Ecology of desert-dwelling giraffe *Giraffa camelopardalis angolensis* in northwestern Namibia

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STATEMENT OF RESPONSIBILITY

This thesis is my original work, except where specifically acknowledged.

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“There is perhaps no animal living more graceful in form, more beautiful in colour, and more stately and majestic in appearance, than the camelopard…measuring eighteen feet from hoof of the fore-leg to the crest of its crown, it stands, as an American would express it, ‘the tallest animal in creation’…a creature so strangely shaped, and possessing so much speed and strength, was certainly designed by the Creator for some other use than browsing upon the leaves of mimosa trees: but that use man has not yet discovered…”

Captain Reid, *The Giraffe Hunters*. vol. 1., London 1867

Abstract

The population size and range of giraffe *Giraffa camelopardalis* have been greatly reduced in Africa in the past century, resulting in geographical isolation of local populations and some herds surviving at the edge of the species' preferred range. Numerous factors have contributed to these declines, but historical analysis indicates that habitat loss and fragmentation, human encroachment, disease and poaching are the main threatening processes. These processes can be expected to continue to impact on giraffe populations, particularly as human populations grow and needs for land and resources increase.

This study used field data and laboratory analyses to investigate the taxonomy, behaviour and ecology of desert-dwelling giraffe *Giraffa camelopardalis angolensis* in the northern Namib Desert. This population resides at the extreme of the giraffe's range. My research also complements the community-based natural resource management (CBNRM) program of the Namibian government, and provides baseline data on the current population status and structure of giraffe in the Kunene Region.

The field data, genetic, habitat and forage samples used in this study were collected by myself and a number of research assistants over a period of two years (2001 to 2003), following preliminary research that I undertook between 1999 and 2001. Laboratory analysis of genetic samples was conducted by Dr R. Brenneman and his team at Henry Doorly Zoo, Omaha, NB., as well as by Mr D. Brown at UCLA, CA. Mr W. Gawa!nab and his team at the agricultural laboratory, Ministry of Agriculture, Water and Rural Affairs, Namibia, conducted chemical analyses on plant samples that form part of the giraffe's diet.

The genetic architecture of Namibian giraffe was investigated, including the samples from the desert-dwelling giraffe of the northern Namib Desert and giraffe from Etosha National Park. The results were compared with genetic profiles of giraffe subspecies throughout Africa, but in particular with *G. c. giraffa* which is the currently-accepted nomenclature of the Namibian giraffe. Results indicated that the Namibian giraffe has five unique haplotypes and is genetically distinct from *G. c. giraffa* or any other extant subspecies; it is considered here, tentatively, to represent *G. c. angolensis*. Furthermore, the Namibian

giraffe has been separated from other populations for an extended period. Some gene flow has occurred between the desert-dwelling and Etosha NP giraffe population, and can be attributed to recent translocations between these regions. Within the study region, a sharing of haplotypes between three studied subpopulations indicated gene flow among giraffe throughout the northern Namib Desert, and this was confirmed by field-based monitoring. Taken together, these findings suggest that Namibian giraffe should be viewed as important for the conservation of overall genetic variation within *Giraffa camelopardalis*, although further investigation into the taxonomy of the Namibian form is warranted.

Following these findings, I then investigated the behaviour and ecology of the desert-dwelling giraffe. As no previous study has been published on the ecology of *G. c. angolensis*, there is an information gap in our knowledge of this subspecies. One hundred and fifty six giraffe were identified individually using field-based identification methods and digital imagery. An assessment of the population structure and dynamics indicated marked variation in numbers, sex and age structure, herd structure and densities between three study areas. These variations possibly arose from differences in study area size, aridity, availability of forage and human impacts. I also investigated levels of associations between giraffe within the population using a simple ratio technique, and observed that increased association occurred in smaller populations; there appeared to be a matrilineal social structure. In one bull-biased population, a higher degree of association between bulls was observed compared to bulls in the other two populations.

To gain further insight into the distribution and range of giraffe, I collected GPS locations from a combination of field-based monitoring and GPS satellite collars. The GPS satellite collars were the first trial of this technology on giraffe in Africa. Using Range Manager, a MapInfo animal location analysis extension program, I estimated 100% and 95% minimum convex polygon for daily, monthly and annual home range sizes of giraffe in the northern Namib Desert. Giraffe were observed to have large home ranges, with the largest individual range for a bull, Africa-wide, being recorded in this study. Large home ranges correlated with low population density, reduced diversity of forage and, in bulls, increased search areas for receptive cows. Giraffe movements occurred predominantly along riparian woodlands, although seasonal use of other habitats was recorded. Observations

and data from four GPS satellite-collared giraffe provided high-resolution data on daily movements, and indicated a pattern of highly biphasic movement behaviour that correlated with ambient temperatures.

Diurnal activity budgets varied between the sexes, with cows spending more time feeding and resting, while bulls walked and ruminated more frequently. Juveniles rested more often than other giraffe. Seasonal variation in activity budgets was evident, perhaps reflecting use of an energy maximiser strategy for cows and an energy minimiser strategy for bulls. The establishment of artificial water points in the Hoanib River during the study period appeared to alter the seeming independence of giraffe on water in the northern Namib Desert, and also resulted in small-scale shifts in use of the riparian woodland by elephant.

To investigate the diet of giraffe, I observed animals feeding in the field and also carried out laboratory analyses of the chemical content of preferred plant species. Seasonal changes in the abundance, moisture and protein content of available food plants correlated with shifts in the diet of giraffe. Giraffe impacted on their preferred forage source, *Faidherbia albida,* causing distinct structural changes in the individual plants and the *F. albida* population. This impact, combined with elephant damage and seasonal flood events, has resulted in a shift in the age structure and dynamics of the *F. albida* population over the past two decades.

Finally, I present a brief overview on the history of conservation and management in the Kunene Region. The established CBNRM program provides a baseline for future wildlife conservation and management, of which the desert-dwelling giraffe could be an integral component for non-consumptive tourism. Long-term research on the population's status, range, behaviour, social structure, habitat requirements, and ecology would help to provide a better understanding of the giraffe's adaptation to the arid environment, while focussed legislation would enable increased control of communal lands and continue to benefit community-based conservancies.

Table of Contents

Acknowledgements

Namibia, the land God created in anger. The old wife's tale that Africa gets underneath your skin and never leaves has proven as true since my first visit to the Dark Continent. In that one year I experienced what part of life is about—entering adulthood and the loss of my old man. To say Africa has played a pivotal influence on my life would be an understatement! The ability to sit back and watch giraffe walk majestically across the dune field is but one of the memories which I have been afforded. True, this thesis focuses on the life and times of the 'Spotted ship of the Namib', but it is more than that—it was a desire, a bet with myself and proof to others that anyone can do it, if they just believe.

Over a decade after I first left the African continent I finally left again, this time with my best friend and wife. We have experienced so much together but there is still so much more to do and see. To dedicate this 'small mammal killer' to you is something small, but you mean more to me than I could ever afford you. Your encouragement, support and love was unwavering during the good, the bad and the ugly of it all. From the field trials to the constant stories of, 'remember when the giraffe …', to the endless giraffe gifts. I would never have started or completed this without you and hope that with it being brought to rest, it will enable us to start the next chapter in our life together. I love you Steph!

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CHAPTER 1. GENERAL INTRODUCTION

1.1. Introduction

This thesis describes the ecology of desert-dwelling giraffe *Giraffa camelopardalis* in the northern Namib Desert, north-western Namibia. It assesses the genetic architecture of the giraffe in the study region and in the nearby Etosha National Park in light of subspecies variation within the genus. From this starting point, the research focuses on the structure and dynamics of the desert population and the behavioural and foraging adaptations of giraffe associated with survival at the extreme edge of the species' range.

In this chapter I briefly describe desert environments and in particular the Namib Desert, followed by general adaptations of biota to deserts. I then discuss the taxonomy, distribution of subspecies and conservation status of giraffe throughout the species' extant range, and the status, historical distribution and population structure of giraffe in Namibia. Finally, I focus on the key research questions addressed in this study.

1.2. Deserts

Deserts comprise one of the most extensive environments on Earth. Occurring on all continents, deserts occupy up to 40% of the land surface (Crawford, 1981; Allan, 1993). Deserts vary markedly in size, climate, soils and diversity, with hot deserts located between latitudes 20° and 35° north and south of the equator, and cold deserts between latitudes 65° and 90° (Degen, 1997). Different disciplines describe deserts based on different structures or processes: ecologists use vegetation biomass and structure, climatologists use rainfall and atmospheric moisture, and geomorphologists focus on soil structure, landforms or surface hydrology (e.g. Giess, 1971; White, 1983; Shmida, 1985; Whitford, 2002). As an example, Koppen deserts are described as having sparse vegetation, high temperatures, annual rainfall less than 254 mm, and conditions where more water is lost through evaporation than is gained from precipitation (Larson, 1970; Lovegrove, 1993).

Temperate to hot deserts comprise the majority of the world's deserts and are generally characterised by low and unpredictable precipitation, low relative humidity, desiccating winds and high temperatures (e.g. Brown, 1974; Allan, 1993; Rundel & Gibson, 1996; Degen, 1997; Dickman *et al*., 1999a). The United Nations Educational, Scientific and Cultural Organization (UNESCO) describes three different desert zones or types: semi-arid (<600 mm rain/year), arid (<200 mm rain/year) and hyper-arid (<25 mm rain/year) (Allan, 1993).

1.2.1. Namib Desert

Located in the driest country south of the Sahara, the Namib Desert lies in the latitudinal range of 18° to 30° S (Lovegrove, 1993). It extends almost 2 000 km north to south along Africa's southwestern seaboard and it is predominantly less than 200 km wide (Louw & Seely, 1982; Seely, 1987; Lovegrove, 1993). Temperatures range from below zero during the cold-dry winter months to above 45°C in the hot-dry summer; rainfall is highly variable with a mean of 5-85 mm per annum at different locations, although prolonged years of no rainfall are not uncommon (Louw & Seely, 1982; Lovegrove, 1993). Precipitation from fog is an important lifeline of the Namib Desert, particularly due to the region's low and highly variable rainfall (Lancaster *et al*., 1984; Pietruszka & Seely, 1985; Henschel *et al*., 1998; Seely & Henschel, 1998). Fog provides essential sustenance for both plants and animals, enabling them to flourish in an otherwise waterless environment.

The desert landscape has undergone continuous change over the millennia due to the influence of episodic climatic events (Armstrong, 1990). As one of the most ancient deserts in the world—it is between 50 and 80 million years old—the Namib Desert is typified by a mass of mobile sand dunes (Seely, 1987; Lovegrove, 1993; Barnard 1998). The Namib Desert is bordered by the Atlantic Ocean to the west, while to the east the 'sand sea' opens up into gravel plains that are dotted with inselbergs (Seely, 1987; Lovegrove, 1993; Barnard, 1998).

The Great Western Escarpment to the east of the northern Namib Desert is categorised by the Etendeka lava field and associated mountain ranges, and separates the coastal desert

from the eastern hinterland (Seely, 1987; Rice & Gibson, 2001). Large 'sand', or ephemeral rivers dissect the arid landscape of the northern Namib Desert, providing a refuge for one of the region's most striking vegetative features—the riparian woodlands (Jacobson *et al*., 1995). Subterranean waters flow beneath the surface of the sand rivers, creating linear oases. Precipitation in the eastern escarpment zone provides valuable water flows along the river courses, providing life to the riparian woodlands. These features consequently form important refugia that provide shelter, food and water for humans and animals alike (Lovegrove, 1993; 2000).

The Namib Desert has remarkably diverse animal life for such an arid environment. Much is owed to the seasonal fog, rather than the limited rainfall, and to the high diversity of succulent plant species (Von Willert *et al*., 1992; Lovegrove, 1993). Both plants and animals exhibit high levels of endemism and adaptations to the arid conditions of the Namib Desert. From *Welwitschia mirabilis* to the head-standing beetle *Onymacris unguicularis*, and Gray's lark *Ammomanes grayi* to the golden mole *Eremitalpa namibiensis*, the Namib Desert is home to a wide array of endemic or near-endemic species, including more than 25 species of reptiles, six birds, two bats, gerbils, invertebrates, lichens and plants (Louw & Holme, 1972; White, 1983; Wessels, 1989; Barnard *et al*., 1998; Branch, 1998; Maggs *et al*., 1998; Seymour *et al*., 1998; Griffin, 1999; Hilton-Taylor, 2000; J. Lalley, unpublished data).

1.2.2. Desert adaptations

The diversity of animal species in desert environments is predominantly dependent on rainfall, but is shaped also by the high and fluctuating temperatures and availability of vegetative cover (Seely, 1987; Broyles, 1995; Rundel & Gibson, 1996). The driest deserts thus contain fewer species than more temperate deserts. Desert plant species, commonly known as xerophytes, show many adaptations for survival, including the following (e.g. Brown, 1974; von Willert *et al.,* 1992; Maggs *et al*., 1998):

- perennial forbs and herbs that germinate rapidly and mature when sufficient moisture is available;
- succulent species that retain moisture;

- deciduous, sclerophyllous shrubs that drop leaves during dry periods;
- geophytes that have most of their biomass underground;
- many taxa with small leaves, waterproofed to limit water loss; and
- grey-green leaves that reflect light and reduce heat absorption.

Both plants and animals obtain heat directly through radiation as well as indirectly via convection from the air and conduction from the substrate, however, plants are often less susceptible to extremes of temperature than animals because of their insulative woody tissues and bark (e.g. Seely, 1978; Louw & Seely, 1982; Louw, 1993; Broyles, 1995; Jacobson *et al*., 1995; Cloudsley-Thompson, 1996; Wickens, 1998; Kitchen *et al*., 2000). Desert animals have developed a range of strategies and have evolved morphological, physiological and behavioural adaptations that enable them to respond to the high temperature variability and fluctuating resource availability that typify deserts. Although some adaptations differ between small and large mammals, reptiles, birds, and other taxa, most serve to conserve water and regulate heat.

Behavioural adaptations vary, from simply avoiding extreme climatic conditions to increasing nutrient and moisture intake during the brief periods when food and water are abundant (e.g. Schmidt-Nielson, 1964; Joubert, 1974; Louw & Seely, 1982; Scheepers, 1992; Bradshaw, 1997; Degen, 1997; Bothma, 1998; Dickman *et al*., 1999a & b; Le Pendu & Ciofolo, 1999; Hudson & Haigh, 2002). Examples include:

- seasonal migrations;
- biphasic, nocturnal or crepuscular activity;
- burrowing, estivation, hibernation, dormancy or torpor;
- orientation of body away from sun;
- urohydrosis;
- selection of moisture-rich forage; and
- collection of fog precipitation from plants and substrate.

Physiological adaptations, such as those listed below, revolve around the ability to overcome the paucity of water in deserts (e.g. Scholander *et al*., 1950; Joubert, 1974; Langman *et al*., 1978; Langman, 1985; Seely, 1987; Louw, 1993; Lovegrove, 1993; MacLean, 1996; Lovegrove, 2000):

- concentration of urea;
- excretion of uric acid;
- expiration of unsaturated breath;
- heterothermy;
- ability to manufacture water metabolically from food sources; and
- nasal heat exchange.

Various morphological adaptations allow avoidance of excessive heat loads (e.g. Miller & Stebbens, 1964; Rundel & Gibson, 1996; Schmidt-Nielsen, 1998; Hudson & Haigh, 2002):

- reflective pelage (coat), feathers and scales that act as barriers to heat transfer or reduce water loss; and
- longer or larger appendage sizes that allow dissipation of body heat.

It is unlikely that all of these responses to arid conditions evolved as adaptations only to aridity (see Gould & Lewontin, 1979). For example, mammalian hair or avian feathers may have been selected for under cooler, non-arid conditions, but provided benefits subsequently when aridity prevailed. Hence, I use the term 'adaptation' loosely here to describe the range of responses exhibited by biota in desert environments.

Adaptations of giraffe to desert environments have not been well researched. Most research has been ecologically based (e.g. Hall-Martin, 1975; Dagg & Foster, 1982; Pellew, 1984a; Ciofolo & Le Pendu, 2002), while physiological studies of giraffe have concentrated primarily on the cardiovascular and respiratory systems (e.g. Robin *et al*., 1960; Patterson *et al*., 1965; Warren, 1974; Hugh-Jones *et al*., 1978; Langman *et al*., 1982). Although limited, some of this latter research suggests that giraffe have physiological adaptations that may be particularly beneficial for survival in arid environments; such as nasal turbinal heat exchange that reduces water loss (Langman *et al*., 1979). However, a study of water retention undertaken by Scheepers (1990) reported that the renal system of Namibian giraffe was not different between the populations of Etosha National Park and those in the arid north-west, and suggested that no specific modification for aridity was evident. It is likely that an array of behavioural, and possibly, physiological adaptations enable giraffe to exist in Namibia's arid regions.

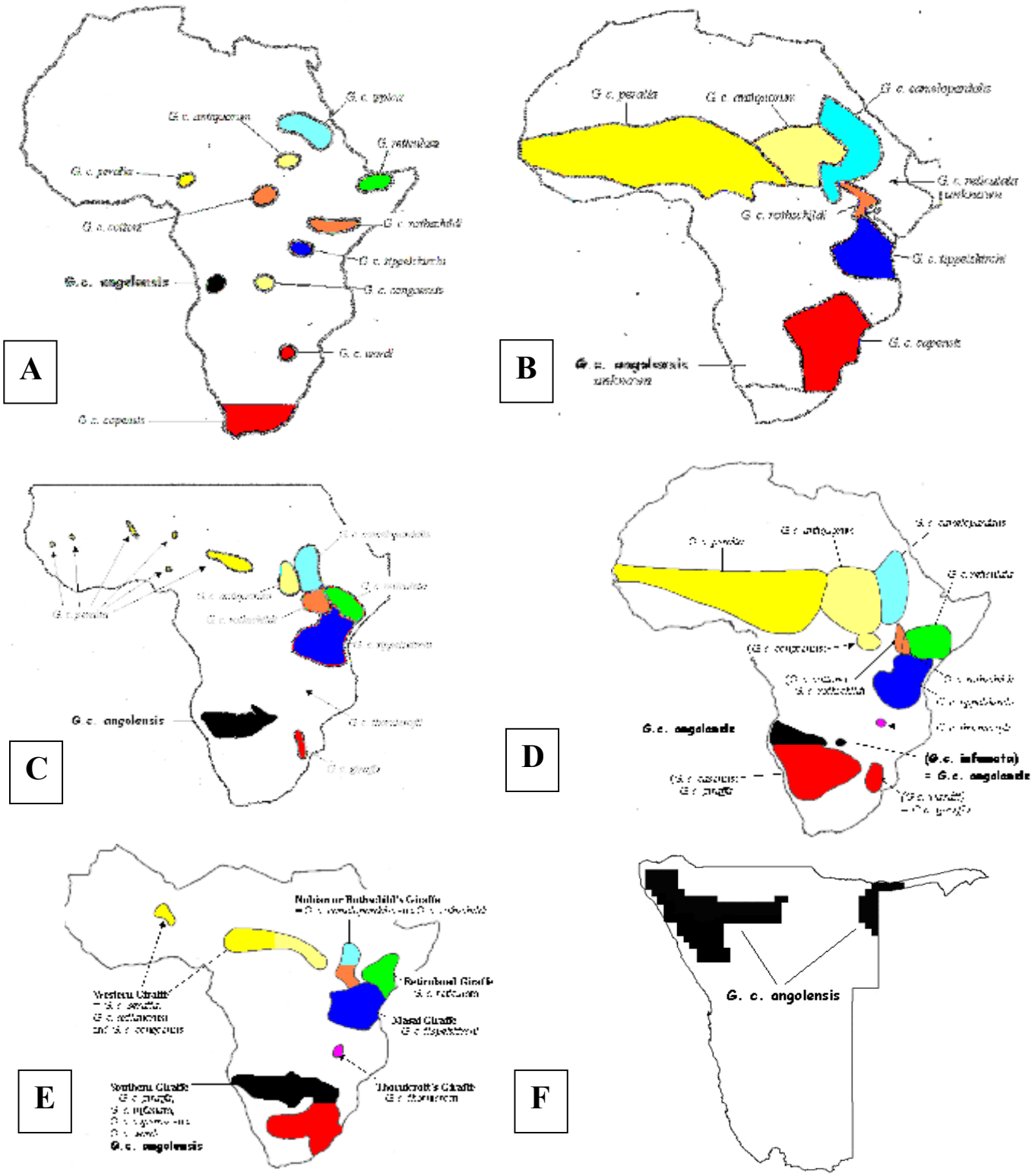
In the present study, I have sought to understand the behaviour, population dynamics and resource use of giraffe in the northern Namib Desert and to unravel the mystery of how giraffe survive in this environment of extreme aridity.

1.3. Taxonomy, distribution and conservation status of the giraffe

The giraffe, *Giraffa camelopardalis* Linnaeus 1758 (Order Artiodactyla, Suborder Ruminantia), is one of two species in the family Giraffidae that exist today. The okapi, *Okapia johnstoni* Sclater 1901, which is close to the giraffe's putative ancestor, is morphologically different and geographically restricted to the forested riverine environment of the north-eastern Democratic Republic of the Congo.

For almost 250 years, and particularly within the last decade, conjecture and confusion have surrounded the classification of giraffe into species and subspecies (e.g. Linnaeus, 1758; Lydekker, 1904; Krumbeigel, 1939; Ansell, 1968 & 1971; Dagg, 1971; East, 1999; Seymour, 2002). In 1848 the generic classification of giraffe was amended to the current scientific name *Giraffa camelopardalis*, following the species' initial classification by Linnaeus (1758) as *Cervus camelopardalis.* The first critical review of giraffe classification occurred almost 150 years after Linnaeus' classification (Lydekker, 1904), although the species was well-known and included in early descriptions by Gray (1821), Gill (1872) and others (review in McKenna & Bell, 1997).

The classification of giraffe by Lydekker (1904), based on the examination of type specimens from throughout the African continent, divided giraffe into two distinct species, *Giraffa reticulata* and *G. camelopardalis*, and the latter into 10 subspecies. This classification was based on pelage pattern, pelage coloration, location and horn (ossicone) structure. Although the paratype samples were limited, classification today (Dagg, 1971) varies little from that described by Lydekker (1904) with the exception that all giraffe are now classified as one species with nine distinct subspecies (Figure 1.1 & Table 1.1).



Legend: *G. c. angolensis* (black); *G. c. giraffa* (red); *G. c. thornicrofti* (pink); *G. c. reticulata* (green); *G. c. tippelskirkirchi* (dark blue); *G. c. rothschildi* (orange); *G. c. camelopardalis (*light blue); *G. c. antiquorum* (cream); and, *G. c. peralta* (yellow).

Figure 1.1. Historical subspecific range maps of giraffe. (A) Lydekker, 1904; (B) Krumbeigel, 1939; (C) Dagg, 1971; (D) Dagg & Foster, 1982; (E) East, 1999; and (F) Fennessy *et al.,* 2003. Illustrations (A-E) redrawn by Seymour (2002) and author.
Note: (F) shows only Namibia and, tentatively (see Chapter 3), *G. c. angolensis*.

The taxonomy of giraffe is complex, both in terms of the species' actual phylogeography and nomenclatural history. Review of the historical literature indicates that authors are generally uncertain about the presence and absence of giraffe across large areas of the continent (e.g. Lydekker, 1904; Krumbeigel, 1939; Dagg, 1971; Dagg & Foster, 1982; East, 1999). For example the reported range of the west African giraffe population has varied from being almost non-existent to widely spread across the continent's north-west, while formerly recognised subspecies have been subsumed into others (e.g. *G. c. congoensis* is now subsumed into *G. c. antiquorum*). In southern Africa, historical estimates of giraffe ranges are varied, particularly for *G. c. angolensis* and *G. c. giraffa*, whose ranges and taxonomic classifications differ widely between studies (Figure 1.1). The taxonomic instability of *G. camelopardalis* spp. is not surprising given our incomplete knowledge of the distribution of giraffe and application of variable character states (e.g. pelage patterns) to distinguish subspecies.

1.3.1. Taxonomy of the Namibian giraffe

The type specimen of *Giraffa camelopardalis angolensis* was collected approximately 240 km south west of Humbe, Angola, north of the Kunene (synonymous Cunene) River (Lydekker, 1904). Lydekker reported that the Kunene and Kavango (synom. Cubango) Rivers form a natural barrier between the Angolan and Namibian giraffe populations, thus effectively separating the ranges of *G. c. angolensis, G.c. infumata* (east) and *G. c. capensis* (south) (the latter synom. with *G. c. giraffa*) (Figure 1.1). Dagg's (1971) review showed that *G. c. infumata* was in fact synonymous with *G. c. angolensis,* and thus the same species, while, both Dagg & Foster (1982) and Seymour (2002) identified that *G. c. angolensis* range extends south and eastwards to the Kwando River, Namibia.

Taxonomically, the giraffe populations of north-western and north-central Namibia have historically been classified as *G. c. giraffa,* which is taken to be synonymous with *G. c. capensis* and *G. c. wardi* (Lydekker, 1904; Ansell, 1968; Dagg, 1971). However, these findings appear to be only loosely, if at all, based on knowledge of the giraffe's actual range. Shortridge (1934) postulated, conversely, that *G. c. angolensis* and *G. c. wardi* could be taken as akin to the extinct *G. c. capensis* from the greater Orange River region of

north-western South Africa and southern Namibia. Numerous authors have described the northern Namibian population as *G. c. angolensis* from as early as 1934, however, this has not translated into the taxonomic literature (Shortridge, 1934; Zukowsky *in* Shortridge, 1934; Krecek *et al*., 1990; Skinner & Smithers, 1990; Scheepers, 1992; ASG, 1996; Fennessy *et al*. 2003). The confusion and indifferent classification of the Namibian population of giraffe indicates divergent views among authors, and also highlights the fact that subspecific classification of giraffe has been based upon limited reference specimens and little knowledge of their ranges.

Authors describing the range of *G. c. angolensis* as occurring throughout northern Namibia have regarded the subspecies distribution to extend to south-western Zambia, throughout northern and western Botswana and into southern Angola (e.g. Shortridge, 1934; Zukowsky *in* Shortridge, 1934; Skinner & Smithers, 1990; ASG, 1996). This original classification of Namibia's giraffe was based on the premise that the Kunene and Kavango Rivers acted as a geographical barrier between the populations in Angola (*G. c. angolensis* sensu stricto) and Namibia. However, the Kunene and Kavango Rivers do not run the length of the shared Angolan/Namibian border and, historically, the river has often been low enough for animals to migrate between the two countries (R. Simmons, personal communication). In hindsight, there is therefore no reason to suspect that the giraffe populations of Angola and Namibia are separate subspecies. As for the giraffe of Namibia and South Africa being taxonomically similar, original samples of giraffe from the region are insufficient and analysis to date has proven to be unclear.

