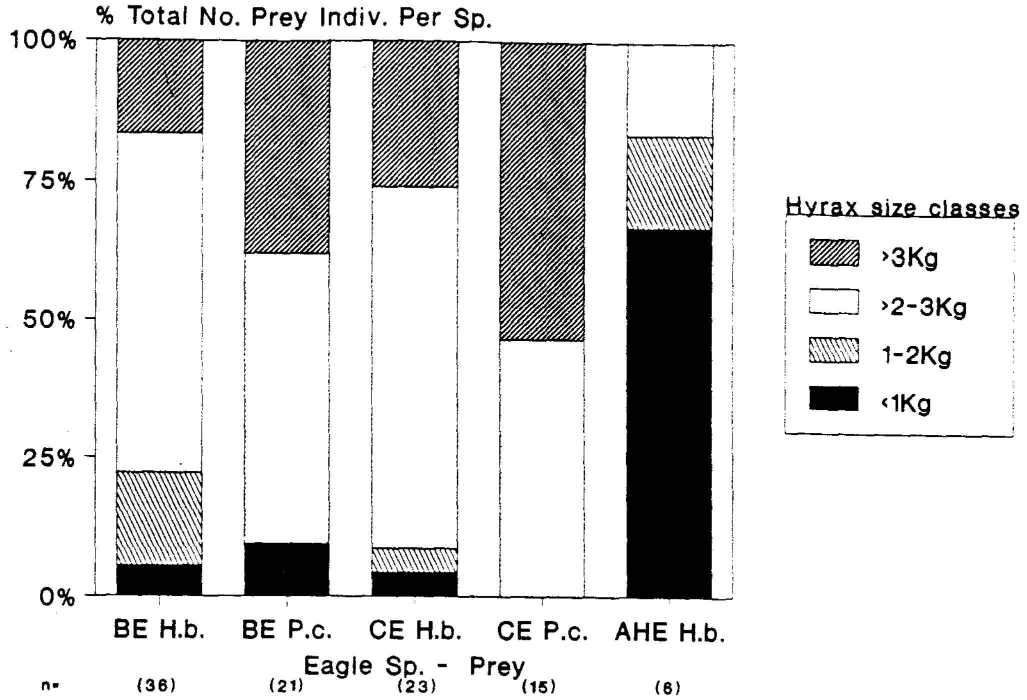

% Total No. Prey Indiv. Per Sp.
100%
75%
50%
25%
0%
BE H.b.
BE P.c.
CE H.b.
CE P.c.
AHE H.b.
Eagle Sp. - Prey
n=
(36)
(21)
(23)
(15)
(6)
Hyrax size classes
>3Kg
>2-3Kg
1-2Kg
<1Kg

Figure 9c.

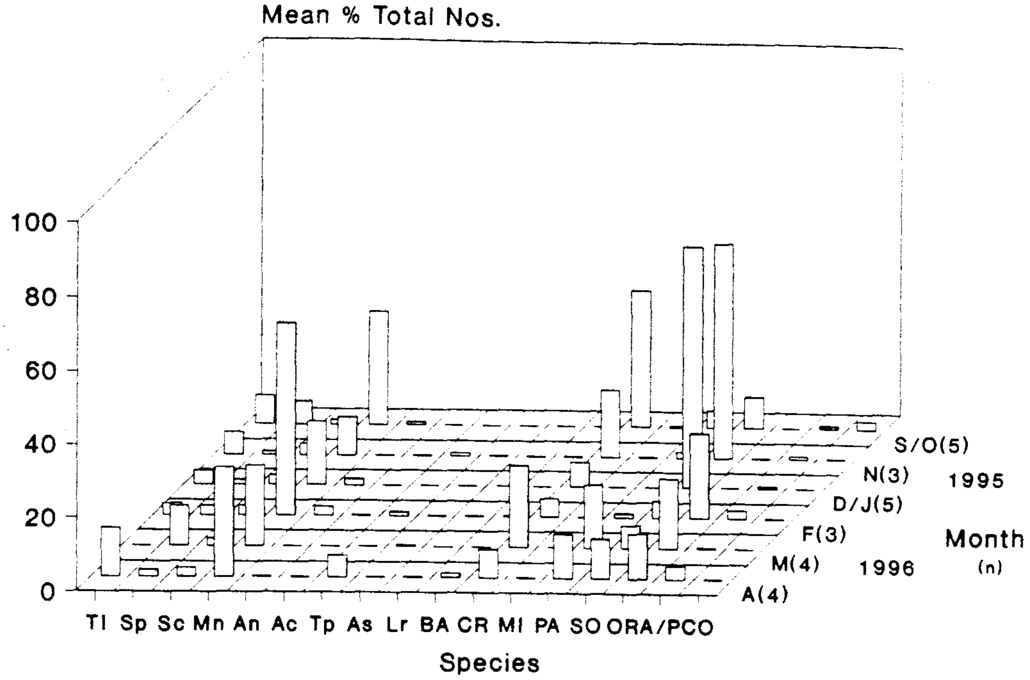

Mean % Total Nos.
100
80
60
40
20
0
Tl
Sp
Sc
Mn
An
Ac
Tp
As
Lr
BA
CR
Ml
PA
SO
ORA/PCO
Species
S/O(5)
N(3)
1995
D/J(5)
F(3)
Month
(n)
M(4)
1996
A(4)

Figure 10a.