Seymour's (2002) recent review of giraffe taxonomy, based on mitochondrial, morphological and pelage pattern variations, hypothesised that individuals from across the entire southern African range (subspecies *G. c. angolensis* and *G. c. giraffa*) belong to a single subspecies. No geographically structured phenotypic variation was observed, while two genetic haplotypes in the region overlapped extensively. However, Seymour (2002) stated that considerable uncertainty surrounds the subspecific placement of the Namibian giraffe with *G. c. angolensis*, and that it was not possible to definitively separate the Angolan subspecies from the other putative southern subspecies. For this reason, Seymour (2002) proposed that *G. c. angolensis* should be maintained as a provisional subspecies until appropriate re-evaluation is undertaken. With such inconclusive results, small sample

size from Angola and Namibia, and a poor understanding of the regional distribution of giraffe, little can be inferred from Seymour's (2002) study on the Namibian giraffe taxonomy.

The results and discussion presented in Chapter 3 provide microsatellite baseline data on the genetic architecture of the Namibian giraffe population and highlight a distinct separation between giraffe populations in the region. These findings will assist in the ongoing review of taxa. For convenience here (based on evidence proposed in Chapter 3), I will refer to the Namibian giraffe as *Giraffa camelopardalis angolensis*.

The typical phenotype of the Namibian giraffe is detailed below:

- bull has two ossicones (horns) (Seymour, 2002);
- large brown body spots, the edges of which are slightly notched (Lydekker, 1904) or with angular projections (Krumbeigel, 1939) on a near-white ground colour;
- body spots are ill-defined (Lydekker, 1904), or well differentiated (Dagg & Foster, 1982) and the margins are clear and complete (Krumbeigel, 1939);
- spots on the neck and rump break up into much smaller spots than the rest of the body;
- legs are fully spotted;
- lower part of the face is spotted; and
- a small white ear patch is present.

Various authors (e.g. Roosevelt & Heller, and Steihardt *in* Shortridge, 1934) have hypothesised that there may be two distinct subspecies of giraffe in Namibia's north-west - one smaller with dark spots, and the other larger with paler, more star-shaped, blotches. This seems unlikely. Although Namibia's desert-dwelling giraffe resembles in part the paler variety noted above, it is not a distinct subspecies from others in the country. However, it is possible that Namibia's desert-dwelling giraffe should be classified as a separate 'eco-type' or 'bio-type', similar to the World Conservation Union [International Union for Conservation and Nature and Natural Resources (IUCN)] status afforded to Namibia's desert-dwelling rhinoceros *Diceros bicornis bicornis* (CITES, 2001; M. Hearn, personal communication) and potentially the desert-dwelling elephant *Loxodonta africana*.

Table 1.1. Taxonomy, distribution, abundance and status of the nine described giraffe subspecies. Adapted from East (1999).

Subspecies type • (synom. subspecies)	Common name	Distribution	Estimated numbers	Country status†	Subspecies status
G. c. angolensis • *(G.c. infumata)*	Angolan	Angola Botswana Namibia Zambia	- 11 700 6 690 Unknown	Ex S/I I S/D	Increasing
G. c. antiquorum • *(G. c. congoensis)*	Kordofan	Sudan	-	Ex	Possibly Extinct
G. c. camelopardalis • *(G. c. typica)*	Nubian	Eritrea Ethiopia Sudan	- 160 -	Ex D Ex	Decreasing
G. c. giraffa • *(G. c. capensis)* • *(G. c. wardi)*	Cape/Southern	Mozambique South Africa Swaziland Zimbabwe	- 7 880 >25 5430	Ex S/I S/I S/D	Stable/Increasing
G. c. peralta	Nigerian	Cameroon Chad CAR* Mali Niger Nigeria	1 360 800 >550 <10 70 -	S/D D D D I V	Decreasing
G. c. reticulata	Reticulated	Ethiopia Kenya Somalia	<140 27 540 -	S/D S/D Ex	Stable/Decreasing
G. c. rothschildi	Rothschild's	Kenya Sudan Uganda	>140 - >150	D Ex S/I	Decreasing
G. c. thornicrofti	Thornicroft's	Zambia (Luangwa valley)	1 160	S	Stable
G. c. tippelskirchi	Masai	Kenya Rwanda Tanzania	17 330 20 28 860	D S/D S/D	Decreasing

†Ex – extinct; S – stable; I – increasing; D – decreasing; V – vulnerable; *CAR – Central African Republic

1.3.2. Conservation status of giraffe Africa-wide

The giraffe has long been considered one of Africa's most charismatic and ecologically and economically important species of megafauna. It was estimated that giraffe numbers exceeded 140 000 individuals throughout Africa in 1998 (East, 1999). This figure is less than a third of the current numbers of the African elephant, which is classified as 'endangered', yet the conservation status and profile of giraffe are very different (ASG, 1996; East, 1999). Specifically, giraffe are not listed in the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES), while the IUCN Species Survival Commission Red List status for giraffe, as classified under 1996 IUCN Redlist categories and criteria version 2.3 is: "Lower risk: conservation dependent" (ASG, 1996). As a species, giraffe do not satisfy the criteria for any of the vulnerable, endangered or critically endangered categories outlined by the IUCN (ASG, 1996). The classification of giraffe as 'conservation dependent' does allow for one proviso should any future change in status occur. That is, if any part of the current conservation programmes ceases, then giraffe may qualify for one of the threatened categories within five years (ASG, 1996).

Historically, the loss of appropriate habitat has had a major impact on the distribution and range of giraffe (Skinner & Smithers, 1990; ASG, 1996; East, 1999). As habitat loss and habitat fragmentation is continuing, it is imperative to undertake continued assessments of giraffe status. The Rothschild's *G. c. rothschildi* and Niger giraffe *G. c. peralta* are two of the nine subspecies whose habitat is diminishing and whose conservation status should be re-assessed with some urgency. But there is little reason to assume that any of the remaining subspecies are secure.

1.3.3. Conservation status of giraffe in Namibia

The population status of the Angolan giraffe *G. c. angolensis* in Namibia, as classified on the Government of the Republic of Namibia's checklist and provisional national conservation status report to the IUCN Red List, is 'Vulnerable (?) & Peripheral' (Griffin, 1999). As indicated by this classification, Namibian giraffe are more than likely to become

endangered if present threatening factors persist (Griffin, 1999). Included in this category are populations or taxa that are:

- decreasing because of over-exploitation, intensive destruction of habitat or other environmental disturbance;
- seriously depleted and whose ultimate security is not assured; and
- still abundant but are under threat throughout their range.

In addition, Griffin (1999) noted that Namibia is not the sole guardian [of this giraffe subspecies] and, while their local disappearance would not necessarily result in the extinction of the taxon, it would reflect deterioration of the Namibian environment. In Namibia, giraffe are one of ten species that are classified by the Ministry of Environment & Tourism (MET) as specially protected. This classification does not limit hunting of giraffe, but rather requires hunters to obtain specific hunting permits from the Namibian Government before a licence is granted. Other countries, including Botswana, Niger and Swaziland, classify giraffe as a specially protected species and do not allow the species to be hunted (Ciofolo, 1995; Monadjem, 1998; East, 1999; T. Reilly & M. Ives personal communication). This conservation status is considered a good indication of giraffe's exalted status in parts of African society.

In the mid to late 1970s a long-term study was undertaken to investigate the status of the desert megafauna (elephant, rhinoceros and giraffe) in the Kaokoveld, northern Namib Desert (Walker, 1978; Hall-Martin *et al.,* 1988). The study reported that all megafauna were in trouble. The desert-dwelling giraffe was described as a mystery animal surviving in an environment with minimal food and water resources. Walker (1978) stated that the desert giraffe represented a 'new dimension' in the animal kingdom and deserved the highest conservation priority. A decade on, Reardon (1986) postulated that the enigmatic desert-dwelling giraffe, as well as the elephant and rhinoceros, had no equivalent anywhere else in the world. Furthermore, he added that ecologically and aesthetically the giraffe is a priority species that is worthy of saving. Despite the hyperbole in some of Reardon's writing, this and other studies highlight the paucity of knowledge available on the Namibian giraffe. This thesis focuses on increasing our understanding, conservation awareness and management of the little-known desert-dwelling population in Namibia.

1.3.4. Historical distribution of giraffe Africa-wide

Historically, giraffe ranged throughout the northern and southern savannah regions of sub-Saharan Africa, from open savannah to scrub and open woodland, apparently avoiding dense forest and desert environments (Dagg & Foster, 1982; Skinner & Smithers, 1990; Estes, 1995; East, 1999) (Figure 1.2). A distinctive broad strip of moist Miombo woodland separates the current northern and southern range of the giraffe.

Lydekker's (1904) interpretation of geographical range of giraffe was simplistic and based upon a limited knowledge of their actual range. In Krumbeigel's (1939) review of giraffe taxonomy, better surveys were available, as were larger sample sizes, and the range map of Krumbeigel is in the generic sense closer to ranges understood today (compare Figure 1.1 & Figure 1.2). A number of authors (e.g. Dagg, 1962; Sidney 1965; Kingdon, 1979; Skinner & Smithers, 1990) have since described the geographical range of giraffe, although most still lack significant ground-truthing and differ greatly from each other.

Today, the range of giraffe is both patchy and discontinuous, from west Africa to the lower reaches of southern Africa (Skinner & Smithers, 1990; Estes, 1995; Dagg & Foster, 1982; Mills & Hes, 1997; East, 1999; IEA, 1998; Seymour, 2002). Over the past two decades, increased translocations of giraffe have resulted in range expansions in some areas, although not always in part of the species' known historical range (D. Gilchrist & T. Reilly personal communication). Similar to other African megafauna, such as elephant, rhinoceros and lion *Panthera leo*, shrinkage of available habitat due to human development, illegal hunting and disease have greatly reduced the numbers and range of giraffe (e.g. Dagg & Foster, 1982; Skinner & Smithers, 1990; Estes, 1995; Mills & Hes, 1997; East, 1999). Appropriate conservation and management steps have been undertaken to aid in the survival and protection of many species and habitats, such as classification of the black rhinoceros as a protected species on CITES Appendix 1 (CITES, 2001; IUCN, 2001), but not specifically of giraffe. It is hoped that findings from this research will be incorporated into a giraffe species survival plan for Namibia, and will contribute to conservation and management of the taxon throughout its extant range.

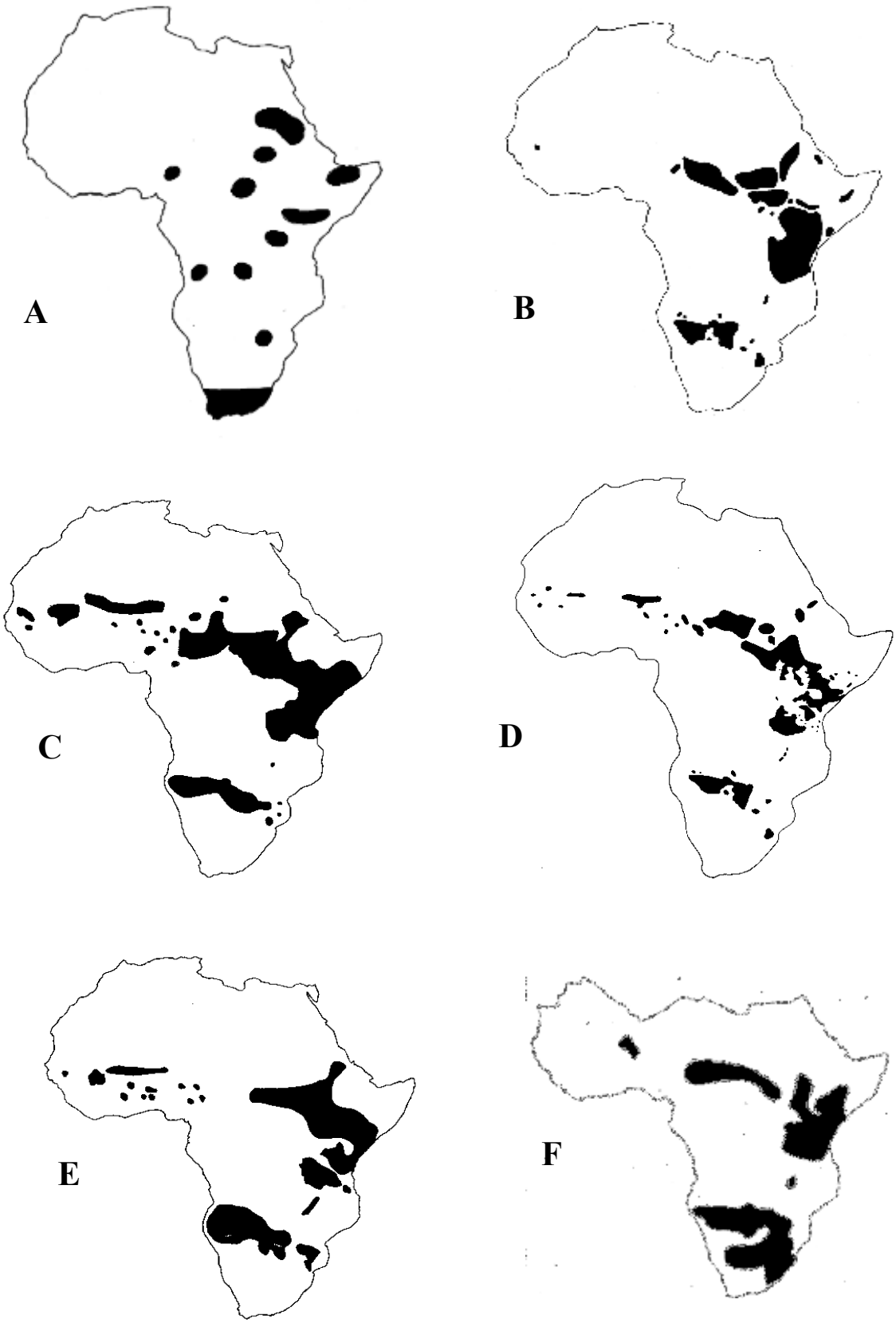


Figure 1.2. Historical range maps of giraffe. (A) Lydekker, 1904; (B) Dagg, 1962; (C) Sidney, 1965; (D) Kingdon, 1979; (E) Skinner & Smithers, 1990; and (F) East; 1999. Illustrations (A-D) redrawn by Seymour (2002) and (E & F) by author.

1.3.5. Historical distribution of giraffe in Namibia

The first recorded account of giraffe in Namibia dates to the travels of Captain Hendrik Hop, who ventured north of the Orange River in 1761 (Scheepers, 1990). During these travels a giraffe was captured and killed in the vicinity of the current day southern border town of Warmbad (Figure 1.3). This is also the first known record of a professional hunt of any wild animal species in Namibia.

Shortridge (1934) observed giraffe ranging throughout the former South West Africa, from Kaokoveld in the north-west, Grootfontein District in the northeast and further east into the Caprivi, east of the Kavango River. Furthermore, Shortridge (1934) postulated that giraffe wandered frequently into the Outjo and Etosha Pan of north-central Namibia, and infrequently into Ovamboland in the north-east (Figure 1.3). Shortridge (1934) estimated 400 giraffe throughout Namibia, of which approximately 200 were in the Kaokoveld and the remainder in the Grootfontein and Caprivi Regions.

The natural distribution of giraffe in southern Namibia is relatively unknown. Rookmaaker (1983) referred to various travellers and expeditions that observed giraffe north of the Orange River. Rookmaaker (1983) added that during Robert Jacob Gordon's expedition to Namaqualand in 1779, a giraffe was shot south of the Orange River, constituting the last record of giraffe in the north-west Cape Province of South Africa. Furthermore, the type specimen of the Cape giraffe *G. c. capensis* came from a sample shot near Warmbad in southern Namibia (Dagg & Foster, 1982; Rookmaaker, 1983). Therefore, it is likely that giraffe either persisted in low numbers or migrated frequently between southern Namibia and north-western South Africa. However, due to a combination of hunting pressure, human population expansion and disease, giraffe have been absent from the area for over a century (Shortridge, 1934; Rookmaaker, 1983). Translocations of giraffe into southern Namibia from the north of the country have only occurred in the past decade; previously they had been extinct from the region (Joubert & Mostert, 1974; 1975; Rookmaaker, 1983; H.O. Reuter, personal communication; personal observation). This recent activity has done little to help understand the historic taxonomy and distribution of the species.

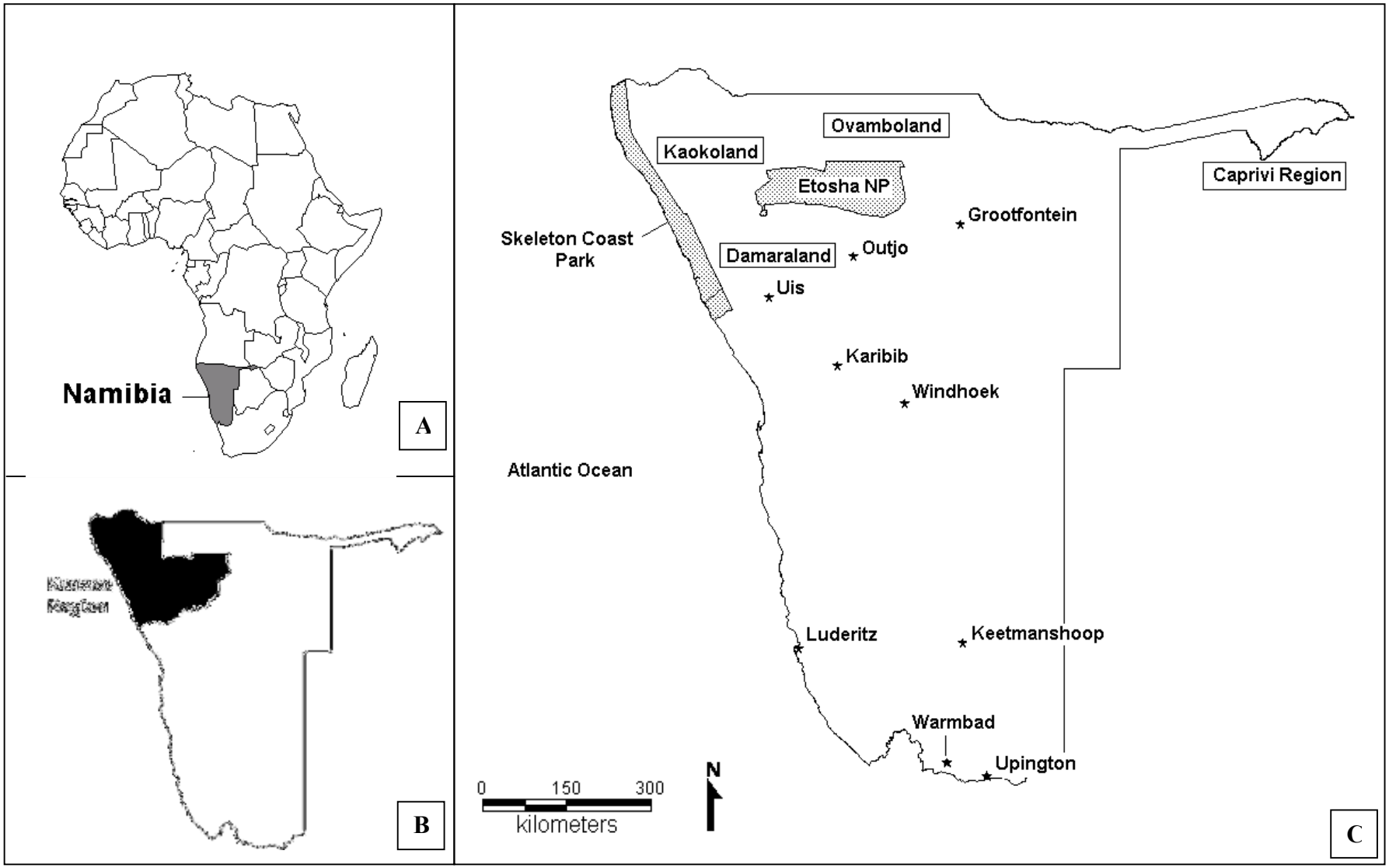


Figure 1.3. (A) Location of Namibia within Africa; (B) Kunene Region in Namibia, and (C) Selected towns, parks and regions in Namibia.

Shortridge (1934) noted that giraffe skull remnants were found in several areas previously assumed to be outside the natural distribution of giraffe. Skulls from a cave in the Karibib district in the central west region of Namibia, from Gobabis in the central east, as well as in the vicinity of coastal Luderitz in the southwest, supported the suggestion that giraffe may once have ranged over much of Namibia. In addition, Shortridge (1934) also stated that folklore surrounding giraffe is evident in the indigenous culture in southern Namibia. It is therefore unclear to ascertain their true historic distribution of giraffe countrywide.

Namibia's desert-dwelling giraffe currently occupy a habitat different from all other giraffe on the African continent. They appear to be almost solely dependent on the riparian environments of the westerly flowing ephemeral rivers. Their presence in this desert environment contradicts the assertions of numerous authorities on giraffe (e.g. Dagg & Foster, 1982; Skinner & Smithers, 1990; Estes, 1995; East, 1999), although evidence supports that, historically, giraffe ranged across much of Namibia's north-west (Shortridge, 1934). Such divergence in learned opinion highlights the very limited research that has been carried out on Namibian giraffe, and specifically the desert-dwelling population.

1.3.6. Historical estimates of giraffe in Namibia

In the 1970s, some 4 000 giraffe were estimated to populate Namibia (Joubert & Mostert, 1975). More recently, cumulative numbers from various population surveys have been tallied to yield estimates of around 5 000 individuals (Iipinge, 1997; Kolberg, 1998; Craig, 2000); however, the African Antelope Database (East, 1999) estimated some 6 690 individuals for Namibia. It is unlikely that the variation in estimation reflects true change in population size. The discrepancies in giraffe population estimates likely result, again, from limited research, a poor understanding of giraffe population dynamics in Namibia, and a lack of standardised methods used in calculating population estimates.

1.3.7. Historical estimates of giraffe in the Kunene Region

Giraffe have roamed Namibia's north-west for thousands of years. Petroglyphs, rock paintings and engravings of giraffe adorn many rock faces throughout the Kunene Region, while their importance as a ceremonial animal for the region's early inhabitants has also been reported (Sherr, 1997; Pager, undated).

According to Shortridge (1934), approximately 200 giraffe resided in the Kaokoveld (Kunene Region) in the early 20th century and had a restricted range to the east (Shortridge, 1934) (Table 1.2). Local residents reported that no giraffe existed in the western desert reaches of the Kunene Region in the early 1900s (Shortridge, 1934), however, this may have been an inaccurate assumption from residents living in the Kunene's east. Almost four decades later, giraffe were widespread throughout this western region with low numbers observed in the eastern Kunene (Owen-Smith, 1970; 1986; Joubert & Mostert, 1974). This situation persisted until the beginning of the 1980s, when small populations of giraffe began re-establishing themselves in the east (Viljoen, 1981). Some authors indicated that the apparent disappearance of giraffe from the eastern Kunene Region in the early part of the 20th century was the result of intensive hunting, predominantly for local consumption and use (Viljoen, 1981; Owen-Smith, 1970; Reardon, 1986; Scheepers, 1990).

Table 1.2. Historical overview of estimated giraffe numbers in the Kunene Region, 1934-2003.

Estimated No.	Survey Year	Source (Year)
200	1934	Shortridge (1934)
<100	1974	Joubert & Mostert (1974)
317	1982	Viljoen (1982)
285	1990	Carter (1990)
~450	1991	Scheepers (1992)
267	1995	Loutit (1995)
548	1998*	Craig (2000)
1 105	2000*	Craig (2000)
922	2002	NRWG (2002)
900	2003	NRWG (2003)

*Confidence Interval – 49.8%

Giraffe numbers in the Kunene Region declined from the 1980s to the 1990s despite observed population increases for all other wildlife in the region and the inception of focused conservation initiatives (Britz *et al.*, 1986; Carter, 1990). The decline may have been the result of giraffe moving onto adjacent commercial farmland to the east as well as due to continued small-scale poaching (Carter, 1990). Conflicting population estimates exist for giraffe for the early to mid 1990s (Scheepers, 1992; Loutit, 1995), while in 1998 the estimate was 548 individuals and in 2000 it was 1 105 (Craig, 2000). This latter increase of approximately 100% is not biologically feasible in the two-year period between surveys, considering that giraffe have a mean gestation period of 457 days (Hall-Martin & Skinner, 1978) and a mean calving interval of 19.9 months (Skinner & Hall-Martin, 1975).

Above average rainfall during the late 1990s and increased conservation awareness and monitoring may have contributed to increased numbers reported since the 1980s. Improved survey methods and analytical techniques have probably also provided better estimates of the population in the Kunene Region, despite the discrepancies noted above (Craig, 2000). More recently, conservative ground surveys have estimated giraffe numbers to be marginally lower than in 2000 (NRWG, 2002 & 2003). However, only limited conclusions can be drawn as sampling methods and extrapolation analyses varied between studies (Craig, 2000; NRWG, 2001).

1.3.8. Historical estimates of giraffe in the study region

This study took place in the catchments of the Hoanib, Hoarusib and Khumib Rivers (see Chapter 2 for overview of study region). No giraffe research or surveys have been undertaken in either the Hoarusib or Khumib River catchments, although it can be assumed that the pressures of local and commercial wildlife poaching in the 1960s-80s would have impacted on giraffe numbers in this part of the northern Namib Desert (Carter, 1990). In 1991, 22 giraffe (twelve bulls and ten cows) were translocated from western Etosha NP to the Purros area, Hoarusib River, to help re-establish the area's population. However, neither pre- nor post-translocation surveys were undertaken, limiting any comparative analyses or assessment of translocation success.

In the Hoanib River catchment, some historical data are available on the giraffe population, but they are neither consistent nor detailed. However, giraffe numbers do appear to have increased over the past 25 years (Cooper, 1980; Tarr, 1986; Scheepers, 1992; Fennessy *et al.,* 2003). An annual increase of 1.6% in the giraffe population was reported over an 11 year period between 1980 and 1991 (Viljoen, 1980; Scheepers, 1992), compared with a 1% increase over the following nine years, from 1991 to 2000 (Scheepers, 1992; Fennessy *et al*., 2003).