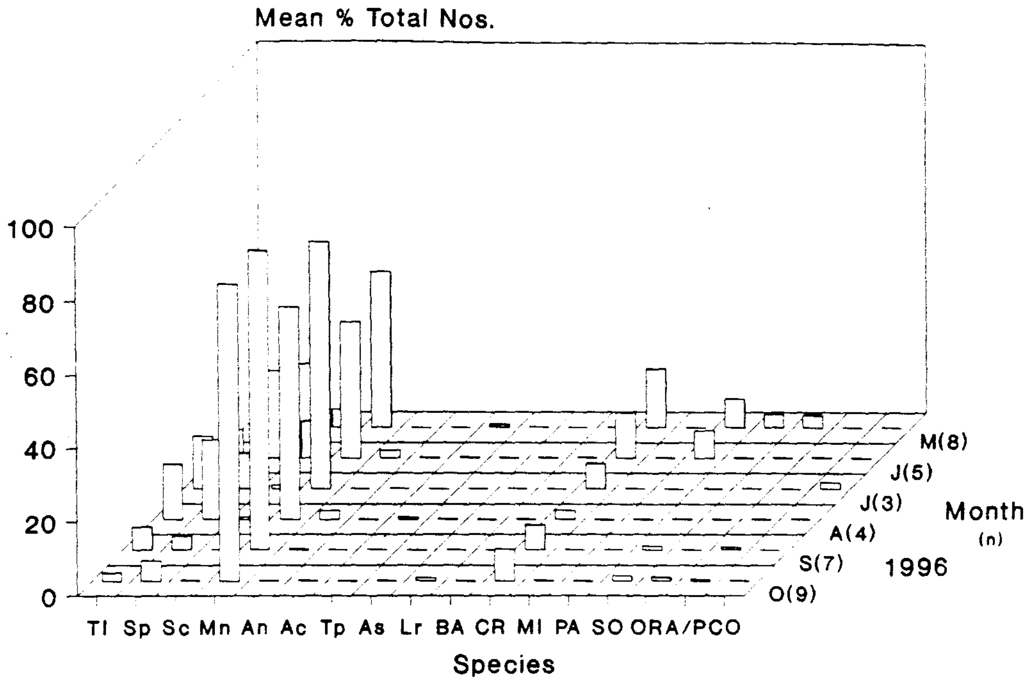

Mean % Total Nos.
100
80
60
40
20
0
Tl Sp Sc Mn An Ac Tp As Lr BA CR Ml PA SO ORA/PCO
Species
M(8)
J(5)
J(3)
A(4)
S(7)
O(9)
Month
(n)
1996

Figure 10b.

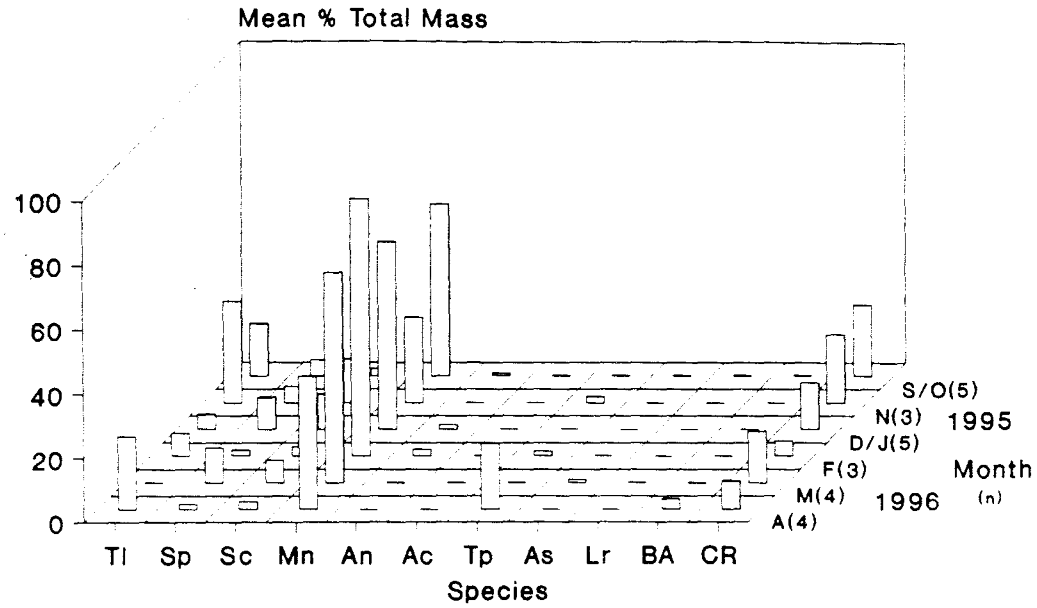

Mean % Total Mass
100
80
60
40
20
0
Tl
Sp
Sc
Mn
An
Ac
Tp
As
Lr
BA
CR
Species
S/O(5)
N(3)
D/J(5)
F(3)
M(4)
A(4)
1995
1996
Month
(n)

Figure 11a.