Scheepers (1992) postulated that the low population growth of giraffe in the Hoanib River catchment compared to other populations was a result of high calf mortality. Similar results had been observed in other giraffe populations (Dagg & Foster, 1982). However, this has not been confirmed (Scheepers, 1992; Fennessy *et al.* 2001; 2003). Movements out of the Hoanib River catchment may account for the low observed population growth (Cooper, 1980; Tarr, 1986; Scheepers, 1992; Fennessy *et al.,* 2003), although little is clearly understood of giraffe dispersal in this area.

1.4. Thesis aims and structure

Little research has been undertaken on the desert-dwelling giraffe population in Namibia, or on the entire giraffe population throughout Namibia. The Namibian Ministry of Environment and Tourism (MET) has recently proposed to down-list the giraffe from its specially protected status within the country. This proposal appears not to be based on any current research, as aside from this work, nothing else has been carried out in the past decade.

One of the driving forces behind the research in this study was to provide an overview of the population dynamics and ecology of desert-dwelling giraffe. Most importantly, I aimed to provide an overdue perspective on current giraffe density and range. Such baseline data would benefit the Namibian community-based natural resource management (CBNRM) program and communal conservancy management practices in providing steps towards economic sustainability in the future. I also aimed to provide valuable knowledge on giraffe survival strategies in an arid environment, as well as to provide data for

informed management decisions. Furthermore, I aimed to contribute to the broader knowledge of giraffe ecology and ethology, as well as to a more general understanding of herbivore adaptations and behavioural strategies in a desert environment.

My study aims specifically to:

- determine the genetic architecture of giraffe in Namibia;
- describe the population structure and dynamics;
- assess the seasonal and year-round movements of giraffe in relation to seasonal forage availability and the role that moisture and/or chemical content play in its selection;
- investigate foraging and activity of giraffe in a desert environment; and
- assess the behaviour of giraffe in a desert environment.

This study was not undertaken to highlight the desert-dwelling giraffe as a keystone species in an arid environment, nor was it the intention to evaluate the role of giraffe in driving biotic processes in the desert. However, evidence of the biotic role played by giraffe was obtained in this study, and emphasises the importance of conserving the species. Thus, it is particularly important to discuss the findings of this study with respect to historical and current conservation management practices and to provide information and baseline data for appropriate population management. It is also salient to identify particular adaptations and behaviours (activity and foraging) of the species at the extreme of its range, in order to gain insight into the best methods to conserve and manage this desert-dwelling megafauna.

The thesis comprises eight chapters. Chapter 2 presents a description of the study region and three main study areas. Chapter 3 provides an overview of the genetic architecture of the Namibian giraffe from two different areas, the northern Namib Desert (desert-dwelling giraffe) and Etosha National Park. In Chapter 4, the population structure and dynamics of the study species in the study region, the northern Namib Desert, are discussed. Chapter 5 presents analyses of home range and movement behaviour of the study species, while Chapter 6 investigates the activity budgets in an attempt to better understand behavioural adaptations in an arid environment. Chapter 7 assesses the foraging behaviour of the study species in relation to seasonal abundance, availability and chemical composition of forage

species, as well as the potential impact of giraffe and other factors on their preferred food plants. Finally, Chapter 8 reviews the main results and conclusions of the previous chapters and provides recommendations on appropriate management to achieve giraffe conservation in Namibia. It also provides a framework for continued research in light of historical conservation efforts and the Namibian community-based natural resource management program.

CHAPTER 2. STUDY REGION AND STUDY AREAS

For the purpose of this thesis, the generic term 'study region' refers to the whole area in which the desert-dwelling giraffe population was researched. The study region consisted of three study areas within the northern Namib Desert; the Hoanib, Hoarusib and Khumib River catchments, in which focused research efforts were undertaken for comparative analysis between and within the giraffe subpopulations.

2.1. Study region

The study region comprised part of the lower catchments of the Hoanib, Hoarusib and Khumib Rivers. These river catchments are the three northernmost of the twelve major westerly flowing ephemeral river systems that occupy the hyper- to semi-arid areas of western Namibia (Figure 2.1). All three ephemeral rivers end in the Namib Desert Sand Sea within the Skeleton Coast Park (SCP). Seasonal rainfall in the catchments is the major driving force behind their seasonal flow and, when heavy enough, results in the rivers flowing into the Atlantic Ocean.

The study region covers approximately 7 500 km^2. Located between a latitude of approximately 18.5°S and 19.5°S, and a longitude of approximately 12.5°E and 13.5°E, the study region ranges in altitude from near sea level in the west to approximately 1 200 m in the mountains. The three river systems in the study region are ecologically linked as wildlife migrates between the catchments (Viljoen, 1988; Jacobson *et al*., 1995). The riparian woodlands of the three catchment areas are the main source of life for all larger mammals of the region, from wildlife to domestic stock, and humans. Only some of the smaller vertebrates, such as the golden mole *Eremitalpa namibiensis* and lacertid lizards (e.g. *Aporosaura anhcietae*), persist in the sand dunes away from the riparian woodlands (Louw & Holm, 1972; Seymour *et al*., 1998). The region predominantly comprises communal farmland, although it extends into the protected SCP in the extreme west of the Hoanib and Khumib River study areas. No fences restrict the free movement of wildlife between communal farmland and the protected SCP. The communal farmland is

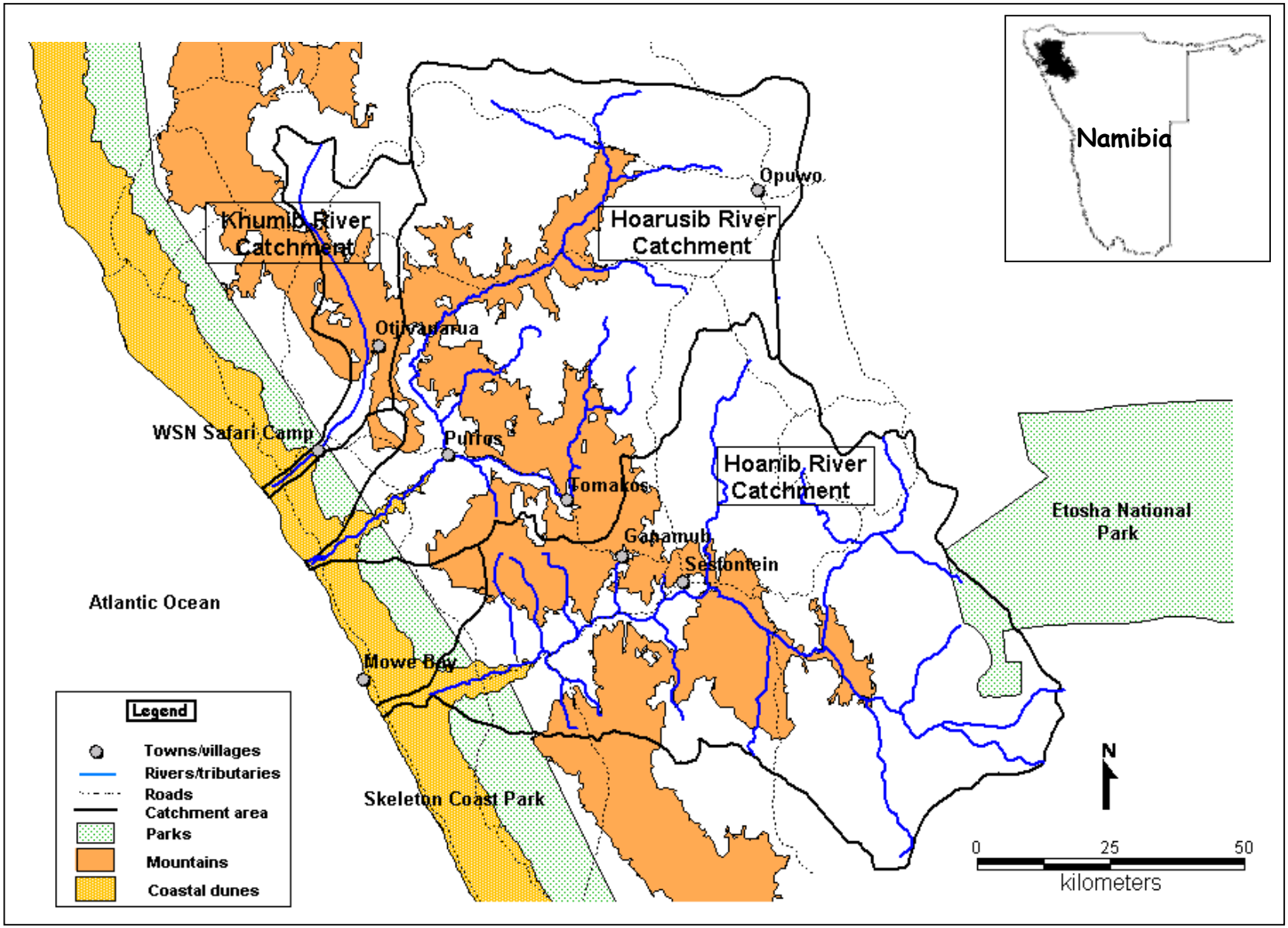


Figure 2.1. Hoanib, Hoarusib and Khumib River catchments in the Kunene Region. (Inset – Namibia with 3 catchments described)

‘organised’ into communal conservancies. A conservancy is a communally owned and managed area where local people manage, utilise and benefit from their wildlife and other natural resources. Conservancies allow people to diversify their livelihoods and provide a greater incentive for sound natural resource management.

Purros conservancy, which includes the Hoarusib River, was one of the first registered conservancies in the Kunene Region (Figure 2.2). The Khumib River study area lies partly within the boundaries of the Sanitatas communal conservancy, while after almost a decade of tribal and political differences, Sesfontein communal conservancy in the Hoanib River study area was registered in 2003 (G. Owen-Smith, personal communication; personal observation). Since 1993 sustainable wildlife hunting has occurred in the north-western conservancies, however, no legal hunting of giraffe has been undertaken in the study region (G. Owen-Smith & C. Nott, personal communication; personal observation).

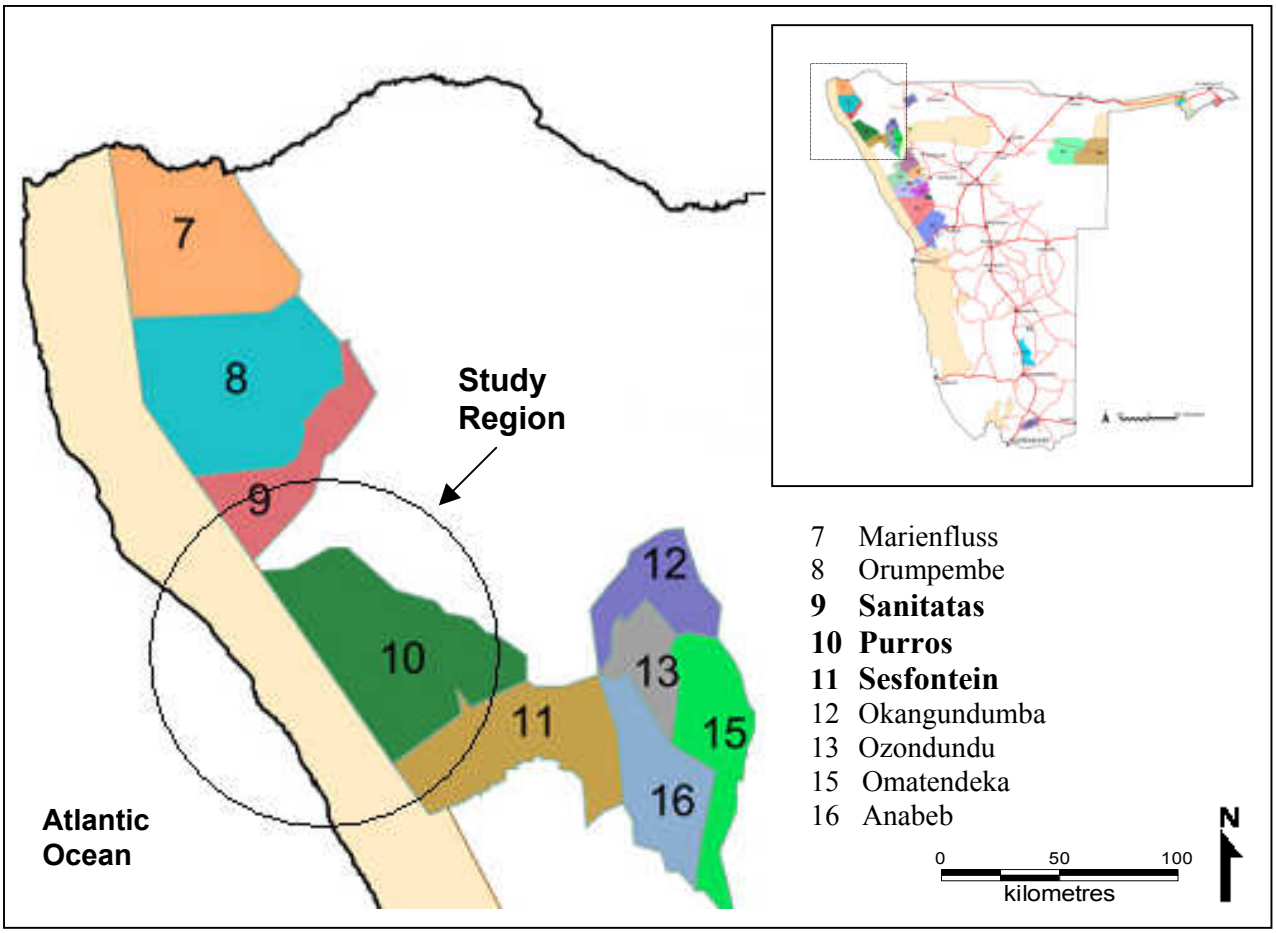


Figure 2.2. Registered communal conservancies in north-western Namibia, indicating those in the study region. Adapted from Tagg (2004).

The density of wildlife throughout the study region is substantial for such an arid environment (Jacobson *et al*., 1995), although the species richness of large mammals is far less than in more densely vegetated, mesic environments (Holmes, 1992; Berger, 1997). The wildlife in the region includes medium and large sized mammals (Table 2.1), as well as many endemic and near-endemic avian species (Griffin, 1999; Jarvis *et al*., 2000).

Table 2.1. Medium to large mammals in the Kunene Region.

African Elephant	*Loxodonta africana*
Black-backed Jackal	*Canis mesomelas*
Black Rhinoceros	*Diceros bicornis bicornis*
Brown Hyena	*Hyaena brunnea*
Chacma Baboon	*Papio ursinus*
Cheetah	*Acinonyx jubatus*
Giraffe	*Giraffa camelopardalis*
Hartmann's Mountain Zebra	*Equus zebra hartmannae*
Lion	*Panthera leo*
Leopard	*Panthera pardus*
Oryx	*Oryx gazella*
Springbok	*Antidorcus marsupialis*
Spotted Hyena	*Crocuta crocuta*
Steenbok	*Raphicerus campestris*
Ostrich*	*Struthio camelus*

*not a mammal but included because of its economic importance in the region.

2.2. Climate

2.2.1. Seasons and precipitation

The study region in north-western Namibia lies in the arid and semi-arid northern Namib Desert. The Namib Desert's climate nearer the Atlantic Ocean is characterised by low average temperatures, high humidity and the presence of fog, with a marked increase in temperature and a decrease in humidity eastwards from the coast (Seely, 1978; Tarr & Tarr, 1989). Precipitation, in the form of rain, is regarded as the single most important

factor in desert and semi-desert ecosystems and a direct correlation between rainfall and vegetation cover has been observed in the northwest (Seely, 1978; Viljoen, 1980; Tarr & Tarr, 1989). In general, rainfall is highly localised and can be described as spatially and temporally irregular (Seely, 1978; Sharon, 1981). Rainfall in the Namib Desert occurs predominantly as localised convective storms, which are relatively stationary and increase in frequency and intensity with altitude inland from the coast (Sharon, 1981).

The climate of Namibia's northwest can be classified into two distinct seasons; a wet and a dry season. The dry season is further divided into a cold-dry and hot-dry season based on ecological considerations, mean monthly rainfall and temperature (Figure 2.3) (Viljoen, 1988). The northern Namib Desert lies in the rain shadow of the Etendeka and other north-south escarpment mountains. It receives limited rain due to the warm Agulhas current on Africa's east coast (Jacobson *et al.,* 1995), therefore seasonal conditions are extremely variable.

The wet season (March to May) follows the long hot-dry season (September to February), and is characterised by higher than average mean rainfall. The cold-dry season extends from June to August. Rainfall throughout most of the study region is extremely low, at <100 mm per annum. The yearly mean rainfall at Möwe Bay is 13.2 mm per annum with 90% variability (Jacobson *et al.,* 1995; MWTC, 2000). Drought, or more appropriately periods of high aridity, is the norm throughout the study region.

The cold-dry season (June to August) has moderate daily temperature changes, and water is still available, although declining, after the rains from the wet season. The availability of free-water is a period when food for herbivores also becomes limited. The hot-dry season has the highest mean temperatures, and is a period of reduced forage and free surface water. Rainfall in October, November and December, the so-called 'small rains', is far less than evaporation and its influence on forage and water availability is limited.

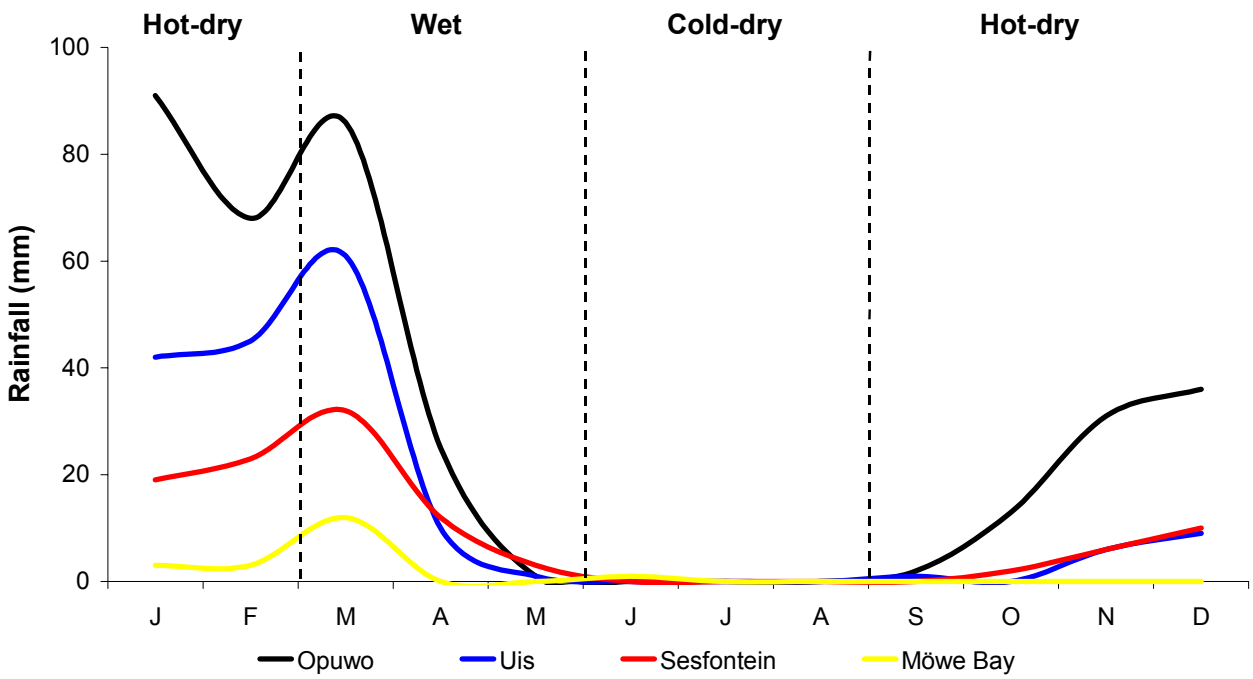


Figure 2.3. Mean monthly rainfall and seasons for areas in the Kunene Region (redrawn from Viljoen, 1988). Rainfall data are based on 50 years of observations from gauges within and surrounding the study region.

Coastal fog, which occurs predominantly during the cold-dry and hot-dry seasons, reaches up to 60 km inland and provides valuable precipitation that can ameliorate conditions for mammals and improve the quality of forage. Studies of fog quantity and frequency have not been undertaken in the study area, however, south in the central Namib Desert, fog evaluation trials have occurred (Henschel *et al*., 1998). There, it has been observed that fog is as much as five times more predictable as a water source than rainfall, with 30–180 mm of fog being deposited per annum; it occurs on 60–200 days per year, and extends up to 50 km inland (Pietruszka & Seely, 1985; Henschel *et al*., 1998; Seely & Henschel, 1998). Seasonal fog and the climate of the study region are influenced by the movements of the south Atlantic anticyclone, the cold Benguela current and offshore upwellings, in conjunction with the southeast trade winds on the coast (Jacobson *et al.,* 1995).

2.2.2. Temperature

Temperatures of the study region correlate with latitude and prevailing seasonal winds. Temperatures range from moderate to extreme, with temperatures in the hot-dry season

often reaching 50°C (Figure 2.4). In the cold-dry season, temperatures are lower and range from 5° to 27°C, particularly when the coastal fog penetrates inland and reduces the temperature markedly. The temperature fluctuations during the wet season are greatest as a lag period from the hot-dry season persists before the rains arrive and the temperature is lowered(MWTC, 2000). Along the coast and inland in the SCP, there are smaller fluctuations in temperature and the climate is markedly cooler.

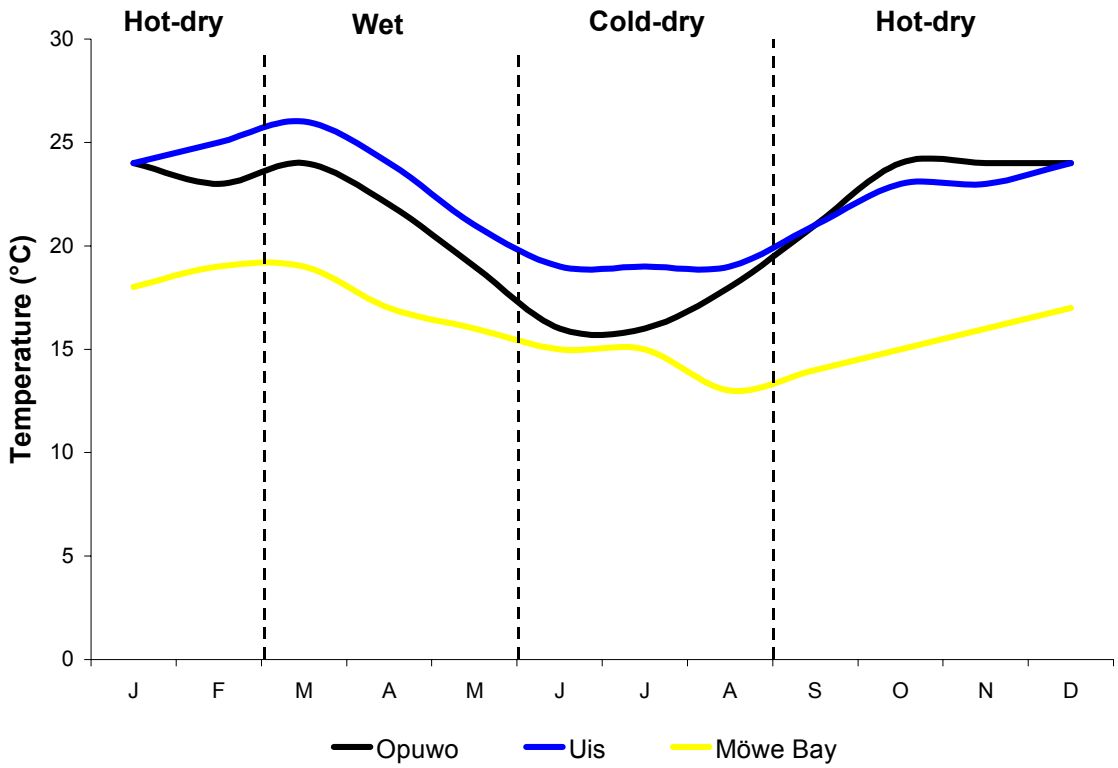


Figure 2.4. Mean monthly temperatures and seasons for areas in the Kunene Region (redrawn from Viljoen, 1988). Temperature data are based on 50 years of observations from gauges within and surrounding the study region.

2.3. Study region broad vegetation and habitat types

Between the dune sea in the west and the escarpment to the east lies the northern Namib Desert, a topographically mountainous region consisting of undulating gravel plains intersected by dry riverbeds and inselbergs, with a diverse and endemic flora (Giess, 1971; Jacobson *et al.,* 1995). The northern Namib Desert is an extension of the southern and central Namib Desert and is classified as hyper-arid in the west to semi-arid in the east (Giess, 1971; Coe & Skinner, 1993: Jacobson *et al.,* 1995; Kingdon, 1997).

Scheepers (1992) described the region's vegetation as sparse, with woody vegetation restricted mostly to riverbeds (see sections 2.4.1-2.4.3 for lists of the dominant plant species). Viljoen (1988) described seven broad habitat types within the study region (Table 2.2).

Table 2.2. Study region habitat types, percentage of region occupied, and broad description of habitat categories. Adapted from Viljoen (1988).

Habitat type	Percentage of study region	Broad description
Floodplains	0.5	Abundance of shrubs and annual grasses on alluvial plains where water accumulates during river floods
Sandy plains	2.4	Wide, deep sandy plains with some perennial grass cover
River courses	2.7	Dry river courses that support large trees and shrubs
Sand dunes	5.9	High semi-permanent dunes with occasional annual grasses
Rocky plains	21.6	Shrubs and annual grasses on plains covered with rocks <300 mm in diameter
Gravel plains	32.0	Annual grasses and herbs on flat gravel plains with no trees
Mountains	34.9	Extremely rocky terrain with mostly shrubs and annual grasses on steep slopes; predominantly 100-600m

Of the various habitat types, the woodlands of the river courses and floodplains are perhaps the most important for large mammals. Although they comprise just over 3% of the study region, these woodlands provide essential forage and shelter for many species on a year-round basis.

2.4. Study areas

2.4.1. Hoanib River study area

The Hoanib River originates on the western edge of Etosha National Park (NP), and flows westerly through commercial and communal farming areas and, near its mouth, traverses the protected SCP. The Hoanib River catchment occupies an area of 17 200 km^2, 3% of which occurs as private farm lands, 91% as communal farm lands and 6% as the protected

Etosha NP and SCP (Jacobson *et al.,* 1995; Leggett, 1999). The Hoanib River constitutes the boundary between the former Damaraland and Kaokoland Homelands. Since Namibian independence (1990) these two areas have been incorporated into the Kunene and Erongo Regions.

The Hoanib River study area is approximately 3 750 km^2 (Figure 2.5). It extends from the Dubis wetlands in the Hoanib River, south west of Sesfontein, westerly towards the Hoanib floodplain inside the SCP, for approximately 60 km. Five tributaries of the Hoanib River form part of the study area, however, access to these (Ganamub, Obias, Mudorib, Swaragab and Tsuxub Rivers) was sometimes restricted by seasonal rainfall.

The Hoanib River catchment is one of the prime wildlife viewing areas in Namibia and contains populations of several species of large mammals (Table 2.1) that are classified by IUCN/Species Survival Commission as rare and/or endangered (Jacobson *et al.,* 1995; ASG, 1996; Leggett, 1999). Up until the 1980s access was restricted to the Hoanib River study area and thus tourism was limited. Today, tourism is the predominant land use in the remote communal land with both self-drive and overland tour groups frequenting the area. The northern bank of the Hoanib River constitutes the northern boundary of the private Palmwag tourism concession area, although access into the concession area, including the Hoanib River, is not restricted. One permanent tourism camp, a small, recently developed communal/non-government (NGO) tourism joint enterprise, is located on the southern bank of the Hoanib River immediately east of the Dubis wetlands. No permanent villages or settlements exist along the Hoanib River, but seasonal settlements occur at the top of the Ganamub River, a northern tributary, as well as east of the Dubis wetlands. The population density is extremely low, with less than 50 communal farmers who migrate seasonally with their livestock into the Hoanib River study area (Sesfontein Conservancy, unpublished data). The Dubis wetlands in the east of the study area are the only permanent waters in the riverbed, while seasonal water is available following flood events.

The vegetation along the Hoanib River changes east-west along a rainfall gradient. On the plains to the north and south of the Dubis wetlands, the vegetation is sparse Mopane *Colophospermum mopane* woodland, while the riparian woodland is forage-rich and consists predominantly of *Faidherbia albida, Colophospermum mopane, Acacia erioloba,*

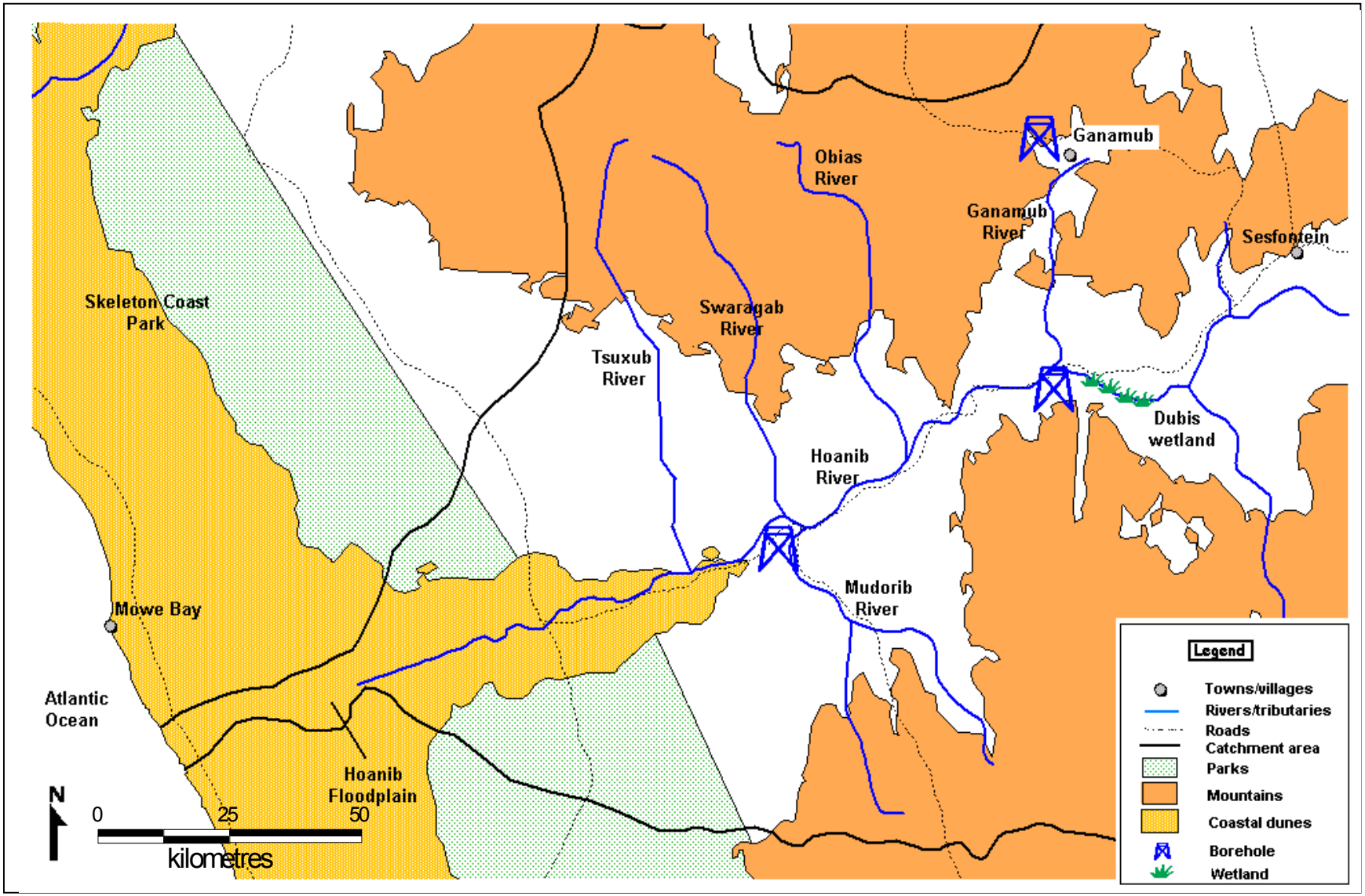


Figure 2.5. Hoanib River study area.

A. tortillis, Combretum imberbe, C. wattii, Salvadora persica and *Tamarix usneoides*. Along the tributaries and into the mountains, *Maurea schinzii, Terminalia prunioides* and *Commiphora* spp. occur, as does an array of perennial and annual grasses, herbs and forbs. Within the SCP no vascular vegetation exists outside the river course. The broad Hoanib floodplain, covering 70 km^2, lies to the east of the coastal dunes and provides seasonal forage for wildlife after flood events (Viljoen, 1988; Jacobson *et al.,* 1995; Leggett, 1999).

2.4.2. Hoarusib River study area

The Hoarusib River is a large-volume river with a broad catchment that encompasses the regional capital of the Kunene Region, Opuwo. The Hoarusib River catchment occupies an area of 15 100 km^2 (Jacobson *et al.,* 1995). Ninety-eight percent of the catchment is on communal land while the remaining 2% is in the SCP (Jacobson *et al.,* 1995). Aside from tourism, there is no formal private sector activity in the study area. Community-based wildlife tourism, predominantly from self-drive and overland tour groups, has resulted in the establishment of a community campsite, a traditional village and an industry based on the sale of locally produced crafts around Purros.

The Hoarusib River study area covers some 2 750 km^2 (Figure 2.6) and extends for 25 km south-west to the Hoarusib Poort (gorge), the confluence of the Hoarusib and Gomatum Rivers. No giraffe or spoor of giraffe has been reported either upstream or downstream of these points in the past decade. The Hoarusib River study area also extends east from the Hoarusib Poort along the Gomatum River for 40 km. The mountainous terrain and tributaries to the south of the Gomatum River were included into the Hoarusib River study area, although seasonal accessibility was limited.

The vegetation along the Hoarusib and Gomatum Rivers differs little from that in the Hoanib River, although the density of trees is greater along the Hoarusib. On the plains adjacent to the Hoarusib River, vegetation is sparse Mopane woodland. The riparian woodlands in the Hoarusib River study area provide a relatively forage-rich habitat consisting predominantly of *F. albida, C. mopane, A. erioloba, C. imberbe, S. persica,*

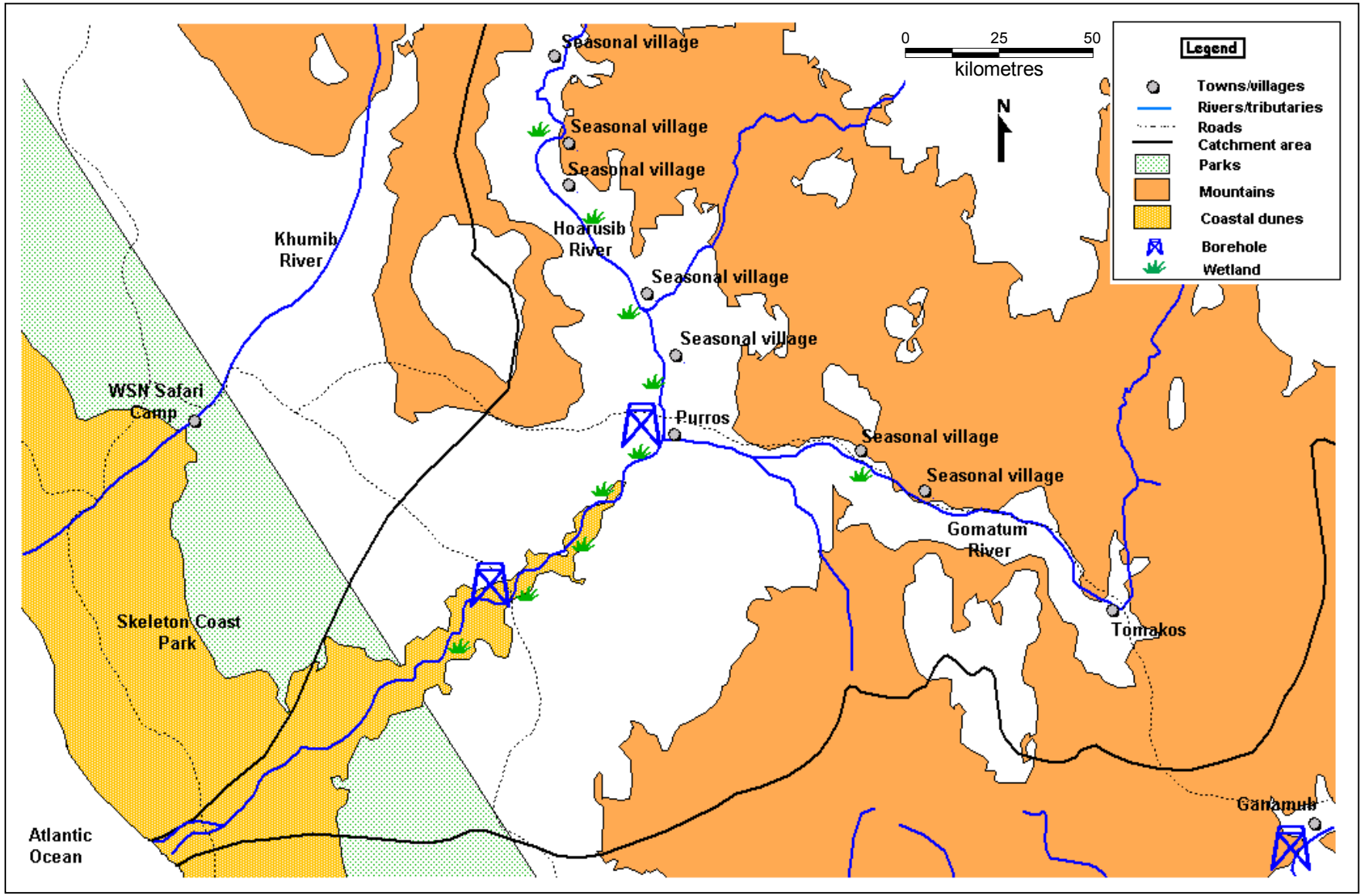


Figure 2.6. Hoarusib River study area.

Euclea pseudebenus, Hyphaene petersiana, Balanites welwitchii and *T. usneoides*. Along the tributaries and into the mountains, *M. schinzii* and *Commiphora* species flourish. Perennial and annual grasses, herbs and forbs are also present. Numerous perennial and ephemeral wetlands occur along the length of the Hoarusib River and provide surface water for wildlife, domestic stock and communal farmers.

Numerous permanent and seasonal villages, including Purros and Tomakos, are located within the Hoarusib River study area. Purros has the largest population west of Sesfontein, numbering up to 250 people at any one time, but is seasonally variable depending on rainfall. Tomakos, to the east of Purros, is a small settlement of less than 20 people. Residents migrate frequently between Purros and Sesfontein with domestic stock. Other seasonal villages are dispersed throughout the study area and are all within close proximity to either the Hoarusib or Gomatum main riverbeds.

2.4.3. Khumib River study area

The Khumib River originates north east of the study area and flows south-west for about 80 km into the SCP (Figure 2.7). The Khumib River catchment occupies an area of 2 200 km^2 – seven percent is in the protected SCP and 93% is on communal land (Jacobson *et al.,* 1995). Human population density throughout the catchment is very low, comprising only 200 people in total. Fewer than 25 communal farmers reside within the Khumib River study area, all of which are nomadic. Inside the SCP a high-price, low-volume fly-in tourism concession, managed by Wilderness Safaris Namibia (WSN), operates an ecotourism venture that accommodates up to 24 guests per week. Currently, this is the only private tourism concession within the SCP and the study area. Very few self-drive and overland tourists explore the Khumib River due to its remoteness and inaccessibility.

The Khumib River study area is some 1 000 km^2 in area. It extends 70 km from the middle reaches of the catchment on communal land, west down river to the WSN lodge inside the SCP. Minor tributaries of the river were also included in the study area, although giraffe were observed predominantly along the bed of the Khumib River and on its adjacent plains.

The vegetation along the Khumib River is the least dense of the three rivers. On the plains upstream, adjacent to the dry riverbed, sparse Mopane woodland predominates. The riparian woodland in the Khumib River is also not as diverse as that of the Hoanib or Hoarusib Rivers, but is still relatively forage-rich for such an arid environment. The riparian woodland consists predominantly of *C. mopane, A. erioloba, C. imberbe, S. persica, E. pseudebenus, B. welwitchii, T. usneoides, F. albida, Acanthosicyos horridus* and *Salsola* spp. Along the tributaries and in the surrounding mountains *B. albitrunca, M. schinzii* and *Commiphora* species occur sparsely, while perennial and annual grasses, herbs and forbs are dominant.

One permanent spring, Sarusas, in the SCP, and numerous seasonal springs in the mountains provide surface water for the wildlife of the area. Seasonal villages exist in the eastern reaches of the Khumib River study area, with communal farmers using hand-dug wells to obtain water for domestic stock.

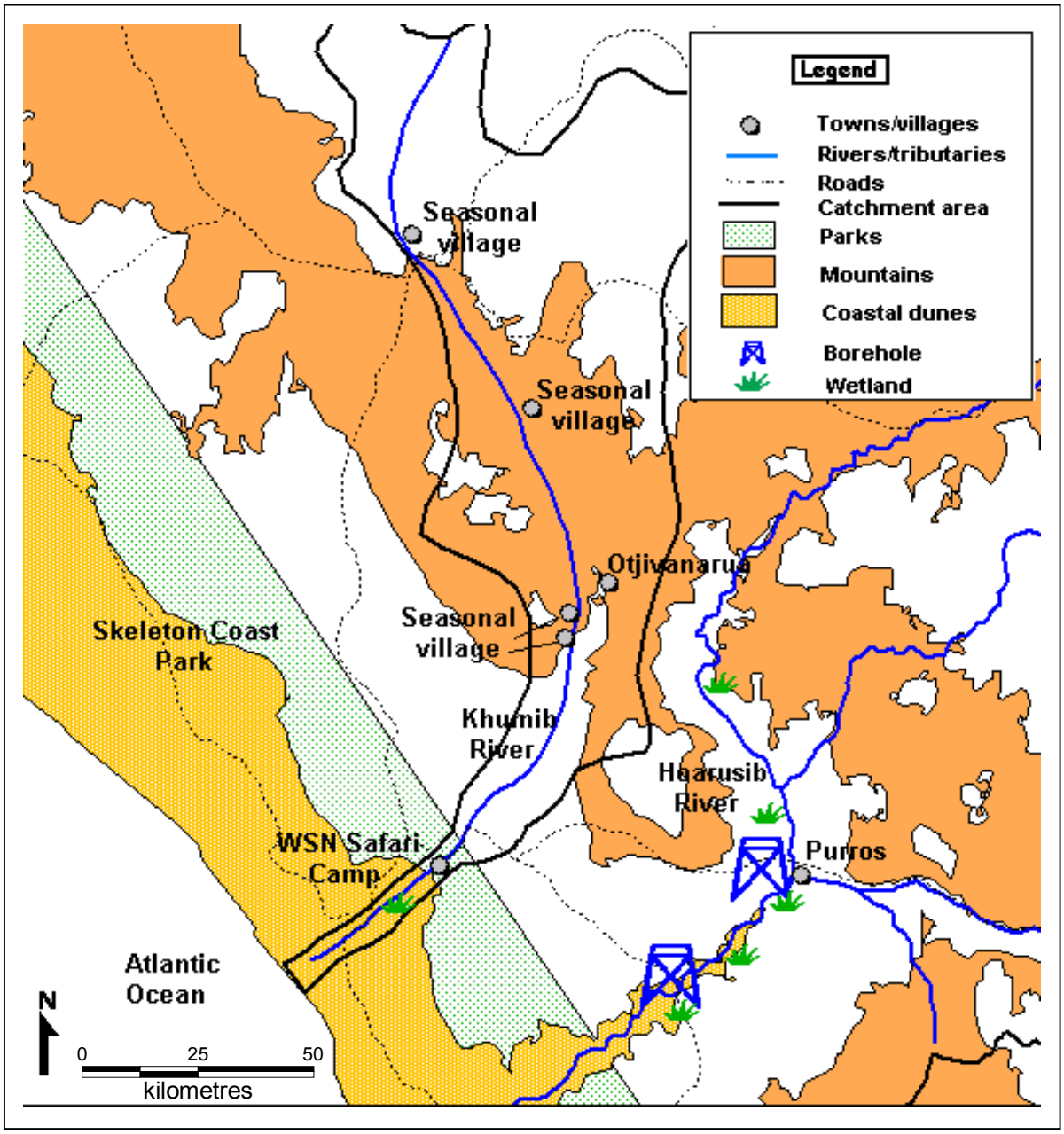


Figure 2.7. Khumib River study area.

2.5. Regional development in the study region

Many development projects are being implemented and planned for the study region and Kunene Region by various Namibian government ministries, including the Ministry of Agriculture, Water and Rural Development and Ministry of Lands, Resettlement and Rehabilitation, as well as NGOs. These proposed developments include the declaration of

Sesfontein as a town and associated increases in infrastructure in the area, focusing on the dense population centres in the central Kunene Region. One of the larger development proposals includes construction of a deep-sea harbour at Möwe Bay, which would be located between the mouths of the Hoanib and Hoarusib Rivers in the SCP (EEAN, 1992; Urban Dynamics Africa, 1999). A preliminary study (EEAN, 1992) recommended that the project should not be undertaken, although more recent plans to upgrade road networks in the region suggest that a re-assessment could be feasible (WSN, unpublished report). Agriculture, mining and tourism activities are ongoing in the SCP and/or on adjacent communal land, and can be expected to increase in the future.

Wildlife and wildlife-based tourism is becoming increasingly important for the livelihoods of the communal residents of Namibia's north-west (e.g. Jones, 1995; Ashley & Barnes, 1996; Vaughan & Katjiua, 2002). The ability to obtain revenue and employment from communal campsites, traditional villages, sustainable hunting and the sale of crafts could improve the livelihoods of many residents. Large-scale tourism operators have recently created joint-venture agreements with several communal conservancies in the Kunene Region, for example, WSN Camp in the SCP (Khumib River study area), with Purros and Sanitatas conservancies. All parties benefit from such joint ventures, such as from profit sharing and employment of local staff for conservancies, to the gaining of exclusive or preferred access for tourism operators to wildlife-rich communal areas and traditional villages (e.g. Jones *et al*., 2002).

The full extent of any proposed developments and/or activities in the Kunene Region, whether small or large-scale, is unknown due to the lack of co-ordination among the government and NGO organisations, as well as to the limited requirement for environmental assessments. One of the greatest limitations facing development in the study region and the greater Kunene Region appears to be water and access to it. If development projects continue throughout the region, increased demand for and consumption of water can be expected to have adverse effects on people, wetlands, vegetation and wildlife.

2.6. Conclusion

The study region extends north-south and east-west across a large portion of the northern Namib Desert. The distinct geographical separation of the ephemeral rivers and the differences in human use associated with them provides a clear methodological separation for assessing subpopulations or study areas in the greater study region. However, as climate, animals and vegetation types are similar between each of the study areas, it allows for the compilation of data sets for analysis where sample sizes obtained were not sufficient enough in each area.

CHAPTER 3. GENETIC ARCHITECTURE OF THE NAMIBIAN GIRAFFE

This chapter describes some aspects of the genetic architecture of two giraffe populations in Namibia, the desert-dwelling giraffe in the northern Namib Desert and in Etosha National Park. The molecular structure within each of the giraffe populations is examined to determine whether the Namibian giraffe is a distinct subspecies, and to evaluate the relationship of the two study populations.

I collected all genetic samples of giraffe and they were then analysed as part of a larger collaborative giraffe research project that included the International Giraffe Specialist Group, Henry Doorly Zoo - Centre for Conservation and Research, Omaha, NB and the University of California Los Angeles (UCLA), CA. Thus, the results are not solely my own, but rather, I am one of the contributing authors (Brenneman *et al*., unpublished data). The results presented are original and have not previously been published.

3.1. Introduction

Similar to many ecologically based scientific investigation, the practice of taxonomy has often been directed by prevailing opinions and theory. For example, debate continues about the merits of the Biological Species Concept versus the Evolutionary Species Concept (see Adams, 1998; Seymour, 2002; Cotterill, 2003 for recent reviews). There is no universally accepted definition of what constitutes a species; more than twenty definitions have been proposed (Frankham *et al*., 2002). Historically, the majority of described species have been defined using morphological criteria and geographical range, although alpha taxonomy of this kind has been subjected to increasing criticism when it is not accompanied by molecular data (Frankham *et al*., 2002).

The subspecific taxonomy of *Giraffa camelopardalis* is similarly contentious. Nomenclature within the taxon is perplexing and often inconsistent within the literature (Ansell, 1971; Dagg & Foster, 1982; Skinner & Smithers, 1990; Seymour, 2002). However, the giraffe is recognised as a monospecific genus (Dagg, 1971), consistent with

the biological species concept (Frankham *et al*., 2002) as all forms of giraffe produce viable offspring when they interbreed. At the subspecies level, reservations have been expressed about our ability to classify giraffe appropriately, particularly with respect to distinguishing subspecies based on traditional skull morphology, pelage pattern and historical range (Dagg & Foster, 1982; Seymour, 2002; Brenneman *et al*., unpublished data). East (1999) could find little evidence to support the separation of populations into subspecies based on geographical barriers.

Recent taxonomic work on giraffe (Seymour, 2002; Brenneman *et al*., unpublished data; R. Brenneman, D. Brown & R. Seymour personal communication) indicates that the southern African populations have an intricate and tangled taxonomic history. This is reflected by uncertainties in their (apparent) historical and assumed current ranges, as indicated in Chapter 1 (Figure 1.1) and by the making of assumptions in some research if comparative data has been limited. For example, East (1999) arbitrarily clumped giraffe populations/subspecies together for the sake of 'ease', although this is inappropriate for conservation management purposes if the populations prove to be different subspecies.

The current subspecies classification of the Namibian giraffe is *G. c. giraffa* (Ansell, 1971). This decision was based on a review of the giraffe species that was undertaken by Lydekker in 1904. Seymour's (2002) recent review of giraffe taxonomy supports the placement of Namibian giraffe within *G. c. giraffa*. However, as discussed in Chapter 1, he also indicated that the Namibian giraffe is morphologically similar to *G. c. angolensis*.

With respect to the genus, Seymour (2002) reported that there was validity in recognising six of seven subspecies (limited samples limited the analysis of the other two recognised subspecies) based on their pelage patterns. However, 'diagnostic' characteristics such as pelage pattern and skull morphology were variable within populations. Similar variability was observed in this study of the desert-dwelling population in the northern Namib Desert, where pelage pattern and colour differ markedly between individuals (see Appendix 1). Seymour (2002) was unable to comment on the subspecific classification by pelage pattern of *G. c. angolensis,* as insufficient sample size limited interpretation.

Using traditional skull morphology as well as landmark-restricted eigenshape analysis, Seymour (2002) showed that southern African giraffe, particularly bulls, are distinct from the northern giraffe populations. Within the southern African populations, evidence suggests that the giraffe are a single entity with little or no geographically structured variation. Thus, the skull morphology of southern African giraffe shows a continuous clinal distribution from southern Angola into northern Namibia and westwards across Botswana into south-western Zambia, western and south-western Zimbabwe into northern South Africa and southern Mozambique (Seymour, 2002). However, as Seymour's study potentially grouped specimens from across the ranges of *G. c. giraffa* and *G. c. angolensis*, it is unlikely that his method would be able to delineate these giraffe taxa.

Using analysis of the mitochondrial DNA (mtDNA), Seymour (2002) proposed that at least two distinct giraffe clades exist; the southern clade (southern African giraffe) and the northern clade (East and West African giraffe). The genetic separation between geographical populations of the southern and northern clades was also supported by using morphological analysis (Seymour, 2002). For management purposes, separate units for conservation management should be considered for each clade as they represent reciprocally monophyletic groups. Within the southern African clade, differentiation in the mtDNA indicates that the population in the west, specifically Namibia, has a unique haplotype. Although this is not quite at the level of clade differentiation, conservation management of such a distinct ecological population is still important. Using nested geographical distance analysis, Seymour (2002) interpreted the mtDNA diversity within the southern African giraffe (east versus west populations) as a consequence of restricted gene flow, due to isolation by distance, and to a sequence of historical range fragmentation and expansion events.

Although the patterns in genetic diversity among southern African giraffe may result from isolation, range expansion or fragmentation, they could also be attributed to recent translocations of giraffe throughout southern African countries (Penzhorn, 1971; Hall-Martin & de Graaf, 1978; Monadjem, 1998; D. Gilchrist & T. Reilly personal communication). Namibia and South Africa have translocated numerous giraffe to Swaziland, Botswana and Zimbabwe, and also within Namibia and South Africa. Many of the areas that Seymour (2002) sampled were in or on neighbouring properties where

giraffe had historically been decimated and subspecies translocated. Therefore, the sampled giraffe may not be representative of assumed remnant genotypes for giraffe subspecies of the region, and thus his observed patterns of genetic diversity may not be informative.