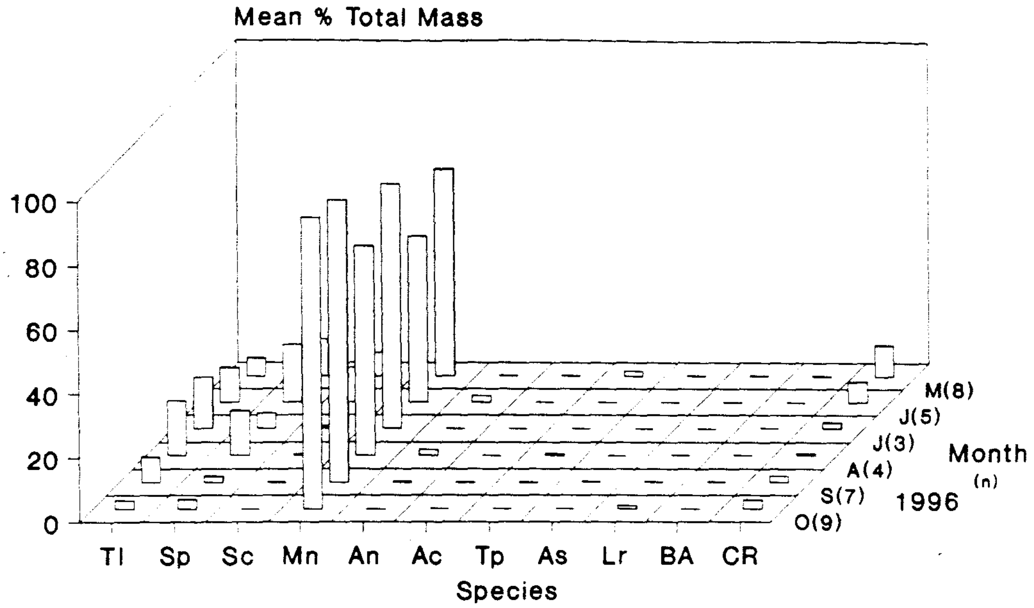
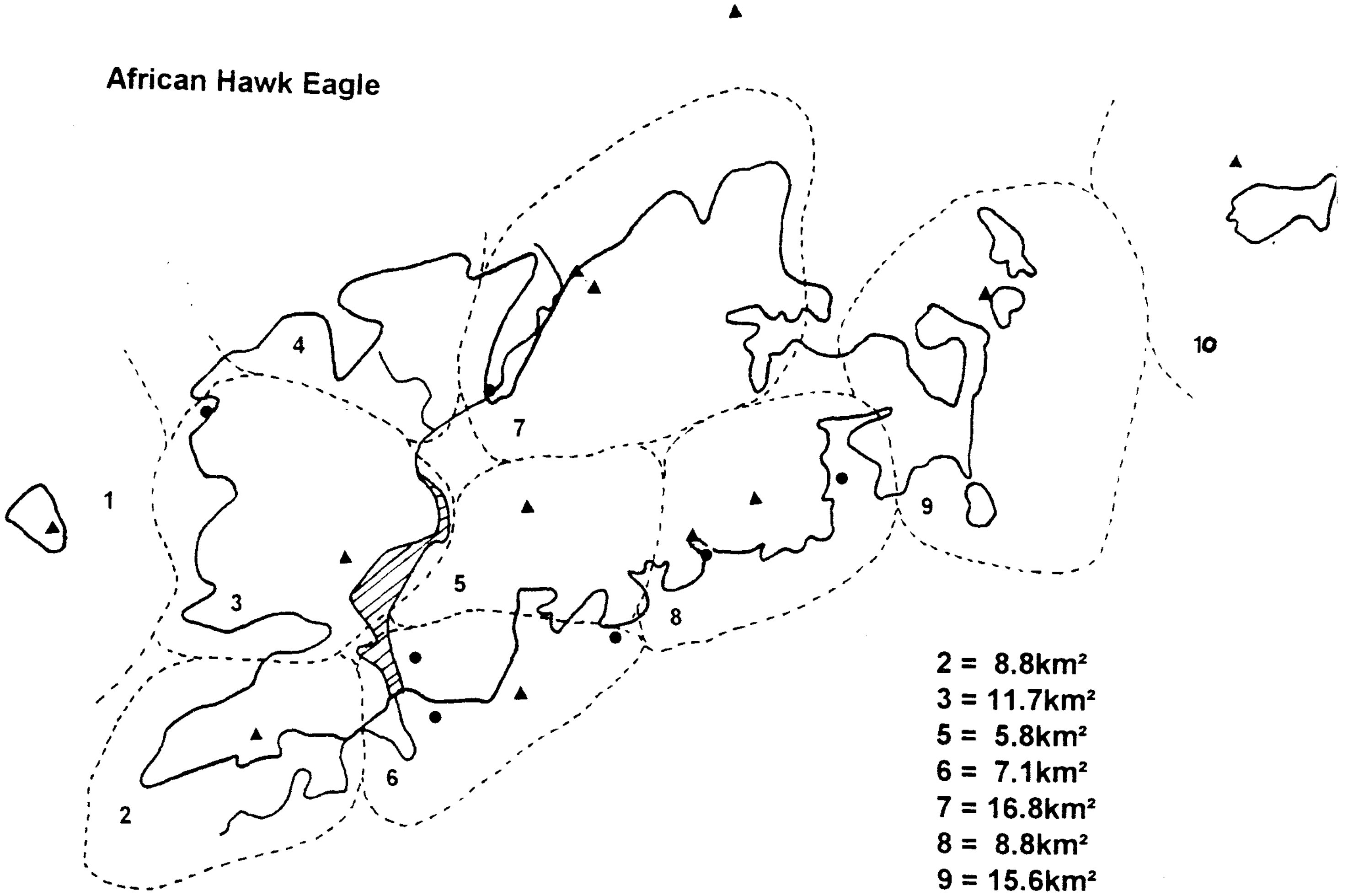

Mean % Total Mass
100
80
60
40
20
0
Tl
Sp
Sc
Mn
An
Ac
Tp
As
Lr
BA
CR
Species
M(8)
J(5)
J(3)
A(4)
S(7)
O(9)
Month
(n)
1996

Figure 11b.