As with the southern populations, there is much conjecture over the subspecific taxonomy of the Namibian giraffe. Although this taxon is classified currently as *G. c. giraffa*, much of the historical and current literature refers to the Namibian population as *G. c. angolensis* (Shortridge, 1934; Zukowsky *in* Shortridge, 1934; Krecek *et al*., 1990; Skinner & Smithers, 1990; Scheepers, 1992; Fennessy *et al*., 2003).

The classification of Namibian giraffe subspecies was based initially on the supposed physical barrier between Namibia and Angola. However, giraffe have historically ranged between the two countries east of the Kunene River headwaters (MET, unpublished data) with separation (if any) being apparent only recently due to human interference. Therefore, it appears likely that populations of the two subspecies may have been contiguous across the two countries.

3.1.1. Aims

This study sought to better understand the genetic architecture of the Namibian giraffe and to help resolve its taxonomic status. To do this, I investigated:

- genetic variation of the Namibian giraffe compared with other extant giraffe populations;
- genetic variation within the study region population and the population in the Etosha NP; and
- genetic variation between the subpopulations in the study region—the northern Namib Desert.

3.2. Methods and materials

Tissue biopsies provide the greatest quantity of high quality nuclear DNA of any biological samples that can be secured readily from free-ranging individuals. Samples for DNA analysis were collected from two separate giraffe populations (study region in the northern Namib Desert and Etosha National Park; Namibian permit no. 597/2002) using a remote biopsy dart delivery system (DanInject CO^2 powered rifle). Samples were skin biopsies, obtained from giraffe in the study region (n = 18; giraffe randomly sampled from each of the Hoanib and Khumib Rivers) and Etosha NP (n = 15; refer to Appendix 2) in October 2002. Additional tissue samples (n = 5) from giraffe in the study region were collected during the satellite-collaring study (see Chapter 5), as well as from incidental mortalities.

While in the field, the tissue biopsy plugs were stored in labelled 1.8 ml Nunc tubes containing 0.5 ml of room temperature tissue preservative (250 mM EDTA pH7.5, 20% DMSO) and then maintained at 4°C. The samples were then couriered to the USA in 0.02% gluteraldehyde solution to ensure digestion of any potential bacterial or viral vectors. This was the protocol specified by the United States Department of Agriculture: Animal and Plant Health Inspection Service (USDA: APHIS) under Veterinary Import Permit #46386-Research.

While I undertook the collection component of the research, the extraction and sequencing component of the genetic research was undertaken as part of a collaborative research effort with Dr Rick Brenneman (Henry Doorly Zoo, Centre for Research and Conservation, Omaha, NB) and Mr David Brown (Ph.D. candidate, UCLA). The following methods are a synthesised overview of the laboratory methods used for the extraction and analysis of the giraffe tissue samples (Brenneman *et al*., unpublished data).

Total DNA was extracted from the biopsy samples in the Genetics Department at Henry Doorly Zoo, using a standard PCI (Phenol-Chloroform-Isoamylacohol) chloroform extraction protocol. An aliquot was sent to UCLA for DNA sequencing. A 656-nucleotide mitochondrial cytochrome-b fragment and a control region gene fragment were amplified and sequenced from 33 individual giraffe samples. This gene region was amplified by standard polymerase chain reaction (PCR) techniques and directly sequenced on a

Beckman CEQ2000 automated sequencer. These sequences were aligned and a neighbour-joining tree constructed using PAUP* v.4.0 (Swofford, 2003).

Microsatellites or nuclear single sequence repeats are the most informative genetic markers available for use today for parentage verification or classification studies. Microsatellite markers have become a standard tool for the analysis of population structure and population comparisons. Standard PCR analysis was carried out using 16 published giraffe-specific microsatellite loci (Huebinger *et al*., 2002) and one novel (unpublished) microsatellite locus under optimised conditions. Genomic DNA was isolated from tissue samples and PCR amplification was performed in a 25 µl reaction volume using an ABI480 thermocycler (Perkin-Elmer; Foster City, CA) with approximately 50 ng of genomic DNA as template. Final amplification conditions consisted of:

- 12.5 pmol unlabelled reverse primer;
- 12.5 pmol fluorescently labeled forward primer;
- 1.5 mM $MgCl_2$;
- 200 µM each dNTP; and
- 0.5 units of *Taq* DNA polymerase (Promega; Madison, WI).

The PCR amplification profile was 95°C for 5 minutes, followed by 35 cycles of 95°C for 30 seconds, a primer-specific annealing temperature for 30 seconds, 72°C for 30 seconds, ending with a single extension of 72°C for 10 minutes.

PCR fragment electrophoresis was carried out on an ABI 377 Automated DNA Analyser (Perkin-Elmer; Foster City, CA), and results analysed with the Genescan software program (Applied Biosystems, Inc.). Two ABI 377 and one ABI 3100 Automated DNA Analysers were used to facilitate the genotyping of all samples utilising this unique suite of microsatellite markers. Multilocus genotypes were assembled for analysis with Genepop v.3.3 (Raymond & Rousett, 1995) for estimation of population genetic parameters, and GenDist. The private alleles method was used to estimate genetic distance, and Bottleneck 3.0 for detection of recent population bottlenecks. Results were then analysed by the WHICHRUN v4.1 (Banks & Eichert, 2000) algorithm, which allowed calculation of the

allele frequency distribution across samples and thus provided the structural evidence needed to support at species decisions about population and subspecies status

A phylogenetic tree was calculated from microsatellite allele frequencies using Nei's Improved Genetic Distance (Nei *et al*., 1983), and the Infinite Alleles Model, with theoretical limits of "0" indicating no differences between two populations (or nodes on the tree) and "1" indicating no similarities. This method was identified as the most likely model to construct the correct tree topology from microsatellite allele frequencies (Takezaki & Nei, 1996).

3.3. Results

3.3.1. Mitochondrial sequence analysis

Thirty-three individual giraffe; 18 from the study region [the Hoanib (HNB, *n* =14), and Khumib (KHB, *n* =4)] (please note that these do not include samples from the satellite collaring or observed mortalities) and 15 from Etosha NP (ENP, *n* =15) were sampled and their tissues analysed for mitochondrial sequencing (refer to Appendix 2). Five unique mtDNA sequences (haplotypes) were identified (Table 3.1). None of the haplotypes in the Namibian giraffe were shared with giraffe from other populations throughout Africa (see Table 3.3 for Africa-wide giraffe populations sampled; Brenneman *et al*., unpublished data).

The Namibian haplotypes indicate a distinctive genetic and geographical separation from other giraffe populations across the continent, and imply that Namibian and other African giraffe have not interbred for many generations. In addition, the presence of unique haplotypes within each of the two sampled Namibian populations indicates limited gene flow between the giraffe of the study region and those in Etosha NP.

Table 3.1. Five unique mitochondrial DNA haplotypes only identified in the Namibian samples of giraffe, and their distribution across the defined sample populations (Brenneman *et al*., unpublished data). Note: these do not include samples from the satellite-collared or mortality giraffe.

Population	Haplotype 1	Haplotype 2	Haplotype 3	Haplotype 4	Haplotype 5
Etosha NP					
ENP-M	4				
ENP-N	4	1			
ENP-O	2	2	1	1	
Study Region					
HNB					13
HSB				1	1
KHB					3

ENP = Etosha National Park; M = Mushara; N = Namutoni; O = Okaukeujo; HNB = Hoanib River; HSB = Hoarusib River; KHB= Khumib River

3.3.2. Microsatellite genotype analysis

Hardy-Weinberg Equilibrium (HWE) was assumed and used as the basis for defining population genetic parameters, as well as for inferring the genetic architectures underlying specific populations. The study region giraffe population was in HWE, while the Etosha NP giraffe was not in HWE (χ^2=90.923; d.f.=26; P<0.001) when analysed as a population (refer to Appendix 3). However, once subdivided into three geographical sample groups; Mushara (ENP-M) in north-eastern Etosha NP, Namutoni (ENP-N) in north-central Etosha NP, and Okaukeujo (ENP-O) in south-central Etosha NP, each subpopulation satisfied HWE (P>0.05) (Brenneman *et al.,* unpublished data). It was not possible to determine individual identification and parentage analysis within the populations due to the low sample sizes per population.

An elevated FIS estimate (an inbreeding coefficient) was observed in the ENP-N subpopulation (Table 3.1). This elevated estimate likely reflects the Wahlund effect of mixing subpopulations detected by FST (effect of population subdivision on inbreeding), confounded with the true FIS of each subpopulation rather than true FIS or inbreeding. It would be expected that if the estimate truly reflected inbreeding in the population, its genetic diversity (HT) would be reduced rather than inflated; this was not the case (Table 3.2). The pertinent parameter estimates (probability of satisfying HWE, observed (Ho) and

expected (He) levels of heterozygosity, estimated inbreeding (FIS), and gene diversity (HT) within each group/population) are consolidated into Table 3.2.

To estimate the relationship between the two geographically separate populations, samples from the study region's subpopulations (Hoanib, Hoarusib and Khumib Rivers) were pooled, as were those from the Etosha NP. The measure of differentiation by FST was relatively small, at 0.0299 (Brenneman *et al.,* unpublished data). An estimation of relationship between the populations in the study region was not undertaken due to the findings presented in Chapter 5.

Table 3.2. Estimate of population genetic parameters for each Namibian sample groups of giraffe, identifying the number of individuals sampled (*n*), probability of satisfying HWE, observed (Ho) and expected (He) levels of heterozygosity, estimated inbreeding (FIS), and gene diversity (HT) within each group/population (Brenneman *et al*., unpublished data).
Note: the increase in the number of individuals sampled (*n*) in the study region is due to the inclusion of additional samples collected during satellite-collaring and from incidental mortalities (see section 3.2).

Population	*n*	HWE	Ho	He	FIS	HT
Etosha NP						
ENP-M	4	0.707	0.525	0.575	0.100	0.343
ENP-N	5	0.209	0.400	0.570	0.231	0.436
ENP-O	6	0.069	0.423	0.490	0.145	0.378
Study Region						
HNB	15	$P<0.001$	0.350	0.404	0.139	0.382
HSB	4	0.317	0.438	0.530	0.198	0.385
KHB	4	0.452	0.396	0.470	0.180	0.341

ENP = Etosha National Park; M = Mushara; N = Namutoni; O = Okaukeujo; HNB = Hoanib River; HSB = Hoarusib River; KHB= Khumib River

The estimate of gene flow by migration between the two study populations was 2.29 migrants per generation using the private alleles method. This estimate is likely to reflect the translocation of 22 giraffe from western Etosha NP to the study region in the northern Namib Desert in 1991. The paucity of unique alleles between the subpopulations and the small sample sizes of those subpopulations, precluded an accurate estimation of gene flow within and between study populations.

Overall, the average number of alleles observed per locus averaged 2.7 among the sampled Namibian populations (Table 3.3). In comparison, the average number of alleles observed per locus detected among 24 populations encompassing six subspecies screened in a larger phylogenetic study of giraffe was 12.8 (Huebinger *et al*., 2002; Brenneman *et al*., unpublished data; R. Brenneman & D. Brown, personal communication). The gene diversity of each of the sampled Namibian giraffe populations was lower than the average of 0.555 observed across the 24 extant giraffe populations (Table 3.2 & 3.3) (Brenneman *et al*., 2004; unpublished data).

The phylogeny and population association of five giraffe subspecies derived from microsatellite analyses is shown in a tree of genetic relationships between giraffe populations and subspecies (Figure 3.1). The genetic distances between the populations, or nodes, indicate that the populations in the study region are more closely related to each other, rather than to the Etosha NP population. The sampled Namibian populations, represented as *G. c. angolensis* on the genetic tree, are more closely associated to each other than to any other populations. The genetic distance between *G. c. angolensis* (Namibian samples) and *G. c. giraffa* (Kruger NP, South Africa) is equivalent to a subspecies level difference.

Table 3.3. Genotypic summary (17 Microsatellite Loci screened) of representative giraffe subspecies sampled in the wild [Data supplied by Brenneman *et al.* (unpublished)].

17 Microsatellite Loci screened with an Average of Alleles/Locus k = 12.8

	Observed			FIS		
	Alleles/Locus	HE	HO	W&C	R&H	*n*
G.c. angolensis						
Etosha NP	**3.0**	**0.479**	**0.391**	**0.178**	**0.193**	**15**
Hoanib River study area	**2.8**	**0.404**	**0.350**	**0.138**	**0.154**	**15**
Hoarusib & Khumib River study areas	**2.4**	**0.489**	**0.405**	**0.155**	**0.149**	**7**
G.c. giraffa						
Kruger NP	3.6	0.417	0.242	0.403	0.308	27
G.c. peralta						
Niger River	3.9	0.540	0.462	0.132	0.153	28
G.c. reticulata						
Meru National Reserve	3.8	0.582	0.513	0.130	0.160	10
Ol Jogi Pyramid	4.8	0.650	0.586	0.096	0.126	23
Ol Jogi Ranch	4.6	0.639	0.615	0.035	0.070	27
Samburu National Reserve	5.5	0.666	0.516	0.217	0.211	20
G.c. rothschildi						
Giraffe Manor	2.6	0.529	0.411	0.254	0.270	6
Lake Nakuru NP	3.7	0.526	0.472	0.068	0.098	18
Ruma National Reserve	3.6	0.517	0.433	0.224	0.212	12
Yoder Flower Farm	3.6	0.579	0.578	0.015	0.063	15
Murchison Falls NP	4.6	0.521	0.415	0.202	0.197	51
G.c. tippelskirchi						
Athi River	4.5	0.523	0.358	0.316	0.263	25
Chyulu Hills	4.5	0.524	0.393	0.254	0.214	25
Seronera Reserve	4.2	0.557	0.436	0.179	0.150	19
Tarangire Reserve	4.1	0.546	0.442	0.165	0.130	17
Manyara Reserve	3.8	0.588	0.487	0.155	0.162	12
Ndutu Reserve	3.9	1.199	0.449	0.231	0.241	16
Grumeti Reserve	2.6	0.569	0.404	0.205	0.239	4
Kirawa Reserve	2.8	0.571	0.515	0.191	0.157	7
Varicho Reserve	3.0	0.609	0.480	0.204	0.213	7
Lake Naivasha NP	2.9	0.624	0.490	0.225	0.218	7

HE = expected heterozygosity; HO = observed heterozygosity; W&C = Weir & Cockerham (1984) FIS estimate; R&H = Robertson & Hill (1984) FIS estimate.

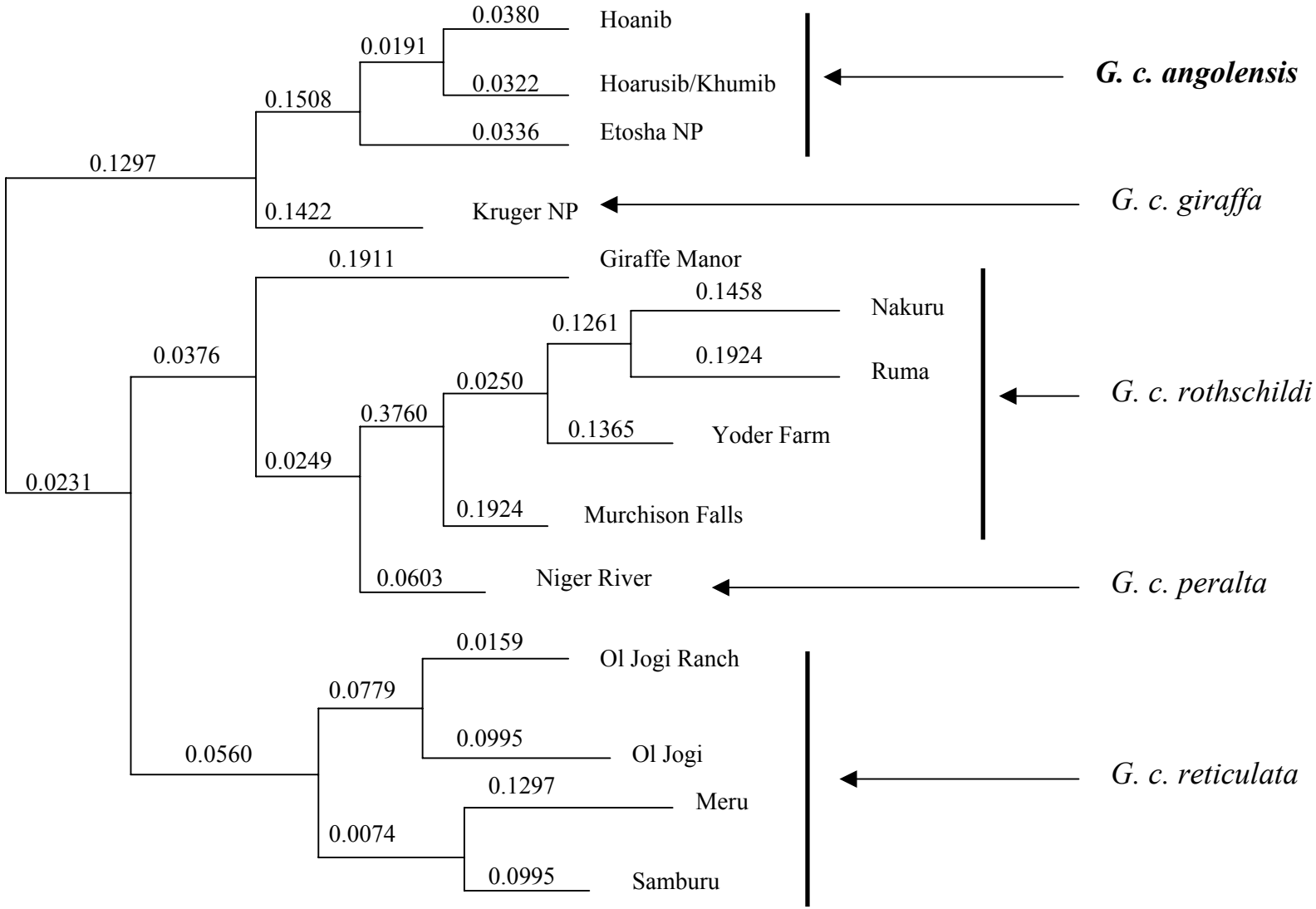


Figure 3.1. Giraffe phylogeny and population association of five putative subspecies derived from microsatellite analyses (re-drawn in part from Brenneman *et al*., unpublished data). Note: numbers used in the phylogenetic tree are Da's, calculated from microsatellite allele frequencies. This is Nei's Improved Genetic Distance from (Nei *et al*., 1983), using the Infinite Alleles Model, with theoretical limits of "0" indicating no differences between two populations (or nodes on the tree) and "1" indicating no similarities. This method was identified as the most likely model to construct the correct tree topology from microsatellite allele frequencies.

3.4. Discussion

3.4.1. Genetic architecture of Namibian giraffe

Five unique haplotypes were observed in the sampled Namibian giraffe population when compared with previous studies on other giraffe populations (Brenneman *et al*., unpublished data; D. Brown, unpublished data). A further two unique haplotypes for the Namibian population have been suggested using a combination of microsatellite and mitochondrial DNA methods (D. Brown, unpublished data), although preliminary results are yet to be published. The number of unique haplotypes found in the Namibian population is the second highest found in all giraffe populations sampled, with only the Masai giraffe *G. c. tippelskirchi* having more (D. Brown, unpublished data). In the desert-dwelling population of *G. c. peralta* in Niger, two unique haplotypes have been observed, while in Rothschild's giraffe *G. c. rothschildi* three unique haplotypes are known. The five unique haplotypes identified in the sampled Namibian population indicate that a biologically significant difference exists between this and other giraffe populations in Africa.

The parameter estimates and population assignment tests demonstrated a close genetic relationship between the two Namibian giraffe populations in the study region (northern Namib Desert) and Etosha NP, although a small genetic difference between the two populations was detected by microsatellite analysis and sequence divergence. The degree of differentiation observed between the two study populations is not uncommon for groups of animals that have been geographically or socially isolated, and can be expected due to genetic drift (Frankham *et al*., 2002). Genetic drift generally results in a gradual decrease in the heterozygosity of a species as particular alleles at given loci are randomly favoured and then driven towards fixation. Fewer alleles were detected in the study region population compared to the Etosha NP population, and subsequently fewer alleles were detected in the sampled Namibian population compared to other extant giraffe populations. These findings are suggestive of genetic drift, and indicate that this is a considerable force acting upon the genetic architecture of the small isolated populations of Namibian giraffe. Unfortunately, an accurate estimation of gene flow or migration by either the private alleles method or by FST could not be determined due to the low available sample sizes.

Additional genetic sampling and investigation of individual movements would enable a better understanding of gene flow within and between populations of giraffe in Namibia. Historically, migration could have occurred between the study region and Etosha NP, as only 300–400 km separates the populations. Furthermore, giraffe continue to exist between the two sampled areas, albeit in declining numbers, potentially facilitating the flow of genetic material between the populations. However, encroachment and development of the land by humans has restricted movement corridors in recent decades, and it is unlikely that natural gene flow or migration between the populations will occur much in future.

Despite the likely occurrence of migrations until recently, it is also possible that populations have been separated for longer than previously assumed, with some of the observed gene flow resulting from the translocations of 22 giraffe into the study region from western Etosha NP in 1991. The single giraffe from the study region that shared haplotype 4 with an individual from the Etosha NP may have been a 'hybrid' offspring of giraffe from both populations following the translocation. This would increase the genetic similarities between the populations and raise the question again about the length of separation between them. Again, sampling the entire population to assess gene flow would be valuable. For conservation management it would be particularly interesting to ascertain whether the two study populations represent evolutionary significant units (ESUs) that have arisen due to long-term isolation and distance, or whether they should be considered primarily in separate management units (MUs) (Moritz, 1994 & 1999).

It must be noted that translocations of giraffe have been occurring for many decades throughout Namibia to stock or re-populate dwindling populations. This would facilitate gene flow. The increase in genetic diversity also should not have a negative effect on population health; indeed, the opposite is likely as isolated, small populations with low genetic diversity, similar to those in the study region and Etosha NP, have higher potential for inbreeding (Hurtrez-Boussès, 1996; Veron *et al*., 2004). If introductions continue, the genetic diversity and architecture of the Namibian population as a whole may increase slowly over successive generations, or at least offset tendencies for reduced genetic diversity that would otherwise occur in small populations with decreasing opportunities for natural dispersal between them.

Moderate levels of inbreeding were detected within the sampled subpopulations, as demonstrated by inbreeding coefficients of 0.12<FIS<0.25 (Frankham *et al*., 2002). However, field observations do not indicate any deleterious effects or inbreeding depression (reduced calving, lowered viability, increased mortality rates or apparent genetic disease) in either the study region or Etosha NP. Inbreeding in giraffe in the wild has been reported, and albino giraffe have been observed (Dagg & Foster, 1982). Inbreeding effects have been observed in the okapi—the only other living giraffid and closest relative to the giraffe (de Boi, *et al*., 1990). Inbreeding is not uncommon in a number of other wild species, (Wathen *et al*., 1985; Laikre & Ryman, 1991; Hurtrez-Boussès, 1996; Laikre *et al*., 1996; Veron *et al*., 2004), particularly mammalian carnivores and ungulates, and deleterious effects often do not appear until inbreeding is extreme.

Molecular systematics, as expressed by the phylogeny and population associations in the phylogenetic tree (Figure 3.1), indicate that the Namibian giraffe are a distinct subspecies from other giraffe populations. Furthermore, the degree of difference indicates that they have not interbred with other giraffe subspecies for an extended time period; indicated by their unique microsatellite architecture. The sampled Namibian population is genetically distinct from *G. c. giraffa* (Kruger NP, South Africa), as well as other extant giraffe populations. C. Baysdorfer (unpublished data) has commented further that captive *G. c. angolensis* were genetically distinct from three East African subspecies of giraffe (*G. c. rothschildi*, *G. c. reticulata* and *G. c. tippelskirchi*), but he did not evaluate genetic variation between any of the extant southern African giraffe populations.

Based on these initial findings, a re-evaluation of subspecific variation in giraffe is warranted. In particular, the molecular evidence indicates that the sampled Namibian population is genetically distinct at subspecies level. Seymour's (2002) morphological and molecular evidence suggested that the Namibian population in Etosha NP (western population in the southern African giraffe clade) was different to other giraffe further east in the continent, while his inadequate sample size also shed little light on any real distinction between *G. c. angolensis* and *G. c. giraffa*. Seymour's (2002) description of *G. c. angolensis* was based on a single specimen from southern Angola, and it was considered to differ from other southern African specimens because of its larger body spot size. However, it must be recognised that pelage patterns of giraffe in Namibia vary markedly within a population, let alone between

habitats (refer to Appendix 1). In addition, recent distribution maps of southern African giraffe (see Chapter 1) show clearly distinct geographical ranges for *G. c. angolensis* and *G. c. giraffa* (e.g. Shortridge, 1934; Zukowsky *in* Shortridge, 1934; Krecek *et al*., 1990; Skinner & Smithers, 1990; Scheepers, 1992; Fennessy *et al*., 2003).

This study indicates that a genetic distinction between Namibian and other giraffe population is clear. In light of the evidence presented in this chapter in comparison with previous taxonomic classification, inclusion of Namibian giraffe within *G. c. angolensis* is recommended, although additional analysis should continue.

3.4.2. Conservation management

Increasing our knowledge of the genetic architecture of giraffe is of intrinsic interest, but it can also assist directly with aspects of management and conservation. For example, not only should we consider giraffe to form two distinct clades across Africa (Seymour, 2002), and therefore two separate evolutionary significant units (genetic differences among these subspecies and populations suggest recognition of these entities as management units) (Mortiz, 1994), recognition of such units should help to inform appropriate conservation management, e.g. translocations and captive breeding.

Positive and negative examples of giraffe management exist. In Namibia, translocations of giraffe onto private game reserves and parks have increased population numbers, genetic diversity and the species' range into areas where giraffe were historically present but had been exterminated. Fortunately, the molecular structure of the Namibian giraffe is similar, at least in the two regions studied, and the genetic integrity of the subspecies has been maintained. It is imperative that future translocations involve only Namibian giraffe to maintain this integrity and to avoid possible negative consequences such as breeding depressions.