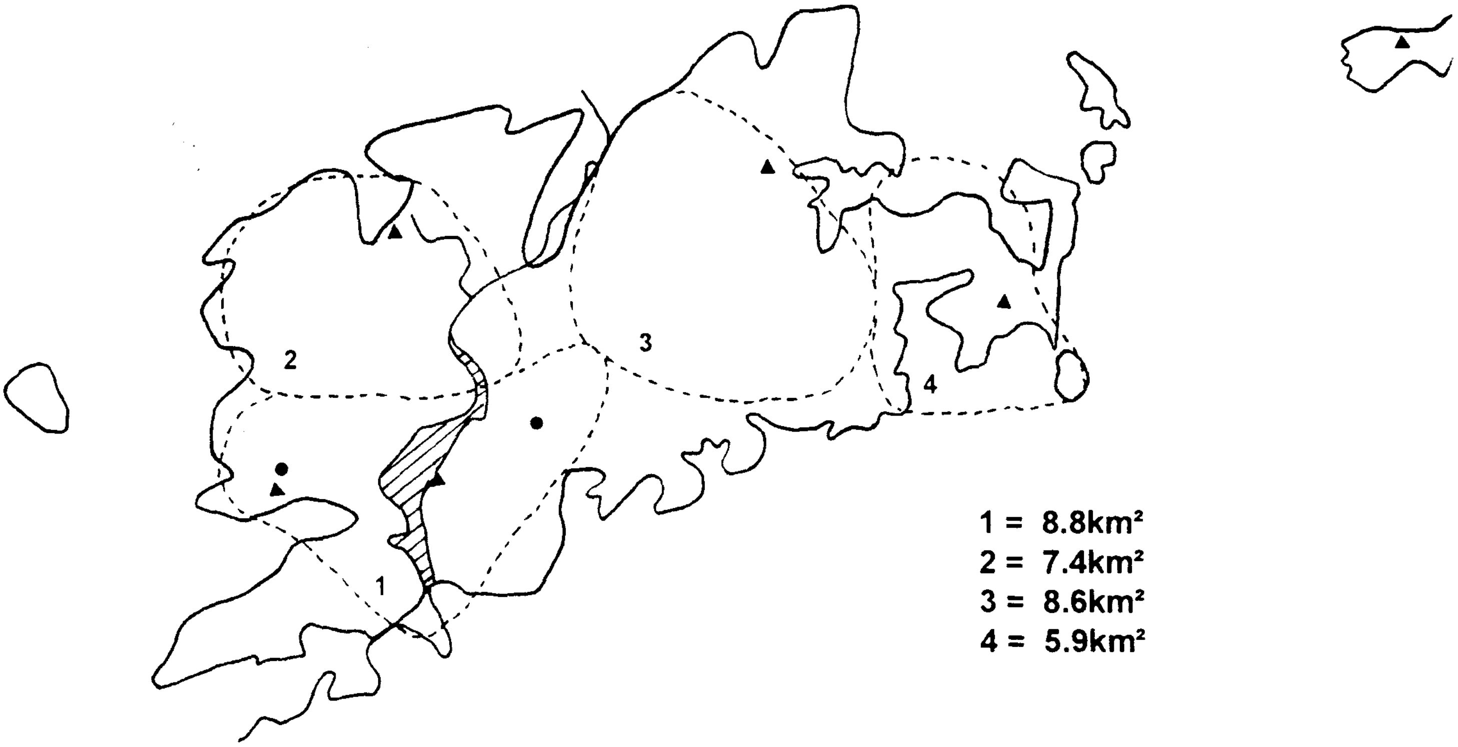


African Hawk Eagle

2 = 8.8km²
3 = 11.7km²
5 = 5.8km²
6 = 7.1km²
7 = 16.8km²
8 = 8.8km²
9 = 15.6km²

Figure 12a.

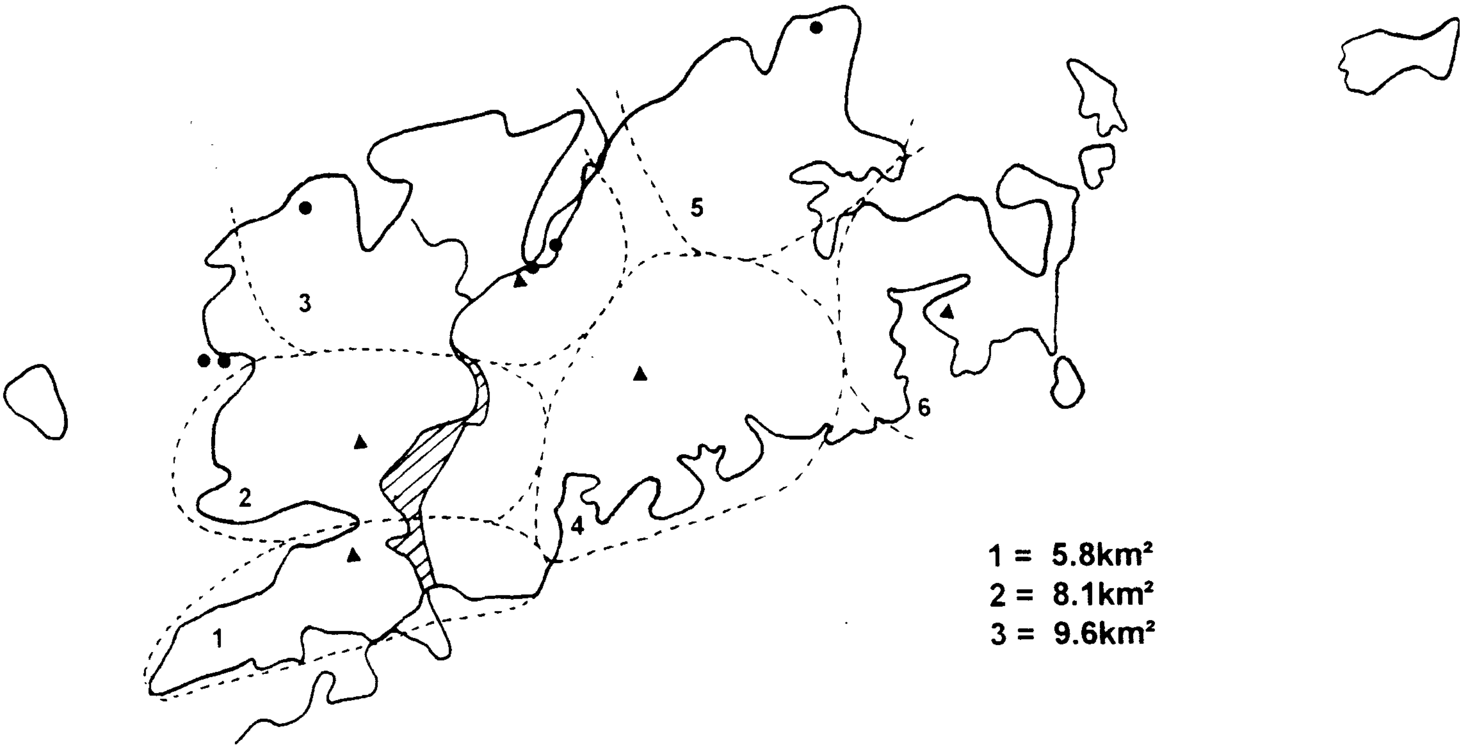
**Black Eagle**



1 = 8.8km²
2 = 7.4km²
3 = 8.6km²
4 = 5.9km²

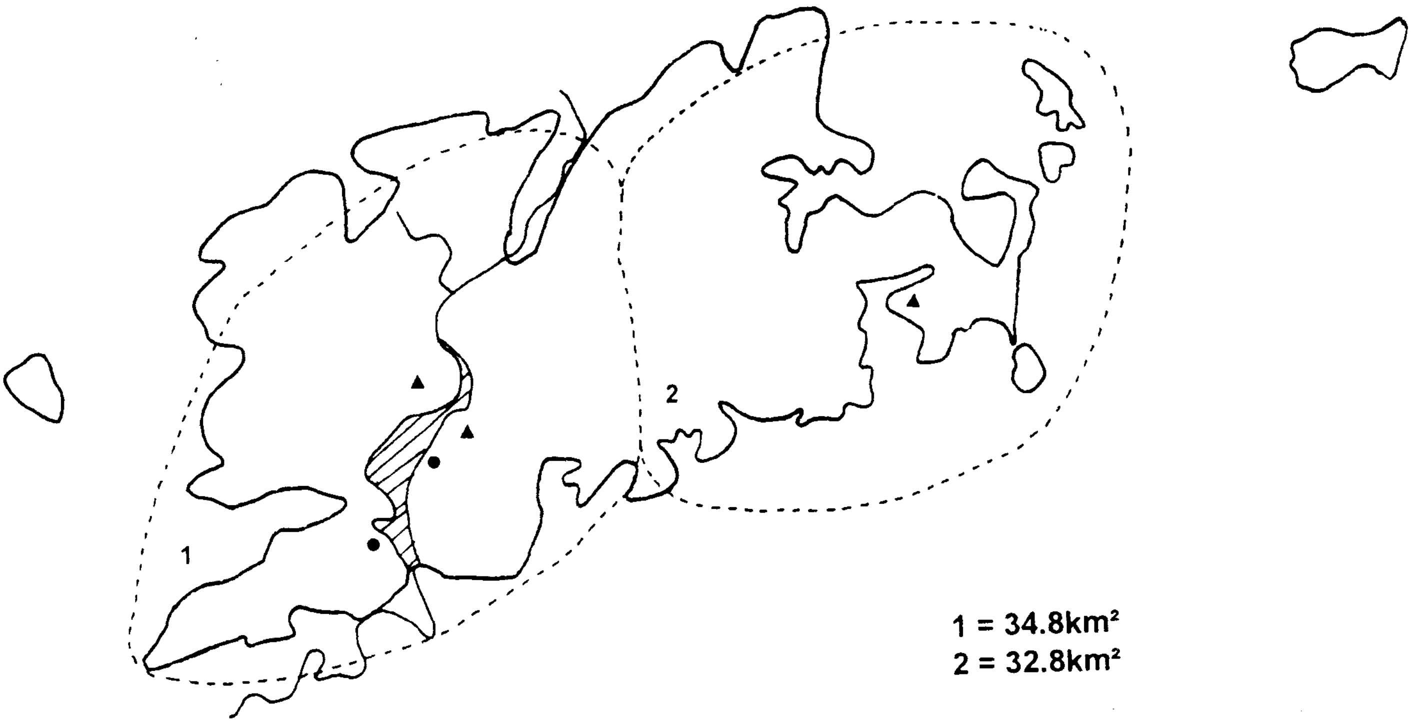
b.

**Crowned Eagle**

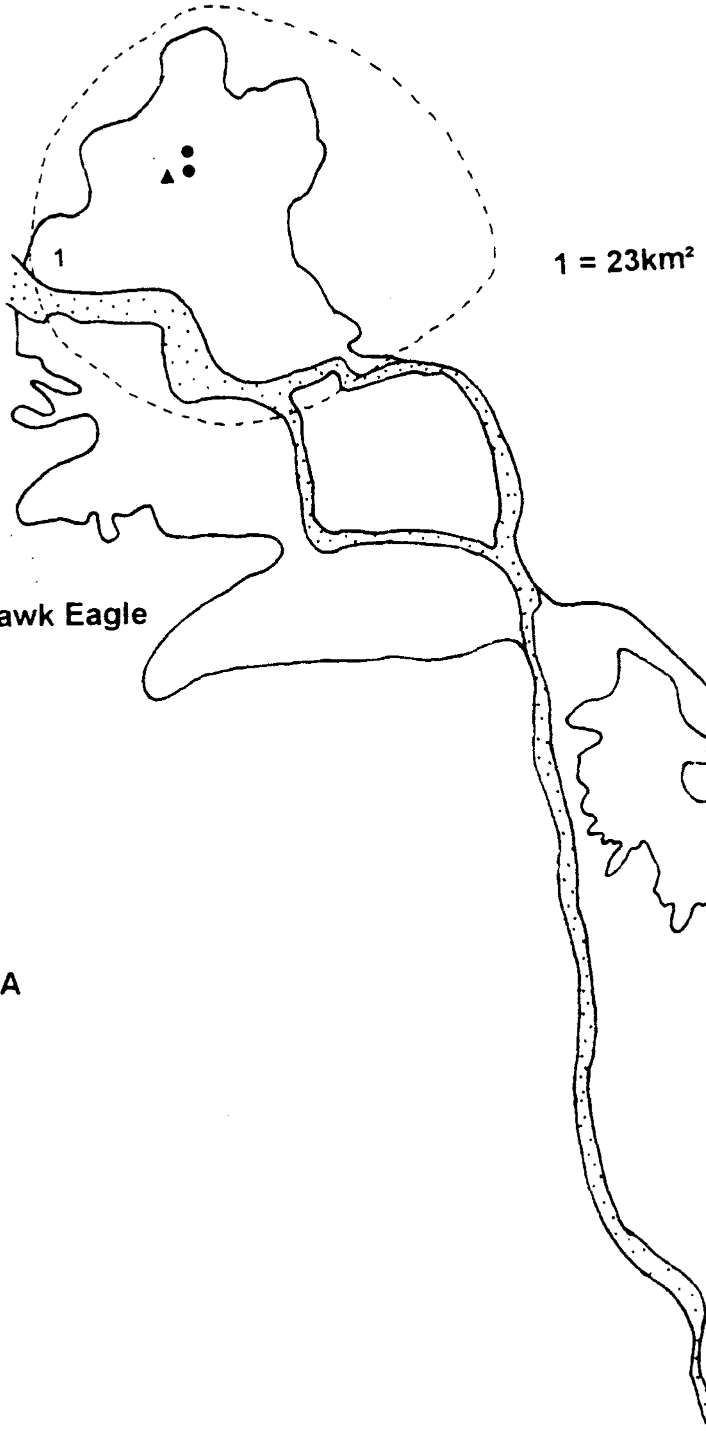


c.

African Fish Eagle



d



African Hawk Eagle

CLSA

e.