As this chapter's genetic findings demonstrate, translocations between and possibly within countries (such as Kenya, where three subspecies exist) should be carried out with great caution, as there is still much uncertainty over the genetic architecture of giraffe at the population and subspecies levels. For example, at times, translocations appear to be ill-

conceived management decisions to artificially populate areas with non-endemic subspecies. Such conservation *faux pas* have been reported elsewhere (e.g. Moritz, 1994; 1999). In 1964, Mupa NP in Angola was proclaimed to aid primarily in the protection of the Angolan giraffe; however, since 1974 no giraffe have been present there. Recent translocations of *G. c. giraffa* from South Africa into Quiçama NP in Angola following decades of civil unrest were part of a greater conservation management program designed to increase species diversity and bolster ecotourism (Kissama Foundation, 2003). However, based on current knowledge, the translocation of a different giraffe subspecies may actually result in reduced intra-specific diversity (e.g. Margan *et al*., 1998; Burrows, 2002; Knapp & Malone, 2003). Throughout Africa and the world, conservation management decisions are still often made with respect to economic and political considerations (e.g. Pearce *et al*., 1990; Barbier & Swanson, 1992). Hopefully, biological and ecological considerations will in time be taken into account to assist in maintaining the long-term survival and diversity of species.

Recent developments in taxonomic classification using microsatellite genotypes have affirmed the importance of genetics as a valuable tool in conservation and species management (e.g. Adams, 1998; Arctander *et al*., 1996 & 1999; Comstock *et al*., 2002; Cotterill, 2003; Lorenzen & Siegismund, 2004). One of the most high profile findings supported by microsatellite analysis has been the recent affirmation of species level genetic differentiation in African elephants; the savanna elephant *Loxodonta africana* and forest elephant *L. cyclotis* (Roca *et al*., 2001; Comstock *et al*., 2002). Although postulated to be distinctive enough based on morphological evidence alone, the microsatellite analysis confirmed that the forest elephant are as genetically distinct from the savanna elephant as Indian elephants are to the African elephants (Roca *et al*., 2001; Comstock *et al*., 2002). Increased genotyping of giraffe, coupled with morphological evidence (Seymour, 2002) for the entire extant population, is ongoing and forms part of a larger study undertaken by the International Giraffe Specialist Group in collaboration with Henry Doorly Zoo and UCLA.

For conservation and management purposes, Namibia's desert-dwelling giraffe population may best be considered as a distinct MU (Moritz, 1994). The population shows distinct genetic differences, has low gene flow (due mostly to recent translocations) between other populations in Namibia and occupies different habitat to other giraffe. It is important that

genetic analysis is not used as a stand-alone tool but rather used as supporting evidence to aid in conservation management.

3.5. Conclusion

The molecular systematics of Namibian giraffe indicate that they are distinct from the subspecies *G. c. giraffa.* Furthermore, the sampled Namibian giraffe have not interbred with giraffe elsewhere in Africa for an extended period, as demonstrated by the presence of several unique haplotypes. These results, coupled with geographical isolation, warrant re-evaluation of the current taxonomic classification of Namibian giraffe. In particular, subspecies recognition of the Namibian giraffe as *G. c. giraffa* should be superseded by *G. c. angolensis* Lydekker, 1904. Distinct geographical populations with limited diversity and gene flow between them were observed in Namibia. The limited gene flow can be attributed to historical migrations and recent translocations of giraffe between the two populations studied and, while the inbreeding estimates were low, no deleterious effects were observed.

Based on the genetic analyses, the desert-dwelling giraffe of the northern Namib Desert is a distinct subspecies from that previously assumed. Our knowledge of this taxon is limited because most previous research on giraffe in southern Africa has focussed on *G. c. giraffa*. Throughout this thesis, I focus on investigating the ecological background of the subspecies *G. c. angolensis*, and in the next chapter examine the current population structure and dynamics of this taxon in the northern Namib Desert.

CHAPTER 4. POPULATION STRUCTURE AND DYNAMICS

This chapter investigates the population structure and dynamics (numbers, density, calving, mortality and herd structure) of the desert-dwelling giraffe in the northern Namib Desert. In addition, it presents a detailed overview of associations among individual giraffe in the three study areas.

4.1. Introduction

While population structure and distribution are usually easy to describe, the factors affecting them are much debated. The majority of studies on population dynamics focus on 'current' ranges of species and their relation to conservation and management (Berry, 1978; Lindeque & Lindeque, 1991; Ciofolo, 1995; Thouless, 1996). However, it is also important to obtain a sound understanding of a species' historical, current and potential (modelled or predicted) distribution and population dynamics before appropriate long-term conservation and management approaches can be established (Caughley & Gunn, 1996).

Numerous short-term studies have been undertaken on the population dynamics of giraffe throughout the current range of the species (Innis, 1953; Foster, 1966; Foster & Dagg, 1972; Berry, 1973; Leuthold, 1979; Pellew, 1984a; Le Pendu *et al,* 2000; van der Jeugd & Prins, 2000). However, few have focussed on populations residing in arid environments (Scheepers, 1992; Le Pendu *et al*., 2000; Fennessy *et al*., 2003).

Precipitation, human disturbances, habitat fragmentation, predation and nutrient and mineral resource availability are extrinsic factors that can affect population density and dynamics (Royama, 1992; Begon *et al*., 1996; den Boer & Reddingius, 1996; Ranta *et al*., 1997; Tedesco *et al*., 2004). Intrinsic factors, such as the Allee effect, stress, intraspecific competition and other density-dependent processes, can have additional influences (Royama, 1992; Begon *et al*., 1996; Dennis & Taper, 1994; den Boer *et al.*, 1996; Gascoigne & Lipcius, 2004). These biotic and abiotic factors can be expected to affect populations differently, with no one population being truly representative of another.

Marked fluctuations in giraffe populations have been reported and are the result of various factors, such as poaching, fragmentation, predation, overuse of forage, and a shift in fecundity (Foster & Dagg, 1972; Scheepers, 1992; van der Jeugd & Prins, 2000). Historical knowledge of a population's dynamics can provide a solid background for management; however, long-term data is often limited. This is the case for giraffe; this limitation has restricted appropriate conservation and management efforts for giraffe species, subspecies and subpopulations across Africa.

Similar to the giraffe in the study area, difficulties in monitoring and researching Namibia's desert-dwelling black rhino have limited our understanding of the population structure and life history strategies of this species (M. Hearn, unpublished data; B. Loutit & M. Hearn personal communication). However, in contrast to research on giraffe, monitoring and research on the desert-dwelling black rhino have been relatively long-term. But, how long is long-term research, and is it essential to fully understand a species' population structure to assist in its long-term conservation? How beneficial is it to understand a species' population structure or any historical and current factors that affect it? Insight into intrinsic and extrinsic regulating factors may be useful in providing baseline information from where appropriate conservation can begin.

For the desert-dwelling black rhinoceros, external factors such as poaching, communal farming and tourism are having a detrimental impact on population size and range (M. Hearn, unpublished data; B. Loutit & M. Hearn personal communication). Increasing human populations in the Kunene Region have and will continue to result in habitat fragmentation, loss of range and increased competition between wildlife and domestic stock (e.g. Yaron *et al*., 1994; Ashley & O'Connell, 1995; Vaughan *et al*., 2003). The increasing potential for poaching is an ongoing concern (e.g. Katjiua *et al*., 2003). The expansion of communal farming populations and the need for resources such as land, water and forage will inevitably result in greater conflict between communal farming and wildlife (e.g. Vaughan *et al*., 2003). Therefore, long-term research and monitoring are important to establish the nature and magnitude of any population change and to provide guidance for effective management.

4.1.1. Individual identification, association and herd structure

Identification of individuals is critical to understanding individual behaviour and important in investigating aspects of species ecology, such as population structure and dynamics, density, distribution and seasonal movement, home range and habitat preference. Single-species studies have adopted many different methods to aid in the quick and easy identification of individuals (e.g. giraffe - Foster, 1966; zebra – Klingel, 1965; Joubert, 1972; Stander *et al*., 1990; elephant - Moss, 1982; impala - Pangais & Stander, 1989), including coat patterns, colour, tail length, tusk length, scars, gait, horn variations, ear notching, mane clipping, painting, branding, collaring and spoor identification. The identification of individuals generally also enables a closer relationship between study species and researcher, allowing collection of high quality data and increased knowledge of species ecology.

Relationships between individuals and family structure in giraffe have been described as loose, fluid and/or temporary (e.g. Innis, 1958; Foster & Dagg, 1972; Moss, 1982; Leuthold, 1979; Dagg & Foster, 1982; Pellew, 1984a; Pratt & Anderson, 1985; Le Pendu *et al*., 2000). Loose relationships are thought to reflect weak herd structure in giraffe and a lack of audible communication. However, recent research suggests that giraffe communicate using infrasound (e.g. von Muggenthaler *et al*., 2001; Bashaw, 2003) similar to that reported for elephants and marine mammals (e.g. Moss, 1982; Berg, 1983; Richardson *et al*., 1995; Ben-Ari, 1999). With knowledge that giraffe communicate using low frequency vocalisations, our understanding of the giraffe's social dynamics can increase.

Weak inter-individual relationships and few preferential associations between giraffe age and sex classes have been reported, with the exception of cow-calf and calf-calf dyads in some populations (Leuthold, 1979; Pratt & Anderson, 1982; 1985; Le Pendu *et al*., 2000; van der Jeugd & Prins, 2000). However, some authors also describe the maternal bond in giraffe (cow-calf) as weak, noting the abandonment of calves for extended periods while the cows venture off to forage or drink (Innis, 1958; Foster, 1966; Dagg & Foster, 1982). Other authors suggest that cows spend periods away from their offspring for different reasons, including the conservation of calf energy, water conservation and increasing calf's

crypsis. However, long associations between cow-calf pairs of up to 22 months have been reported (Langman, 1977; Pratt & Anderson, 1982).

4.1.2. Aims

It is important to understand population dynamics and structure and to consider how sub-populations within a species may vary with respect to social structure, seasonal responses and habitat. In order to clarify these issues, in this chapter I investigated:

- population structure;
- calving periods;
- density;
- herd structure;
- mortalities; and
- inter-individual associations of giraffe.

Differences in sub-population structure and dynamics in each study area (Hoanib, Hoarusib and Khumib Rivers) were assessed by treating each area as a separate unit. The investigations were also intended to provide an overview of the giraffe population in the study region, its social structure and dynamics. It also sought to obtain a better understanding of seasonal changes in the population and the effect that study area size may have on population structure.

4.2. Methods and materials

Giraffe (individuals and as a population) were observed on a monthly basis in the study region over a two year period, predominantly by vehicle and sometimes on foot. Giraffe were observed from sunrise to sunset. While the study focused on the riparian woodlands, the plains, dunes, floodplains and some mountain areas were also traversed each month.

The Hoanib and Hoarusib River study areas were visited more frequently (five to 10 days per month) than the Khumib River study area (two to three days every second month) due

to time, distance and logistical constraints. Herd and individual giraffe locations and co-ordinates were recorded using a Garmin II *plus* Global Positioning System (GPS) that was fixed to the vehicle with an external antenna. GPS co-ordinates, along with relevant bio-data on giraffe (see below) were then stored in a Microsoft Excel Professional 2000 database and co-ordinates mapped using the MapInfo Professional 6.5 Geographical Information System (GIS) program.

4.2.1. Age standardisation

Limited standardisation exists in the classification of giraffe age classes (Innis, 1958; Foster, 1966; Foster & Dagg, 1972; Berry, 1973; Leuthold, 1979; Pratt & Anderson, 1982; Young & Isbell, 1991; Le Pendu *et al.,* 2000; van der Jeugd & Prins, 2000). This study classified individuals and herd members into the appropriate sex class (bull or cow) and into one of three different age classes. Only three age classes were used to standardise data collection and for comparative analysis between some other published studies.

- Adult >5 years
- Subadult 1-5 years
- Juvenile <1 year

Unless born during the study period, it was difficult to accurately classify giraffe into appropriate age classes. Therefore, validated height-age estimates were used (Dagg & Foster, 1982). During a preliminary study I observed that once juveniles reached approximately one year old they became relatively self-sufficient and their behaviour was similar to that of adults and subadults (personal observation). Therefore, all giraffe were classified as subadults from one year of age, and subadults were re-classified as adults after five years when they had reached a height of about 4–4.5 m. This age interval correlates with sexual maturity and social presence (Hall-Martin, 1975; Dagg & Foster, 1982).

4.2.2. Population structure, density and calving

Population structure, calving periods and densities were assessed for each study area. Seasonal variation in herd sizes was also investigated. Aggregations in herd sizes have been observed in numerous plains ungulates, representing responses to the dispersion of food and/or predator numbers (Caro, 1999; Fischer & Linsenmair, 1999; Leggett *et al.,* 2003a). Densities were calculated on the assumption that all giraffe in the study region were identified. The number of giraffe first identified in each of the study areas was used as the baseline for density, from which density relative to the study area size was calculated.

Population sex ratios within each study area and between the study areas were tested by Chi-Squared for deviations from parity. Seasonal herd size aggregations in the study areas were compared using the Kruskal-Wallis test and Kendall's coefficient of concordance, while solitary bull to cow herd sizes were compared using the Chi-Squared test.

4.2.3. Herd structure

There is little standardisation regarding descriptions of giraffe herd structures, with concepts of a giraffe herd or group being continually re-defined (e.g. Backhaus, 1961; Foster, 1966; Foster & Dagg, 1972; Leuthold, 1979; Scheepers, 1992; van der Jeugd & Prins, 2000). Backhaus' (1961) definition of a herd 'any number of the same species that moves together and engages in the same activity, at any one time', has been the baseline for much giraffe herd structure analysis, however, specifics between studies do vary. Preliminary research for this study and the observations published by others (e.g. Scheepers, 1992; Fennessy *et al*., 2001; Brashaw, 2003; personal observation) support the concept that giraffe exhibit loose and gregarious social structures, although this has not been quantified in the wild.

This study defined herd structure as individual or group associations. However, herds were not determined necessarily just by proximity of individual giraffe (social distance) as determined in other studies e.g. Foster (1966). It was considered irrelevant whether giraffe

were 100 m or 1 000 m apart—this also varied between published giraffe studies e.g. Foster (1966) and van der Jeugd & Prins (2000), or whether they were engaged in the same activity at any one time (Backhaus, 1961). The definition of herd structure was placed, instead, in relation to the daily social structure of the population and determined by continuous monitoring and observation. When two giraffe were observed associating with one another for an extended period (>10 minutes), for example feeding next to each other or moving in the same direction, it was deemed as two giraffe in one herd. However, if an individual or herd traversed an area coincidentally and did not proceed to associate with other giraffe, even though they may have fed in the same vicinity, two different herds were recorded. This distinction has not previously been standardised in other studies. Behavioural observations and seasonal movements were collected to determine herd structure.

4.2.4. Individual identification

The giraffe, the tallest terrestrial mammal, is possibly the most recognisable and charismatic member of the African megafauna. Giraffe have a pelage pattern that does not change throughout its lifecycle, however colour intensity can either fade or darken over time. Ossicones, another distinctive feature, may increase in size over time, particularly in bulls (Dagg & Foster, 1982; Seymour, 2002). Consequently, individuals remain distinguishable, especially when observed at frequent intervals. Their size, and the ability of researchers to identify them individually, makes giraffe an ideal study species. Many authors have developed and/or adapted identification methods for individual giraffe in their studies (Innis, 1958; Foster, 1966; Leuthold, 1979; Pratt & Anderson, 1979; Pellew, 1983; Young & Isbell, 1991; Le Pendu *et al.*, 2000; van der Jeugd & Prins, 2000).

For my research, I used a preliminary study to validate the use of a combination of identification methods. During this study digital photographs of the right and left pelage patterns of individual giraffe and their ossicones were used for identification, as were sex, age, colour and tail length. A Fuji S1 Pro digital camera body with Nikon AF telephoto compatible lenses, up to 400 mm focal length, was used to photograph individuals for identification and creation of a pictorial database. Digital photographs were manipulated

using Ulead PhotoImpact 3.02 and generic databases were created in Microsoft Excel and Word 2000 Professional.

Individual identification sheets (double-sided) were developed and completed for each giraffe. Recorded data included the name, nomenclature, age class, sex and tail length (Figure 4.1). Prominent scars, ossicone size or shape, and pelage colour were also described (Figure 4.2). Nomenclature was important to establish associations among individual giraffe, population structure and home range. In the field, additional notes were made on prominent pelage patterns and markings directly onto individual identification sheets. This method enabled continuous updating of the giraffe identification sheets as more images were obtained or new recognisable features were observed. Nomenclature was based on the study area in which an animal was first observed, and sex and number of individuals in the population. Furthermore, 'popular' names were given to each individual, e.g. Angelo (Figure 4.1). These names aided recognition of individuals more easily in the field.

Examples of the nomenclature system are given below:

HNBM1	HNB	- refers to the Hoanib River, area of first observation
	M	- refers to the individual being a bull (male)
	1	- refers to the first bull observed in that study area
HSBF2	HSB	- refers to the Hoarusib River, area of first observation
	F	- refers to the individual being a cow (female)
	2	- refers to the second cow observed in that study area
KMBJ34	KMB	- refers to the Khumib River, area of first observation
	J	- refers to the individual being a juvenile (calf)
	34	- refers to the nomenclature number of the juvenile's mother

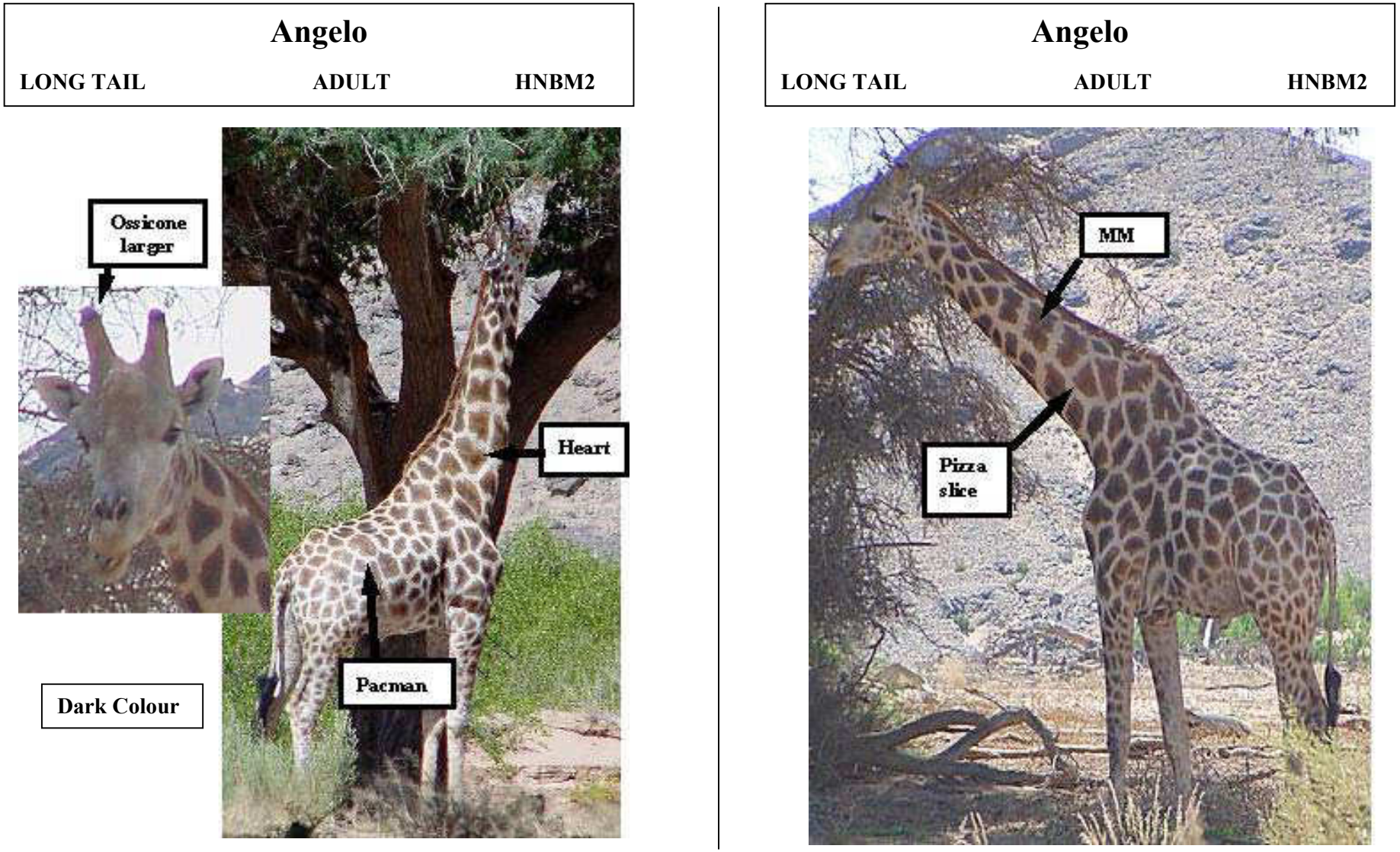


Figure 4.1. Example of giraffe identification field manual developed during this study.

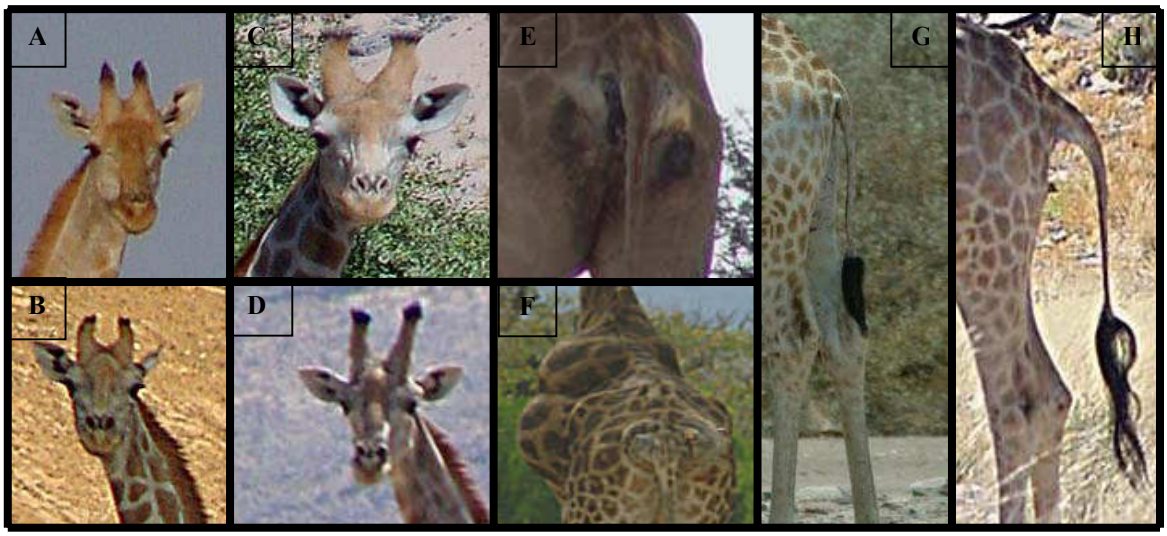


Figure 4.2. Prominent identification features used to assist in recognising individual giraffe in the study region [(A-D) ossicones; (E) markings; (F) tumours; (G-H) tail length].

After completion of fieldwork for this study, the database of individual giraffe in the region was made accessible to the wider conservation community. Hard copies and electronic versions were provided to communal conservancies, NGOs and the MET for personal references and use in the CBNRM program.

4.2.5. Inter-individual associations

Indices of association between identified individuals were initially computed using the half-weight index, more commonly known as Dice's or Sorensen's index (e.g. Leuthold, 1979; Ginsberg & Young, 1992). However, this index is reported to double count sightings as well as deflate the denominator by a given average (Cairns & Schwager, 1987; Ginsberg & Young, 1992; Le Pendu *et al*., 2000; van der Jeugd & Prins, 2000). Therefore, indices of association were computed using simple ratio (SR) method, which reportedly provides a more accurate assessment of inter-individual association (Cairns & Schwager, 1987). Association indices were calculated for known individuals that were observed a minimum of nine times over a one year period or longer, as suggested in Le Pendu *et al*. (2000), a study of giraffe in Niger.

The index is calculated as:

$$SR = \frac{X}{(X + Y)}$$

where X = number of times that two known individuals were observed together, and Y = number of observations of two known individuals (A and B) recorded separately (i.e. when only A was observed plus when B was observed), or when both A and B were located separately.

An index of 0.5 or greater was taken here to indicate a strong or close association between two known individuals (e.g. Cairns & Schwager, 1987; Ginsberg & Young, 1992; Le Pendu *et al*., 2000; van der Jeugd & Prins, 2000). The mean value of SR was then calculated for different sexes and age classes to determine any preferential associations (Le Pendu *et al*., 2000).

4.2.6. Mortality

When dead giraffe were observed, a rapid method of ageing was applied. Firstly, a quick visual assessment of the giraffe and surrounding area was undertaken. Size, pelage pattern, colour and dentition aided in identifying the individual, as well as determining the possible cause of death; for example, predation, natural senescence or poaching. Secondly, the age of the giraffe was assessed using a tooth wear method (Hall-Martin, 1976). GPS co-ordinates of all mortality locations were recorded.

Swab and skin samples were also taken from one individual for analysis by the State Veterinary Services, Namibian Ministry of Agriculture, Windhoek, for anthrax (*Bacillus anthracis*) analysis.

4.3. Results

4.3.1. Population structure

During the study a total of 156 giraffe were identified in the study region: 40 adult bulls, 47 adult cows, 33 subadult bulls, 25 subadult cows and 11 juveniles that were not sexed (Table 4.2; see Appendix 4). The smallest population of giraffe within the study area was recorded in the Khumib River study area with 17 individuals, 11% of the regional population. Forty-seven giraffe, 30% of the population, were recorded in the Hoarusib River study area while 92 individuals, 59% of the population, were recorded in the Hoanib River study area.

Table 4.2. Population structure (sex and age class distribution) of giraffe in the study region.

	Study region							
	Khumib River		Hoarusib River		Hoanib River		Total	
	Bull	Cow	Bull	Cow	Bull	Cow	Bull	Cow
Age class								
Adult	3	3	20	10	17	34	40	47
Subadult	6	4	11	3	16	18	33	25
Juvenile	1		3		7		11	
Study region								
Total no. of bulls & cows	9	7	31	13	33	52	73	72
Sex ratio (bull : cow)	1 : 0.78		1 : 0.42		1 : 1.6		1 : 0.99	
Total no. giraffe	17		47		92		156	
% of total no.	10.9		30.1		59		100	

In the study region the sex distribution was even (bull : cow = 1 : 0.99), even though a significant difference in sex ratios occurred among the three study areas (χ^2 = 11.85; d.f.=2; P=0.003). Differences in sex ratios were observed within the Hoanib (χ^2 = 4.247; d.f.=1; P=0.039) and Hoarusib River study areas (χ^2 = 7.364; d.f.=1; P=0.007) but not the Khumib River study area (χ^2 = 0.25; d.f.=1; P>0.05). The Hoanib River study area was strongly cow-biased (1 : 1.6), while both the Hoarusib (1 : 0.42), and Khumib River study

areas (1 : 0.78) populations were bull-biased, the latter because of a slight preponderance of subadult bulls. Juveniles comprised 6–8% of the population in each study area.