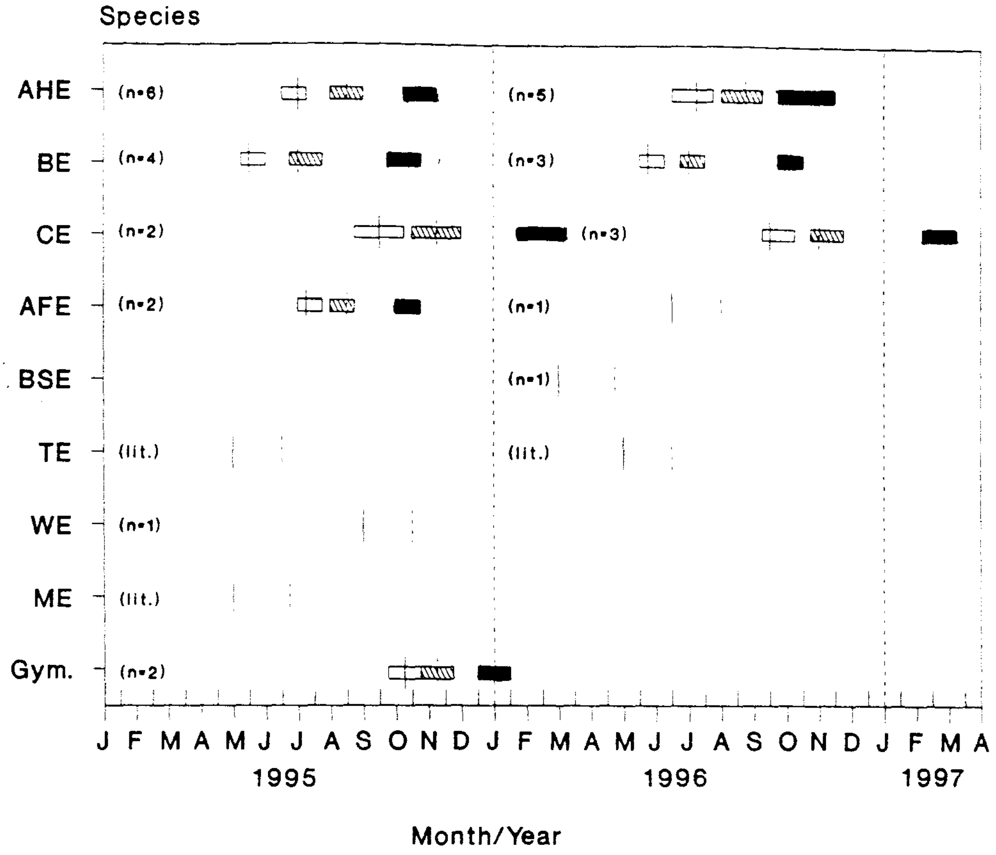

Species
AHE
(n=6)
(n=5)
BE
(n=4)
(n=3)
CE
(n=2)
(n=3)
AFE
(n=2)
(n=1)
BSE
(n=1)
TE
(lit.)
(lit.)
WE
(n=1)
ME
(lit.)
Gym.
(n=2)
J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1995
1996
1997
Month/Year

Figure 13.

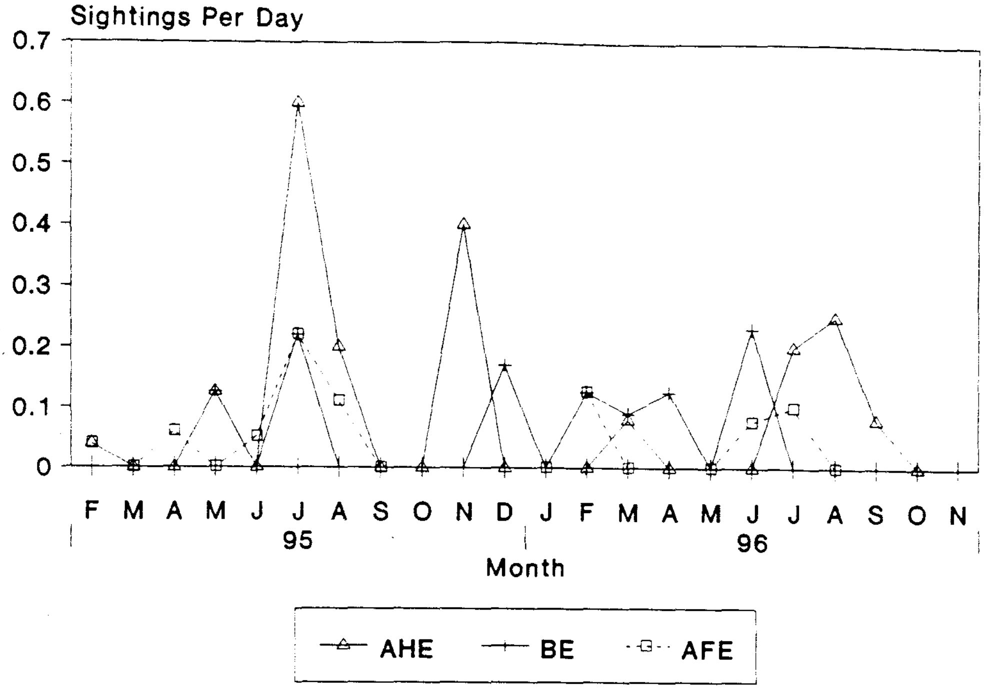

Sightings Per Day
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
95
96
Month
AHE
BE
AFE

Figure 14.

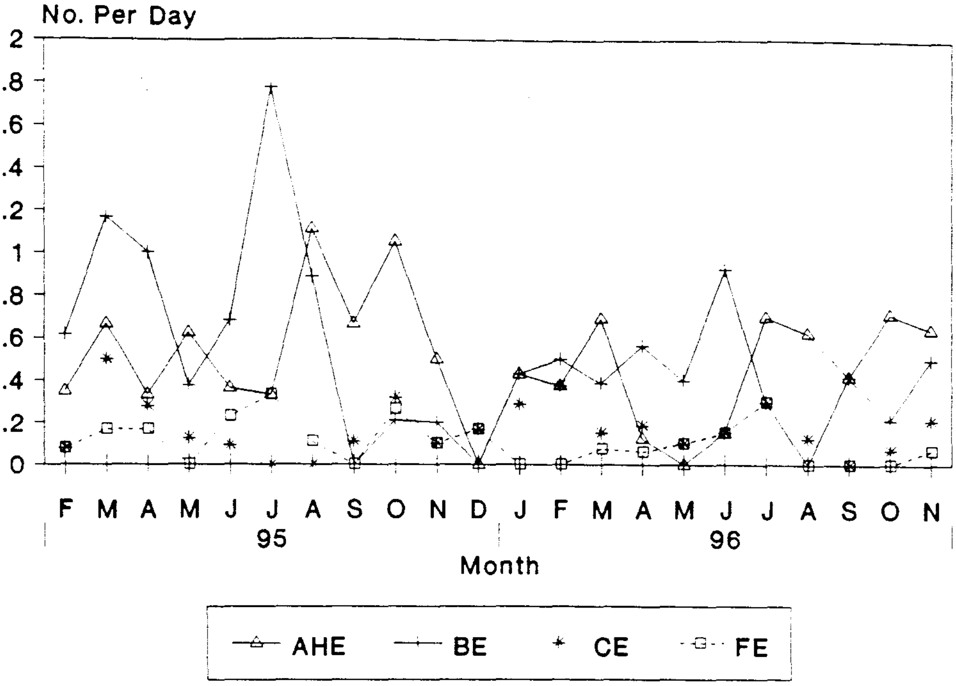

No. Per Day
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
F M A M J J A S O N D J F M A M J J A S O N
95
96
Month
AHE
BE
CE
FE

Figure 15a

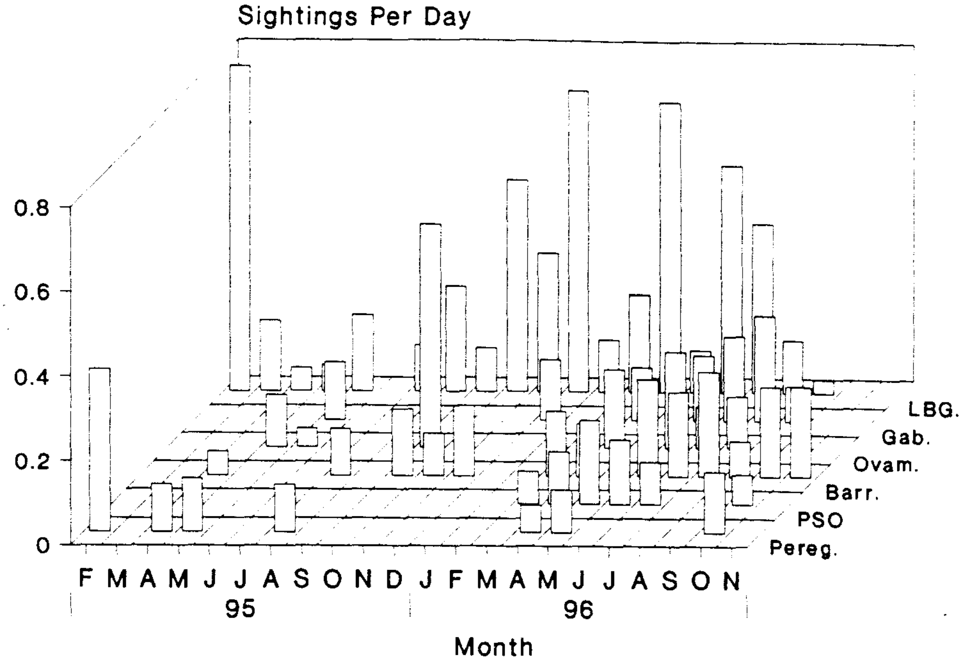

Sightings Per Day
0.8
0.6
0.4
0.2
0
LBG.
Gab.
Ovam.
Barr.
PSO
Pereg.
F M A M J J A S O N D J F M A M J J A S O N
95
96
Month

Figure 15b

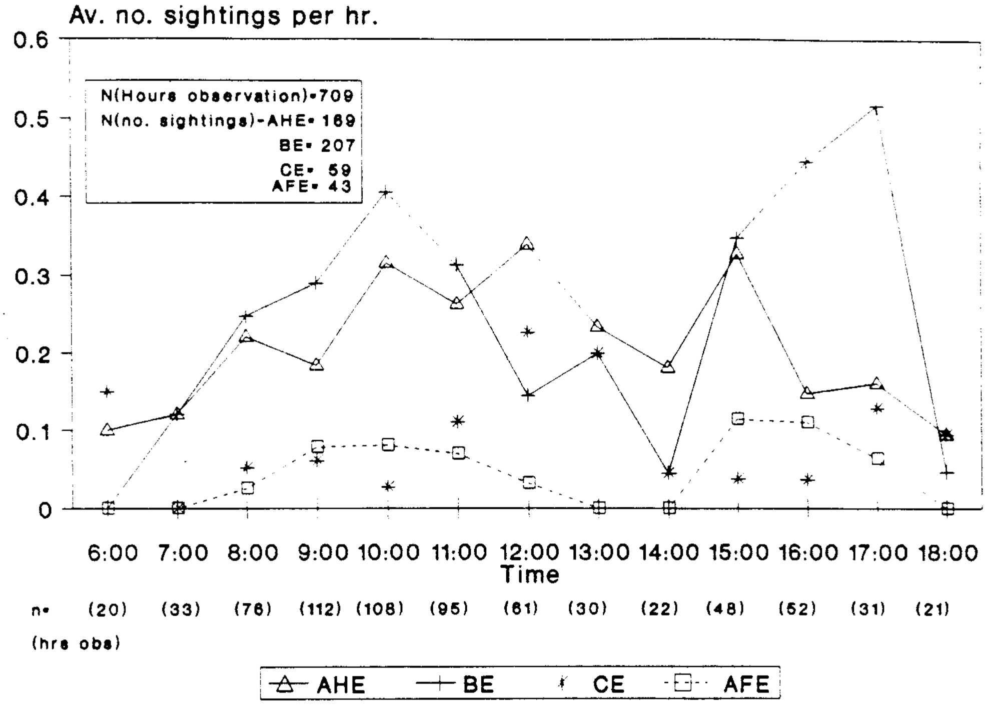

Av. no. sightings per hr.
0.6
0.5
0.4
0.3
0.2
0.1
0
N(Hours observation)=709
N(no. sightings)-AHE= 169
BE= 207
CE= 59
AFE= 43
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
Time
n=
(hrs obs)
(20)
(33)
(76)
(112)
(108)
(95)
(61)
(30)
(22)
(48)
(52)
(31)
(21)
AHE
BE
CE
AFE

Figure 16a.