The combined age class categories (adult : subadult : juvenile) in the regional study population indicated an age class ratio of 1: 0.67 : 0.13 (adult population of 55.8%, subadult 37.2% and juvenile 7%). However, within the different study areas, subadults dominated in the sparse Khumib River population (1 : 1.67 : 0.16) and adults dominated in the Hoarusib River study area (1 : 0.47 : 0.1). Age class ratios for the Hoanib River study area were similar to those observed for the total study region.

Study area populations were positively correlated with study area size (r = 0.93, P=0.25, but 1 d.f. is available). A large giraffe population was observed in the larger Hoanib River study area and smallest giraffe population in the smaller Khumib River study area.

4.3.2. Densities

Within each of the Hoanib, Hoarusib and Khumib River study areas, giraffe densities (0.024, 0.017 and 0.017 /km^2 respectively) were low and only marginally higher than the entire giraffe densities for the Kunene Region (Table 4.3). The density of giraffe in the Kunene Region (0.01 km^2) is equal to the lowest recorded density across the extant range of giraffe (0.01 km^2 in the desert-dwelling giraffe population in Niger) (Le Pendu *et al.*, 2000).

Table 4.3. Densities of giraffe across the three study areas, study region and Kunene Region.

Study area	Size (km^2)	Density (n/km^2)	Source
Khumib River	1,000	0.017	This Study
Hoarusib River	2,750	0.017	This Study
Hoanib River	3,750	0.024	This Study
Study Region	7,500	0.02	This Study
Kunene Region	72,000	0.01	Fennessy *et al.,* 2003

4.3.3. Calving periods

Only nine calving events (*n* =9) were observed during the study. These low numbers restricted any rigorous analysis, however, a distinctive hot-dry season calving peak was evident, with 66.6% of all births occurring at this time (Table 4.4).

Table 4.4. Giraffe calving events by month during the study period (*n* =9).

		Wet season			Cold-dry season			Hot-dry season					
	n	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
Births	9	1		1			1			1	3	1	1

4.3.4. Herd structure

Seasonal aggregations and mean herd sizes differed between the three study areas. A strong negative correlation was observed (r = 0.928, d.f.=7, P<0.001; using data from three seasons and three study areas) between mean herd size and number of study area giraffe (e.g. the Hoanib River study area had the lowest mean herd size and largest population) (Table 4.5). The Khumib River study area had the largest mean herd size (4.6±3.1 s.d.), which increased from the wet through to the hot-dry season. In the Hoarusib River study area, larger herd sizes were observed in the cold-dry season, while in the Hoanib River study area herd sizes were similar in all seasons (Table 4.5). Changes in herd structure sometimes occurred throughout any day. This, in turn, resulted in some inflation of apparent animal numbers above the numbers of individuals actually present (Table 4.2).

No significant difference in seasonal herd sizes was observed in either the Hoanib (Kruskal-Wallis: H = 0.445; d.f.=2; P=0.801) or Khumib River study areas (Kruskal-Wallis: H = 3.126; d.f.=2; P=0.209). In the Hoarusib River study area significant differences in the seasonal herd sizes were observed (Kruskal-Wallis: H = 11.919; d.f.=2; P=0.003).

Table 4.5. Seasonal herd sizes of giraffe within the study region.

	Number in herd																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	21	Total herd no.	Mean herd size (± s.d.)
Khumib River																		
Wet (%)	28.6	14.3	28.6	14.3	14.3												7	2.7 ± 1.5
Cold-dry (%)		20.0	10.0	10.0	10.0	10.0	30.0	10.0									10	5.1 ± 2.2
Hot-dry (%)	10.5	26.3	15.8		5.3			15.8	15.8		10.5						19	5.21 ± 3.6
Total (%)	11.1	22.2	16.7	5.6	8.3	2.8	8.3	11.1	8.3		5.6						36	4.6 ± 3.1
Total herd no.	4	8	6	2	3	1	3	4	3		2						36	
Hoarusib River																		
Wet (%)	25.0	22.9	25.0	12.5	2.1	6.3	2.1		2.1	2.1							48	2.98 ± 2.1
Cold-dry (%)	16.9	11.9	8.5	11.9	10.2	6.8	5.1	8.5	5.1	3.4	3.4	1.7	5.1	1.7			59	5.4 ± 3.7
Hot-dry (%)	29.5	11.5	7.7	10.3	15.4	7.7	6.4	3.8	2.6	1.3	2.6	1.3					58	3.95± 2.9
Total (%)	24.3	14.6	12.4	11.4	10.3	7	4.9	4.3	3.2	2.2	2.1	1.1	1.6	0.5			185	4.2 ± 3.1
Total herd no.	45	27	23	21	19	13	9	8	6	4	4	2	3	1			185	
Hoanib River																		
Wet (%)	36.4	14.6	17.3	10.0	3.6	2.7	2.7	5.5	2.7			0.9	0.9	0.9	0.9	0.9	110	3.48 ± 3.5
Cold-dry (%)	27.9	21.6	16.2	12.3	7.8	7.4	3.4	1.0	1.0	0.4	1.0						204	3.08 ± 2.11
Hot-dry (%)	32.6	17.6	11.6	11.2	9.4	4.9	5.2	4.5	0.7	1.4	0.3	0.3				0.3	267	3.34 ± 2.7
Total (%)	31.5	18.4	14.3	11.4	7.7	5.3	4.1	3.4	1.2	0.9	0.5	0.3	0.2	0.2	0.2	0.2	581	3.3 ± 2.7
Total herd no.	183	107	83	66	45	31	24	20	7	5	3	2	1	1	1	1	581	

Herd sizes varied between each of the three study areas. In the Khumib River study area herd sizes ranged from one to 11 individuals, in the Hoarusib River study area from one to 14, and in the Hoanib River study area from one to 21. Solitary or lone giraffe were dominant in both the Hoanib and Hoarusib River study areas (31.5% and 24.3%, respectively) while groups of two and three were dominant in the Khumib River study area (22.2% and 16.7%, respectively) (Table 4.5).

There was strong concordance between season and number of giraffe in a herd in the Hoanib River (Kendall's: W=0.89; d.f.=15; P<0.001) and Hoarusib River study areas (Kendall's: W=0.887; d.f.=13; P=0.001). However, herd size varied seasonally in the Khumib River study area (Kendall's: W=0.361; d.f.=9; P=0.361). Between 11.1% and 26.7% of all sightings of solitary giraffe in the three study areas were bulls (Table 4.6). Solitary bulls were observed more often than solitary cows in both the Hoanib (26.7% vs. 4.3%) and Hoarusib River study areas (23.2% vs. 1.1%). No solitary cows were observed in the Khumib River study area.

Groups of two or three giraffe were common in all three study areas although group composition differed. Group sizes of three or fewer giraffe comprised 50% of all observations in the Khumib River study area, 51.3% of those in the Hoarusib River study area and 64.2% of those in the Hoanib River study area. In total, 60.2% of observations in the study were groups of three giraffe or fewer (Table 4.6). Bull-bull associations dominated the Hoarusib River study area, while cow-juvenile associations dominated the Khumib River study area. An even distribution of mixed group compositions was observed in the Hoanib River study area.

Historical surveys of giraffe herds in the Kunene Region have varied markedly in both survey quality and quantity. Few comparative data could be drawn from these historical surveys with the exception of long-term mean herd sizes. Between 1981 and 2000, 786 surveys were undertaken in the Kunene Region, with a total of 2,944 observations of giraffe being made (Loutit, 1998; MET, 1998; Fennessy *et al.,* 2003). Based on these surveys, the long-term mean herd size for giraffe in the Kunene Region is 3.7±0.5 s.d. individuals per herd. Combined mean herd sizes for this study were very similar to the long-term mean for the Kunene Region (3.54 ±2.8 s.d.) (Table 4.5).

Table 4.6. Giraffe herd sizes and composition with ≤3 individuals as percentage of the total numbers in herds observed in the study region.

	Study areas			
	Khumib River	Hoarusib River	Hoanib River	Study Region
No. of sightings	36	185	581	802
Solitary animals	11.1%	24.3%	31.5%	28.8%
1 m	11.1%	23.2%	26.7%	25.2%
1 f	0	1.1 *	4.3 *	3.4 *
1 j			0.3 *	0.2 *
Two animals	22.2%	14.6%	18.4%	17.7%
m-m	0%	14.1%	4.6%	6.6%
f-f		0.5%	6.2	4.6
j-j			0.2	0.1
m-f	5.5		4.6	3.6
f-j	16.7		2.8	2.8
m-j				
Three animals	16.7%	12.4%	14.3%	13.7%
m-m-m	0%	10.9%	2.6%	4.4%
f-f-f	8.3	0.5	1.7	1.7
j-j-j			0.2	0.1
m-m-f		0.5	1.9	1.5
m-m-j			0.2	0.1
m-f-j			0.7	0.5
f-f-m	5.6	0.5	5.0	4.0
f-f-j			1.4	1.0
j-j-m				
j-j-f	2.8		0.3	0.4

m: bulls, f: cows; j: juveniles; * $P<0.001$, χ^2 test on raw frequencies.

4.3.5. Inter-individual associations

Inter-individual associations were calculated for giraffe dyads in the study population. The number of observed dyad associations in the Khumib River study area was considerably lower than those in the Hoanib and Hoarusib River study areas (Table 4.7). Although fewer dyads were observed in the Khumib River study area, observations were recorded over a one year period and can therefore be considered representative of herd dynamics there.

Table 4.7. Number of dyad associations observed in the three study areas (n = 1 239).

Study area	Bull/Bull	Cow/Cow	Bull/Cow	Juvenile*	Total
Khumib River	13	12	21	11	57
Hoarusib River	286	-	66	7	359
Hoanib River	161	212	369	81	823

*Juvenile associations were with bulls, cows or other juveniles. N.B. Adult and subadult age classes are combined in all groupings.

The SR index identified six strong inter-individual associations in the Hoanib River study area, eight in the Hoarusib River study area and six in the Khumib River study area (Figures 4.3 to 4.6).

Strong inter-individual associations (SR ≥ 0.5) were observed in 0.5% of all cow-cow associations in the Hoanib River study area compared to 25% of all cow-cow associations in the Khumib River study area. Few observations were made of cows and juveniles in the Hoarusib River study area thus limiting any association analysis. However, personal observations indicated that strong associations probably existed between cows and their calves.

In the Hoarusib River study area strong associations were observed in 2.8% of all bull-bull dyads, in 0.6% of all bull-bull associations in the Hoanib River study area and in 8% in the Khumib River study area. Strong associations were observed in 0.5% of all bull-cow associations in the Hoanib River study area and 4.8% of all bull-cow associations in the Khumib River study area. In the Hoanib River study area strong juvenile associations were observed in 2.5% of all combined juvenile associations and 9.1% of all juvenile associations in the Khumib River study area.

Association was deemed to be due to chance for SR values less than 0.2 (Cairns & Schwager, 1987). These low values were found in 84.3% of all bull-bull associations in the Hoarusib River study area, 93.2% of all bull-bull associations in the Hoanib River study area and 46.2% in the Khumib River study areas (Figure 4.3). SR values were less than 0.2 in 88.2% of cow-cow associations in the Hoanib River study area and 17% of cow-cow associations in the Khumib River study area (Figure 4.4). SR association values

were less than 0.2 in 96.7% of bull-cow associations in the Hoanib River study area, 89% in the Hoarusib River and 47.6% in the Khumib River study area (Figure 4.5). In 92.6% of juvenile associations in the Hoanib River study area and 27.3% of juvenile associations in the Khumib River study area, SR association values were less than 0.2 (Figure 4.6).

All strong dyad associations in the Hoanib River study area were between cows and their calves (four associations) and subadult-subadult giraffe from crèche groupings (two associations). One strong bull dyad was observed, however, that was an individual that was originally identified in the Hoanib River and moved to the Hoarusib River. Similar dyad associations were observed in the Khumib River study area (cow-calf dyads: four associations; subadult-subadult crèche dyads: two associations), however, a close adult bull-subadult bull dyad was also observed. In the Hoarusib River study area, dyad associations were observed only between bulls; adult bull-adult bull (five associations) and adult bull-subadult bull (three associations).

Analysis of preferred group associations between giraffe of specific sex and age classes indicated no close associations in either the Hoarusib or Hoanib River study areas (Table 4.8).

In the Khumib River study area mean SR values were all less than 0.5, but the mean association values were considerably greater than those in the other two study areas. The highest mean association values in the Khumib River study area were adult cow-juvenile (0.42), adult cow-subadult cow (0.4) and subadult cow-subadult cow (0.39) dyads.

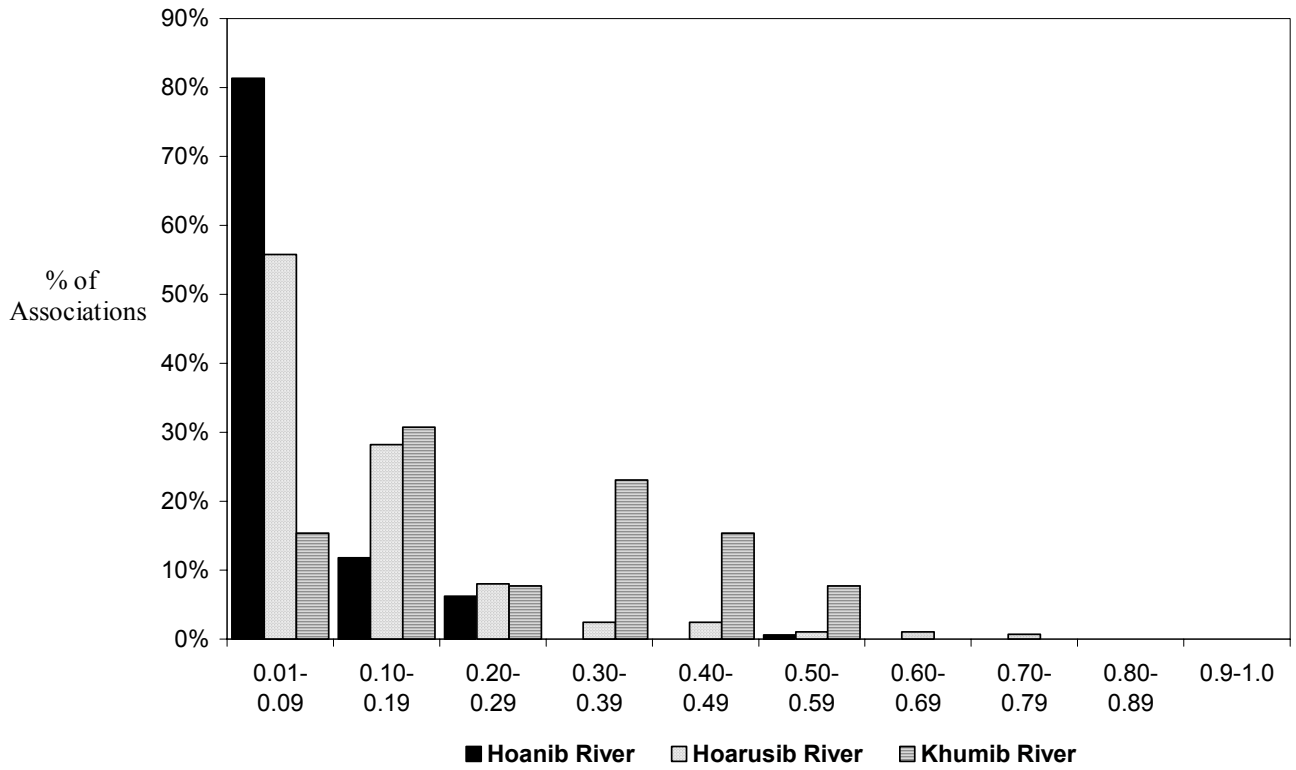


Figure 4.3. SR Index for inter-individual dyad associations of giraffe bulls in the study region.

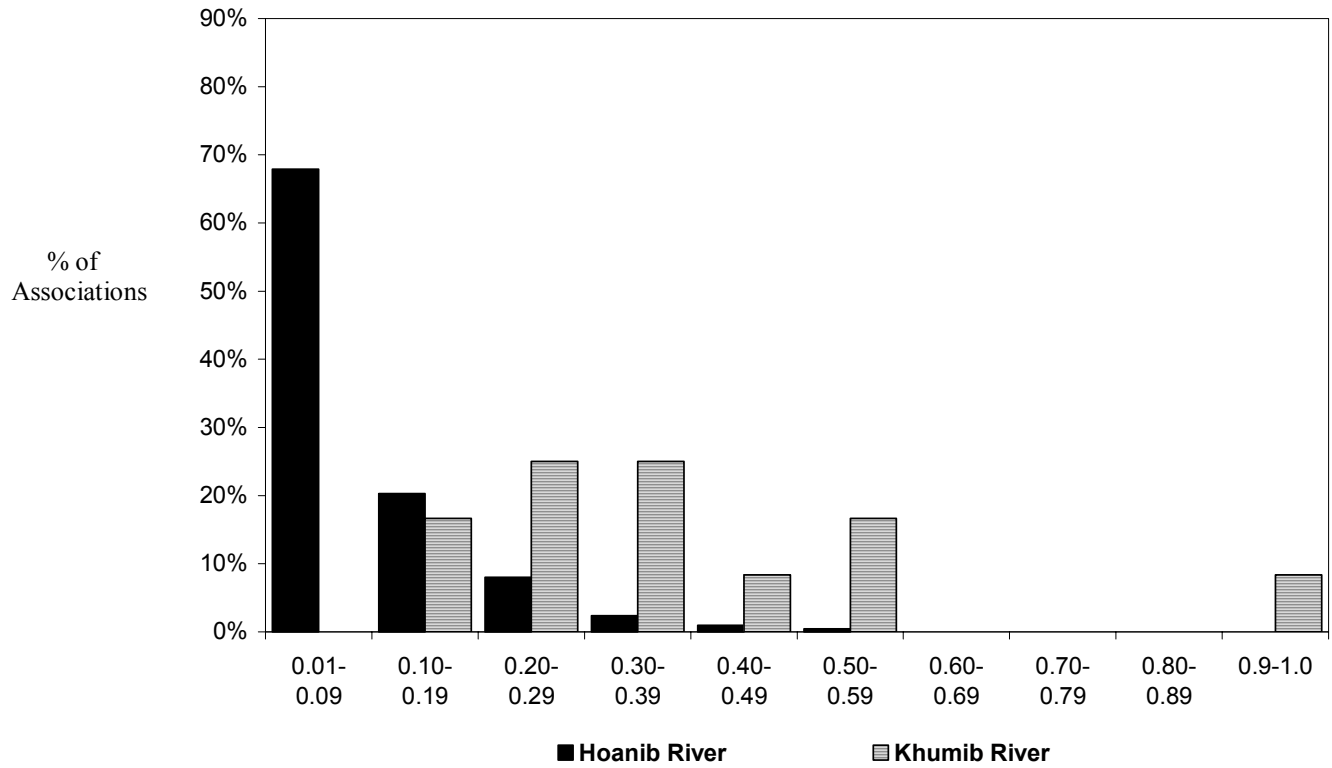


Figure 4.4. SR Index for inter-individual dyad associations of giraffe cows in the study region.

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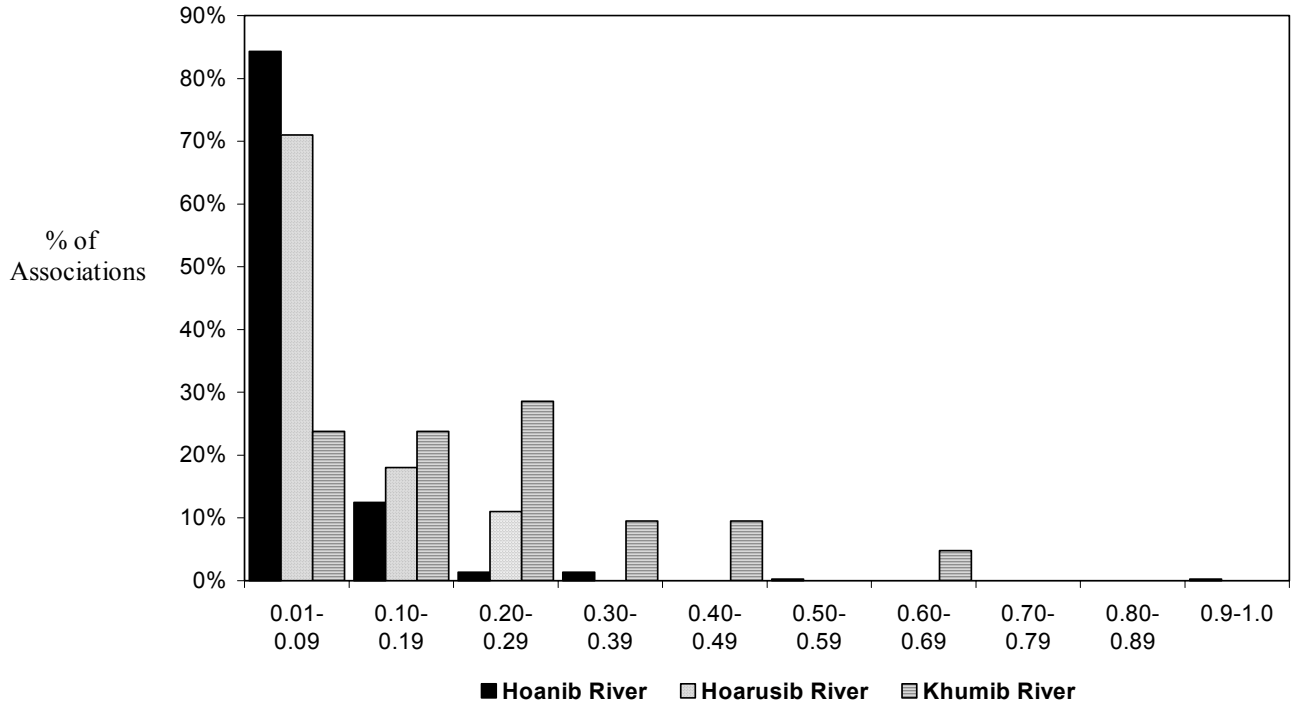


Figure 4.5. SR Index for inter-individual dyad associations of giraffe bulls and cows in the study region.

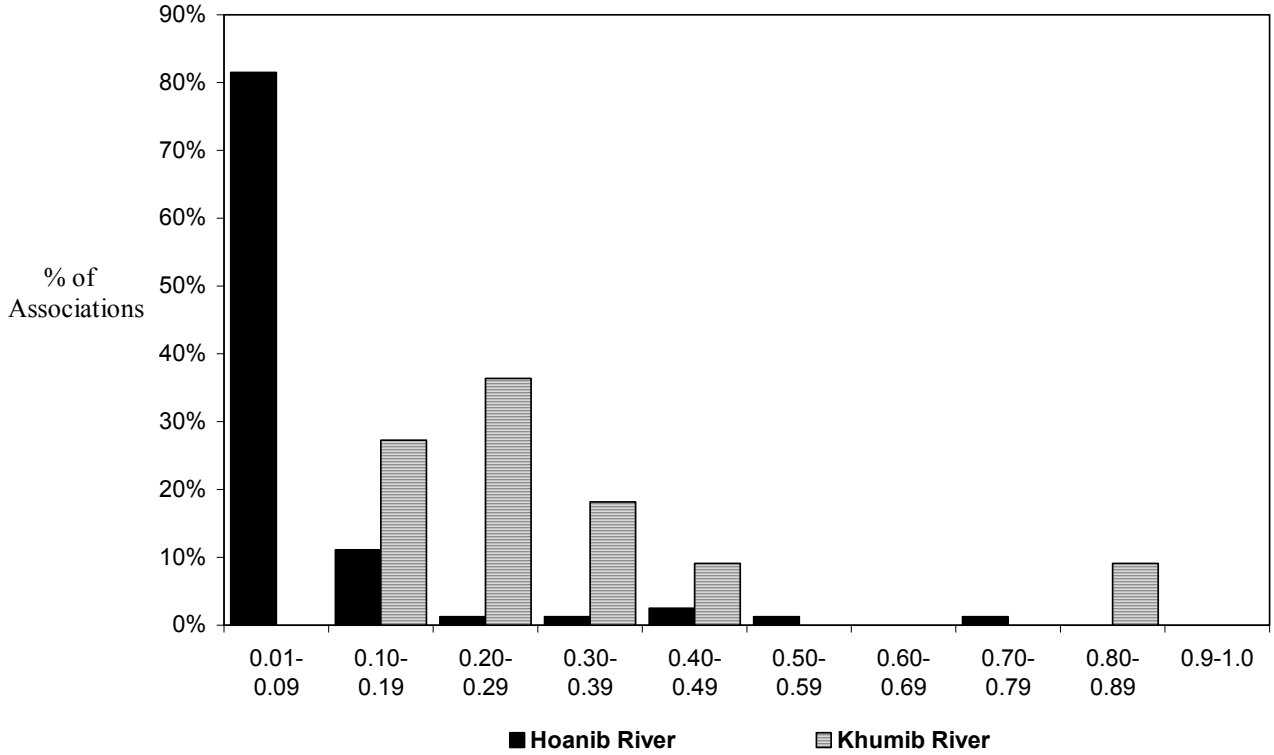


Figure 4.6. SR Index for inter-individual dyad associations of juvenile giraffe in the study region. N.B. No SR indices were calculated for Hoarusib River as number of associations <10.

Table 4.8. Mean simple ratio (SR) values ± s.d. between the different age and sex classes of giraffe.