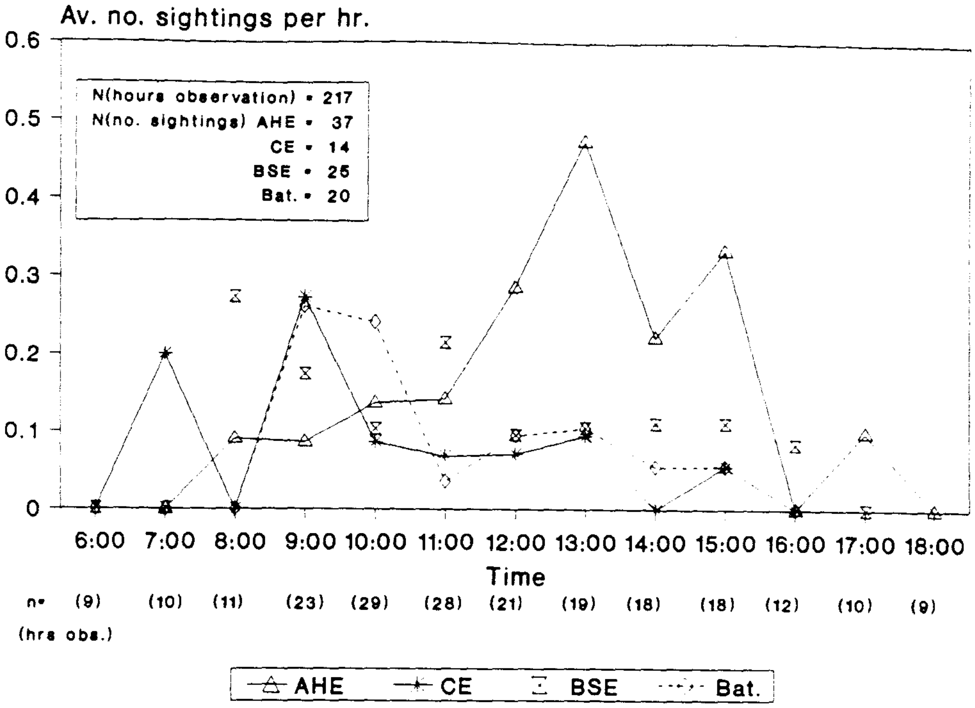

Av. no. sightings per hr.
0.6
0.5
0.4
0.3
0.2
0.1
0
N(hours observation) = 217
N(no. sightings) AHE = 37
CE = 14
BSE = 25
Bat. = 20
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
Time
n=
(9)
(10)
(11)
(23)
(29)
(28)
(21)
(19)
(18)
(18)
(12)
(10)
(9)
(hrs obs.)
AHE
CE
BSE
Bat.

Figure 16b.

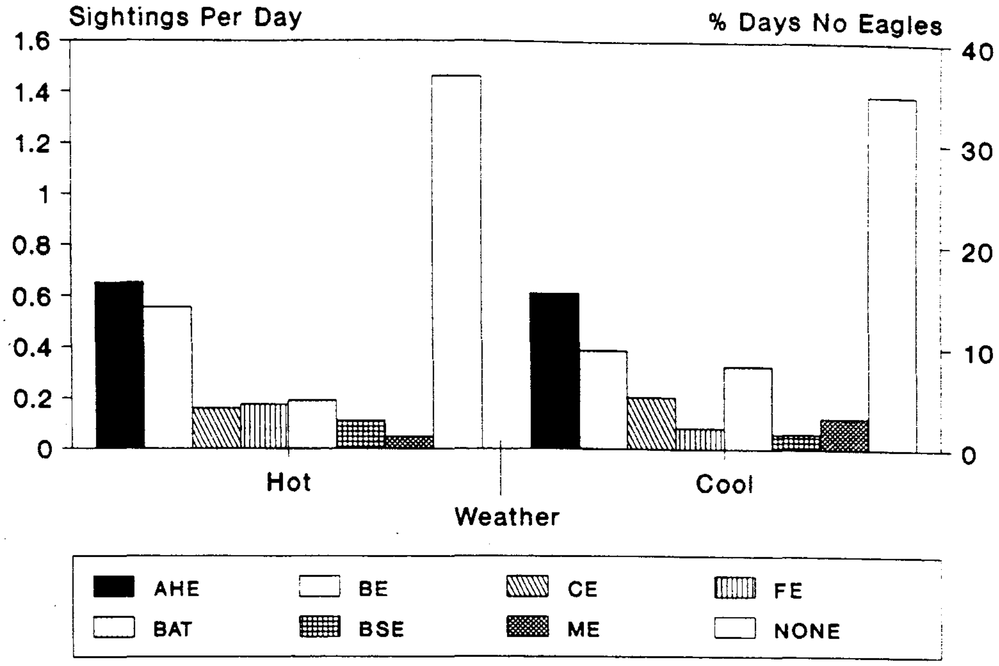

Sightings Per Day
% Days No Eagles
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
40
30
20
10
0
Hot
Cool
Weather
AHE
BE
CE
FE
BAT
BSE
ME
NONE

Figure 17a.

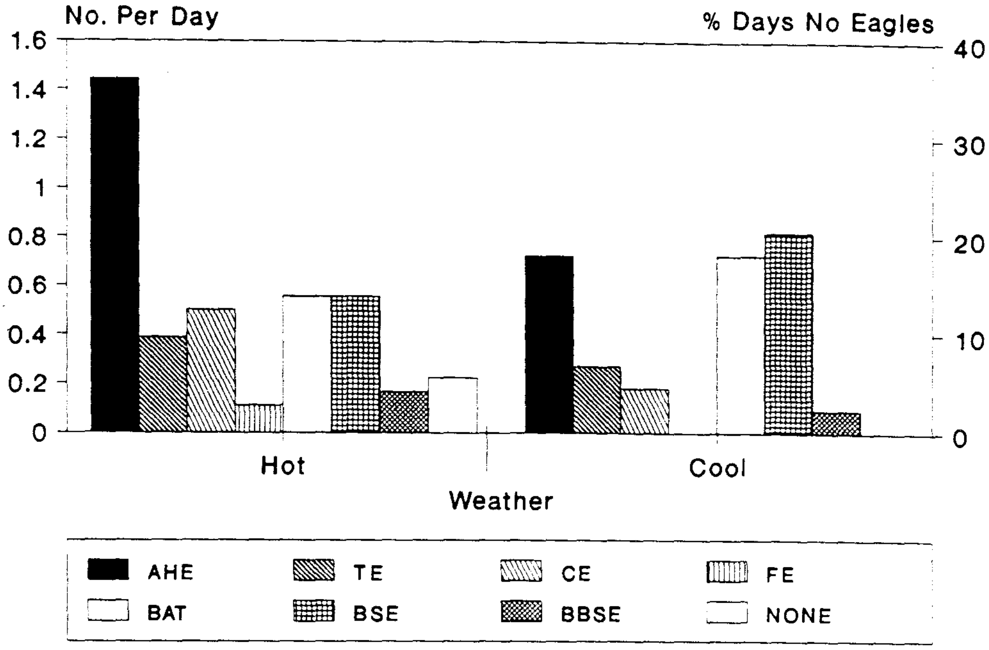

No. Per Day
% Days No Eagles
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
40
30
20
10
0
Hot
Cool
Weather
AHE
TE
CE
FE
BAT
BSE
BBSE
NONE

Figure 17b.