Study area	Juvenile	Subadult bull	Adult bull	Subadult cow	Adult cow
Hoarusib River					
Juvenile	-				
Subadult bull	0.08 ± 0.05	0.11 ± 0.09			
Adult bull	0.08 ± 0.05	0.11 ± 0.12	0.13 ± 0.13		
Subadult cow	-	0.07 ± 0.04	0.04 ± 0.03	-	
Adult cow	-	0.08 ± 0.05	0.04 ± 0.02	-	-
Hoanib River					
Juvenile	0.05 ± 0				
Subadult bull	0.04 ± 0.02	0.11 ± 0.12			
Adult bull	0.04 ± 0.02	0.05 ± 0.04	0.07 ± 0.07		
Subadult cow	0.09 ± 0.09	0.09 ± 0.09	0.04 ± 0.03	0.11 ± 0.12	
Adult cow	0.12 ± 0.16	0.08 ± 0.10	0.04 ± 0.03	0.09 ± 0.09	0.09 ± 0.07
Khumib River					
Juvenile	-				
Subadult bull	0.31 ± 0.18	0.27 ± 0.20			
Adult bull	0.23 ± 0.01	0.25 ± 0.18	0.22 ± 0.16		
Subadult cow	0.25 ± 0.10	0.23 ± 0.19	0.21 ± 0.21	0.39 ± 0.23	
Adult cow	0.42 ± 0.38	0.24 ± 0.14	0.17 ± 0.08	0.40.± 0.31	0.29 ± 0.04

4.3.6. Mortality

Five giraffe deaths were recorded in the study population (Table 4.9), equating to a 3.2% mortality rate over a four and a half year period, or 0.7% per year. Natural mortalities were observed only in the hot-dry season. Using Hall-Martin's (1976) technique of age determination based on wear patterns of the maxillary first molar, the deceased giraffe bulls and cows were classified as adults.

The first observed mortality was that of an unknown adult bull in the Hoanib River study area in November 1999. On visual examination no immediate cause of death could be ascertained and hence it was assumed to have died of natural causes. Anthrax swabs and skin samples were taken for analysis. The Central Veterinary Laboratory, Namibian Ministry of Agriculture, analysed the samples and ruled out anthrax (unpublished data).

Table 4.9. Mortalities of giraffe in the study region.

Nomenclature	Sex	Age Class	Month of death	GPS/Location °S	°E	Cause of death	Anthrax test result
Unknown	Bull	Adult	11/1999	-	-	Natural	Negative
HSBM23	Bull	Adult	11/2002	18.82152	13.12603	Disease	*
HNBM14	Bull	Adult	2/2003	19.35210	13.15723	Lion	N/a
HNBF6	Cow	Adult	3/2003	19.32807	13.23327	Lion	N/a
HNBJ6	-	Juvenile	3/2003	19.32708	13.23466	Lion	N/a

*Corpse was dried out and decomposed, no sample possible; N/a: not applicable.

A second adult bull (HSBM23) died of unknown causes in the Hoarusib River study area in November 2002 and was found approximately one month later. The carcass had dried and unfortunately no blood or swab samples could be obtained for analysis. Calluses and remnants of lesions were observed on the carcass. A month prior to its death this giraffe had been sighted with large tumour-like protrusions on both sides of its body, as well as around the rump, exuding a milky white 'pus-like' substance (Figure 4.7). It was assumed that these growths resulted in the giraffe's death. Namibian wildlife, and former MET, veterinarian Dr H.O. Reuter, was consulted but he was unable to provide an explanation for the growths other than they might have been due to cancerous tumours or viral infections, such as 'lumpy disease'. Lumpy disease is a highly infectious viral disease that predominates in cattle in sub-Saharan Africa, and is becoming more prevalent in other ungulate species.

A third adult bull (HNBM14) was killed in the Hoanib River study area by two adult lions in February 2003. This was the first observed lion predation of giraffe in the study area in over a decade. On examination of the giraffe carcass, puncture wounds on the upper neck indicated suffocation.

In March 2003 n adult cow (HNBF6) and her calf (HNBJ6) were killed during one attack by three subadult male lions in the Hoanib River study area. Tooth punctures were observed in the upper skull of both giraffe, indicating that the lions were inexperienced killers.

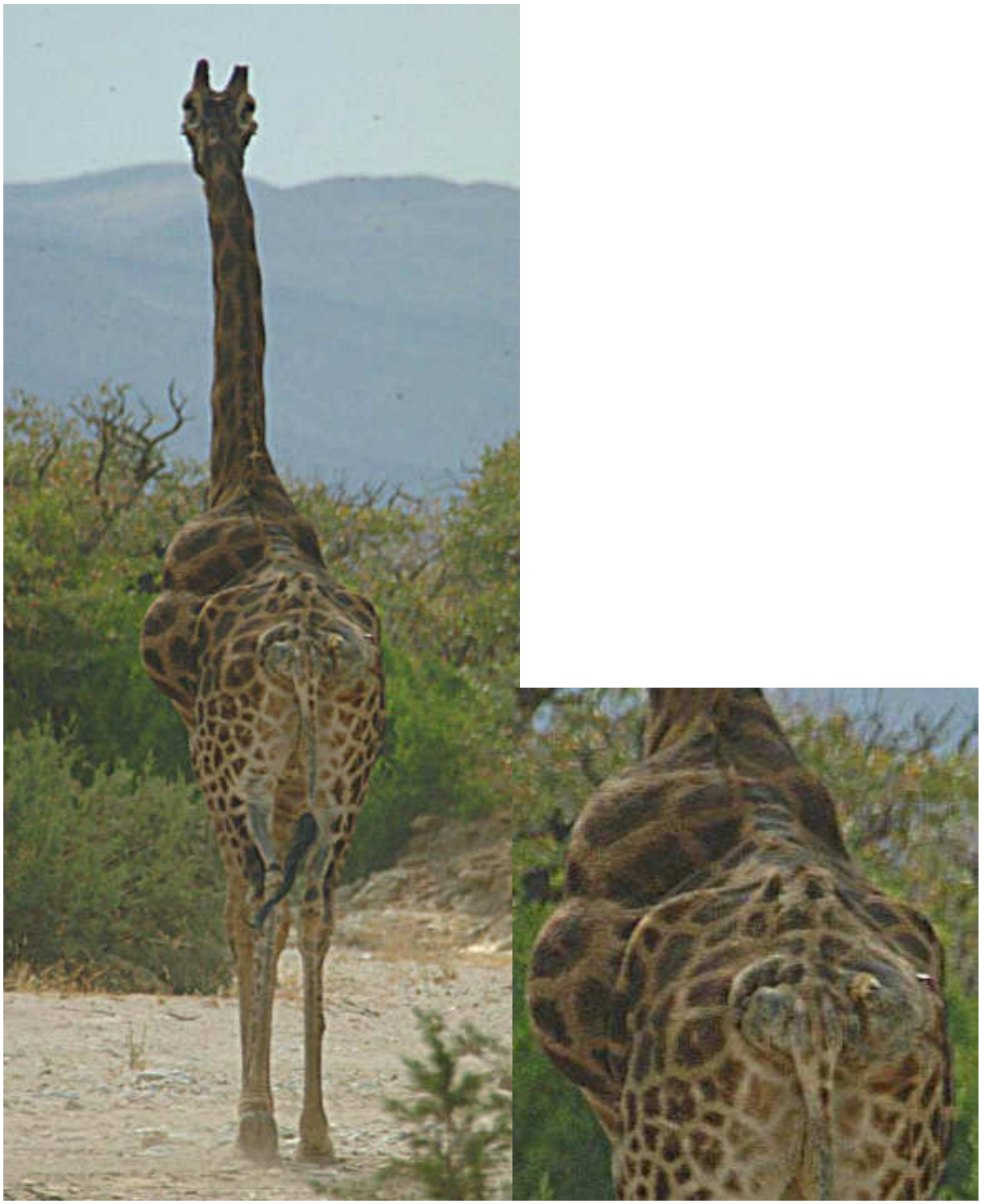


Figure 4.7. HSBM23 sighted one month prior to its death in the Hoarusib River study area. Note large tumour-like protrusions on both sides of the body and around the rump.

4.4. Discussion

4.4.1. Population structure

The current estimate of 92 giraffe in the Hoanib River study area is considerably greater than previously published data has suggested (Scheepers, 1992; Fennessy *et al*., 2003). Individual identification of giraffe during this study provided a more accurate baseline of the giraffe population. All previous estimates were based on time-dependent surveys, and hence did not succeed in providing accurate estimates of giraffe numbers in the Hoanib River (Scheepers, 1992; Fennessy *et al*., 2003). Earlier wildlife surveys also did not include the Hoarusib and Khumib River study areas, and a comparison of this study's population estimates with historical data was therefore not possible.

Population numbers differed between the three study areas, as did age and sex ratios. Study area population sizes were correlated with study area sizes, with the largest giraffe population residing in the Hoanib River study area and the smallest population in the Khumib River study area. As a consequence, densities in each study area were similar; 0.017 animals/km^2 in the Hoarusib and Khumib study areas, and 0.024/km^2 in the Hoanib. The high numbers of giraffe in the Hoanib River study area can thus be attributed, in part, to area but probably also to relatively dense forage that was available in its riparian woodland. The study region experiences decreasing rainfall from northeast to southwest. When overlaying a rainfall map with giraffe numbers, it appears that lower population numbers correlate with lower rainfall across the study region and hence reduced primary productivity, as well as with study area size.

Dominant adult to subadult to juvenile age class ratios are consistent with other findings and are indicative of a stable population with low fecundity (Dagg & Foster, 1982; Le Pendu *et al*., 2000). Only the Khumib River study population differed, having a slight subadult to adult bias. The increased number of subadults in the Khumib River study area might be a result of external factors such as poaching, drought or giraffe bulls migrating out of the population. The latter would offer an explanation for the strong bull bias in the adjacent Hoarusib River study area and higher reproduction rates.

Prior to this study, no follow-up research had been undertaken on the 22 giraffe that were translocated from western Etosha NP to the study area in 1991. During this study five of the translocated giraffe, three cows and two bulls, were observed. A communal farmer reportedly shot one bull some years earlier (J. Patterson personal communication). At least two of the translocated cows had calved since residing in the study area, with one giraffe calving twice. Of these identified giraffe, only one bull resided in the Hoarusib River, the original site of the translocation release. The other four translocated giraffe had moved to the southern tributaries and mountainous terrain between the Hoarusib and Hoanib Rivers. The move away from the Hoarusib River was apparently due to the conflict with communal farmers and associated permanent village of Purros and seasonal satellite homesteads. By avoiding communal farmers and their livestock, these giraffe would have reduced competition and conflict. The observations of this study indicate that giraffe can be successfully translocated from the higher rainfall area of Etosha NP to the arid study region and can survive and reproduce successfully. The exchange of genetic material (haplotypes) between the translocated Etosha NP and desert-dwelling giraffe, reported in Chapter 3, support this inference.

4.4.2. Sex ratio

Sex ratios differed markedly between the three study areas, although the population sex ratio for the three areas combined was approximately 1:1. The marked variation in sex ratios ranged from a large bull-bias at the Hoarusib River, to a large cow-bias at the Hoanib River study area. The bull-biased sex ratio in the Hoarusib River study area was the largest recorded for giraffe across their extant range (see Appendix 5). However, it is unclear why this persisted. Migration of bulls from adjacent areas to the Hoarusib River study area was observed. Cows showed a preference for environments, such as the Hoanib River, with reduced conflict and competition with humans and livestock (Caister *et al.,* 2003), although possibly a factor of the small populations size.

The cow-biased population in the Hoanib River study area was similar to that reported by Scheepers (1992). It appears that while giraffe numbers in the study area have increased in recent years, and assuming a natural calving sex ratio of 1:1, only migration of maturing

bulls into adjacent systems, such as the Hoarusib River study area, could have maintained the observed bias in sex ratio (Scheepers, 1992).

The sex bias within the three study areas was also reflected in the herd structures. Increased observations were recorded with two and/or three giraffe bulls per herd in the Hoarusib River study area compared to the other two study areas, correlating with the stronger bull-bull associations detected there. Single bulls were observed more often in the Hoanib River study area, perhaps reflecting more solitary behaviour of older, and potentially more dominant bulls in this study area (e.g. Foster & Dagg, 1972; Leuthold, 1979; Pellew, 1983).

4.4.3. Densities

Giraffe densities in the Kunene Region (0.01 giraffe/km^2) were equal to the lowest recorded densities across the extant range of the species (Le Pendu *et al.*, 2000). Similarly low giraffe densities have been observed only in the desert-dwelling giraffe population of Niger (Le Pendu *et al.*, 2000). Within each of the three study areas, giraffe densities were only marginally higher than those recorded for the Kunene Region. These marginal increases in densities were probably the result of the giraffe aggregating in the forage-rich riparian woodlands of each study area. On communal lands, giraffe densities are usually considerably lower than in protected areas, reflecting the impact of increased human encroachment, illegal hunting and high legal hunting quotas (Carter, 1990; Ciofolo, 1995; Caro, 1999). Similar conflicts have been reported to have detrimental effects on giraffe conservation and survival in this study region (Hall-Martin, 1988; Carter, 1990). Furthermore, the extreme arid conditions, large seasonal rainfall variability, lack of surface water and limited forage resources contribute to low giraffe densities and a low population carrying capacity in the region.

Throughout their range, giraffe vary in density between and within subspecies, across habitat types and under different conservation management approaches (see Appendix 6; Innis, 1958; Foster & Dagg, 1972; Hall-Martin, 1975; Leuthold, 1979; Dagg & Foster, 1982; Pratt & Anderson, 1982; Le Pendu *et al.*, 2000; Birkett, 2002). Previous research in

higher rainfall habitats has reported that giraffe achieve relatively high densities, small home ranges, stable herds and low mobility (Dagg & Foster, 1982; van der Jeugd & Prins, 2000; Le Pendu *et al.*, 2000). In contrast, the arid conditions in the study region have resulted in lower giraffe densities, larger home range sizes (see Chapter 5), less stable groups and increased mobility. Giraffe residing in more arid environments have been reported to have lower densities generally (Le Pendu *et al.*, 2000). Herd structure is further discussed (see below), while home range and mobility are discussed in Chapter 5.

4.4.4. Calving peaks

A strong calving peak was observed in the hot-dry season, coinciding with the podding of *Faidherbia albida* and a leaf flush of *Colophospermum mopane*. Scheepers (1992) reported a calving peak in the warm wet season for the Hoanib River study area. However, it should be noted in Scheepers (1992), seasons differed to those in this study (warm wet season—January to March; cold-dry season—April to August; warm dry season—September to December). Therefore, the calving peak in the warm wet season reported by Scheepers (1992) partially coincides with this study's hot-dry season peak. Seasonal calving peaks have been reported in giraffe elsewhere, and all correlate with seasonal flushes of forage (Ansell, 1960; Hall-Martin *et al.,* 1975; Dagg & Foster, 1982; Skinner & Smithers, 1990). However, it was also evident that giraffe in the study region and throughout their extant range calve year round (Foster & Dagg, 1972; Hall-Martin *et al,* 1975; Dagg & Foster, 1982; van der Jeugd & Prins, 2000; Le Pendu *et al,* 2000). Food resources must therefore be present year round in sufficient quantity to sustain reproduction, albeit at lower levels outside the hot-dry period.

Giraffe have a mean gestation period of 457 days (Skinner & Hall-Martin, 1975). Extrapolating conception dates from calving dates for this study, the majority of conceptions would have occurred in the late cold-dry and hot-dry season. This is similar to the findings of Scheepers (1992) for the Hoanib River study area. In other studies, however, conception has been reported to increase in the wet season, correlating with higher plant production and seasonal rainfall (Berry, 1973; Field & Blakenship, 1973; Dagg & Foster, 1982). In the northern Namib Desert, some conceptions did occur in the

wet season, perhaps correlating with aggregation of giraffe in the riverbeds and seasonal production of some preferred plant species, such as *Faidherbia albida*. It is also possible that the low numbers of calving events precluded the detection of any real pattern e.g. low survivorship.

Throughout the study period the mean annual calving rate giraffe was approximately 3%, double that reported by Scheepers (1992), but substantially lower than the 9.3% reported by Viljoen (1982) for the Hoanib River study area. However, when comparing population numbers from the Hoanib River study area in 1990 (Scheepers, 1992) with population numbers recorded in this study, the mean annual calving rate equates to less than 1%. Low calving rates are common in giraffe (e.g. Foster & Dagg, 1972; Dagg & Foster, 1982), while calf predation increases calf survival markedly. Only one fifth of all giraffe reach sexual maturity (Foster & Dagg, 1972; Dagg & Foster, 1982; Scheepers, 1992). During this study only one calf was killed by predators, which could result from the low predator density in the study region (see below). Other factors such as resource availability and competition, low and variable rainfall, low fecundity and limited forage availability may affect calving rates of giraffe in the study region.

4.4.5. Herd structure

During the study nearly all combinations of herd structure were observed, comprising different age and sex classes. However, no bull-juvenile herd groupings were observed, indicating that bulls lack a paternal bond with their calves in the study area. A negative correlation between mean herd sizes and study area population numbers also implies a looser herd structure in the more populated Hoanib River study area compared to the Khumib River study area.

Approximately 60% of all giraffe in the study region were sighted in herds of three or less individuals. Similar herd sizes have previously been reported for giraffe in the Hoanib River study area (Fennessy *et al*., 2003). Solitary giraffe were most commonly observed, as in other giraffe populations throughout Africa (see Appendix 7) (Innis, 1958; Foster & Dagg, 1972; Leuthold, 1979; Scheepers, 1992; Le Pendu *et al.,* 2000; van der Jeugd &

Prins, 2000; Fennessy *et al*., 2003). Solitary bulls were observed more frequently than solitary cows, while solitary cows were observed more frequently than solitary juveniles. Mate searching by giraffe bulls (Dagg & Foster, 1982) likely results in their solitary existence, although singleton status may result also from bulls avoiding each other due to intolerance.

Solitary cows were not commonly observed in this study. Solitary cows in the Hoanib River were previously reported only in a pre-partum isolation period before pregnancy (Scheepers, 1992), but this was not observed in this study. One cow in the Hoanib River study area was observed alone on numerous occasions, however, giraffe were more often observed in mixed herds. Only one solitary juvenile, aged between six and 12 months old, was observed. This individual was separated from its mother for less than two hours, in contrast to reports of cows often leaving their calves for hours, or days, on end (Foster & Dagg, 1972). On all other occasions juveniles were observed in mixed herds or crèche groupings.

In the Hoarusib River study area, bachelor herds predominated. Due to the high number of bulls, few combinations other than bull-bull were observed. The greatest variation in age and sex per herd structure was observed in the Hoanib River study area, although solitary bulls and mixed herd combinations (bull/s-cow/s) were the most frequent herd compositions. The Khumib River study area had different herd compositions to the other study areas, and herd sizes of two or three giraffe were dominant. Herd structures in this study area most frequently comprised cows and their calves, cows only or cows in combination with subadult cows and/or bulls and/or juveniles. Variances in herd composition in the Khumib River study area may have resulted from lower numbers, reduced forage availability, a strong social structure and inter-individual associations between cows.

Giraffe herd sizes differed seasonally between the three study areas. Increased herd sizes were observed during the wet season in the Khumib River study area, during the cold-dry season in the Hoarusib River study area and during the hot-dry season in the Hoanib River study area. Although there was some movement of bulls into the Hoarusib River, no large-scale seasonal movements of giraffe from one study area to another study area were

observed. Movements across the study area therefore did not affect seasonal herd aggregations. Seasonal shifts in availability of food and local rainfall have been reported to increase herd sizes elsewhere in Africa (Hall-Martin, 1974; Hall-Martin *et al,* 1975; Pellew, 1984b; Le Pendu & Ciofolo, 1999). Giraffe did not appear to aggregate for predator protection, as reported for other ungulates (Bertram, 1979; Siegfried, 1980), possibly due to low predator densities within the study areas.

It was not apparent why herd sizes differed seasonally in the three study areas. Increased herd sizes in the wet season may be attributed to an increase in moisture-rich forage (Hall-Martin, 1974; 1975); this opportunism may extend also into the cold-dry season, particularly in years of late seasonal rainfall. Herd aggregations in the hot-dry season in the Hoanib River study area could be attributed to increased use by giraffe of the main riverbed to access podding *Faidherbia albida* and a flush of *Colophospermum mopane* leaves. This period is a time when few other moisture- and protein-rich resources are available in the study area, and these forage sources are consequently important (Hall-Martin, 1974; 1975; Styles & Skinner, 1997; Fennessy *et al.,* 2003).

4.4.6. Inter-individual associations

A low degree of association was observed between giraffe in the study population, with the majority of dyad interactions being weak. However, these results indicated stronger inter-individual associations in non cow-calf dyads, than compared to other populations (e.g. Leuthold, 1979). Other studies have reported generally loose associations between giraffe, with the only strong bonds being between cows and their calves (Leuthold, 1979; Pratt & Anderson, 1982; Le Pendu *et al*., 2000; van der Jeugd & Prins, 2000). A stronger cow-calf association would be expected based on the need for calves to be nurtured and protected.

Within each of the three study areas, varying SR indices and sex-age associations were observed. However, across the study population the overall degree of association was low. No strong associations were observed between giraffe from different study areas. Only bull-bull dyads showed strong associations (n=8; both adult-adult and adult-subadult) in the Hoarusib River study area, correlating with this area's bull-biased population. In

contrast, strong associations in the Hoanib River study area comprised one subadult bull dyad, one subadult cow dyad, two bull-cow dyads and two cow-calf dyads. No adult bull or adult cow dyads were observed, while the strong subadult cow dyad was between two giraffe that had associated as juveniles in a crèche grouping.

The smaller population in the Khumib River study area exhibited several strong inter-individual associations, as well as relatively more dyads with indices greater than 0.3. The highest mean SR indices were identified for adult cow and calf dyads and adult cow and subadult cow dyads. The subadults in the dyads were the offspring of the associated cow. Relatively strong subadult cow-cow associations reflected the maturation of a relationship from crèche juveniles into subadults. The maturation of two associated crèche juveniles into subadulthood was also observed for two subadult bulls in the Hoanib River study area. Strong juvenile-juvenile associations following break-up of a crèche have previously been reported only in captive populations (Bashaw, 2003).

The observations in this chapter support the concept that stronger bonds and associations between giraffe stem from matrilineal associations of similar age/sex. This stronger association among cows, as observed in the Khumib River study area, has previously been assumed in other giraffe populations (Le Pendu *et al*., 2000; van der Jeugd & Prins, 2000) but not confirmed. Furthermore, juvenile cows, as opposed to juvenile bulls, have been reported to associate longer with their mothers following maturation (Pratt & Anderson, 1979). This relationship is similar to that observed for elephant, where a strong matrilineal association exists (Moss, 1982; Bashaw, 2003).

In bulls, maturation is associated with progress from social to more solitary behaviour (Pratt & Anderson, 1985). Strong adult bull-bull associations have not previously been reported, as bulls spend much of their time seeking cows in oestrus (Dagg & Foster, 1982; Pratt & Anderson, 1982; van der Jeugd & Prins, 2000). However, it was apparent that old bulls in the study area associated less often with other giraffe, independent of age and sex, and became more solitary as they aged (Dagg & Foster, 1982; personal obs). The strong bull-bull dyads in the Hoarusib River study area reflected a small group of individuals in a bull-biased population that associated frequently within a larger grouping consisting of nine bulls. Of these, two or more were usually observed together at any one time,

irrespective of age. The strong bull-bull associations in the Hoarusib River study area were not reflective of the entire bull population in the study region.

The smaller population and higher mean herd size in the Khumib River study area correlated with stronger inter-individual associations. The population in the Khumib River consisted of two core herds, both with dominant cows and their calves (juveniles and subadults, bulls and cows). The strong associations may have been matrilineal. Herds were often observed together for days, even weeks, at a time, however, throughout the year they continually separated and re-formed. This is similar to the clan relationship in elephant (Moss, 1982). The strong association between giraffe herd members in the Khumib River study area was not observed in the other study populations, nor has it been recorded in other wild giraffe populations in Africa.

Studies of captive giraffe support the concept that cows are more social, particularly with their calves (Bashaw, 2003). Matrilineal relationships in captive studies suggest strong associations. However, limitations of captive studies restrict the translation of findings into the wild (Bashaw, 2003). Limitations include creation of groups of unnatural social composition and density, restriction in movement and association, artificial dispersion, restricted reproduction, forage and water manipulation.

Further analysis of matrilineal relationships through long-term monitoring and study of genetic architecture would likely provide greater insight into the population dynamics and conservation of giraffe. Further research may also shed light on whether increasing numbers and maturation of bulls in the Khumib River population result in their migration into adjacent river systems, whether the strong crèche bonds established between giraffe persist throughout their lives, whether herd associations are coincidental, and whether dominant relationships occur within or between adults of both sexes.

4.4.7. Mortality

Of the five deaths of giraffe recorded during the study, none were directly attributable to debilitation due to the arid conditions. The causes of death varied from natural senescence

and disease to predation by lion. Giraffe mortalities are usually highest in the first year of life, due to lion predation, but predation by leopard and hyena have also been reported (Foster & Dagg, 1972; Dagg & Foster, 1982; Henschel & Skinner, 1990; Cooper *et al*., 1999). No deaths in the study region were caused by leopard or hyena, but they are known to occur in the nearby Etosha NP (Scheepers & Gilchrist, 1991).

Prior to this study, no observations of lion preying upon giraffe had been reported for the study region in the past decade (Braby, 1990; Scheepers, 1992). The usual prey of lion in the Kunene Region include gemsbok, ostrich and springbok, and more rarely black-backed jackal, cape fur seal *Artocephalus pusillus*, porcupine *Hysterix africae-australis* and white breasted cormorant *Phalacrocorax carbo* (Bridgeford, 1985a; Scheepers, 1992). Predation by lion is the major threat to giraffe in most other habitats, but low lion density and continued persecution by communal farmers have minimised this impact in the study region (Stander & Hannsen, 2000; Hannsen, 2004).

Historically, disease, in particular rinderpest, foot and mouth and anthrax, has decimated giraffe and other wildlife populations across the African continent (e.g. Young, 1969; Ebedes, 1976; Foster & Dagg, 1982; East, 1999). Several giraffe deaths from anthrax were reported in Etosha NP between 1963 and 1990, and were a result of an over-concentration of wildlife at water points and adjacent feeding grounds, coupled with a natural anthrax epizootic (Ebedes, 1976; Berry, 1997). During this study, one bull died of symptoms similar to anthrax, but laboratory analysis returned a negative anthrax result. The dead bull had excessive tooth wear that prevented it from feeding, suggesting that it probably starved. The smaller population numbers and limited availability of surface water in the study region may reduce the susceptibility of giraffe to diseases such as anthrax, but the recent construction of permanent artificial water sources in the Hoanib River area may result in increased transmission of disease between wildlife populations in the long-term (e.g. Young, 1969; Ebedes, 1976).

In the arid environment of the study area, drought often kills livestock and wildlife (Scheepers, 1992; D. Gilchrist & R. Loutit, personal communication). Although drought did not cause the death of a single giraffe in the study area, it could contribute to mortality rates. Giraffe have the ability to feed solely on larger desert trees and shrubs, and often on

plants that are least dependent on local rainfall. Furthermore, the ability of giraffe to range across large distances, coupled with slow breeding, ensures that their numbers do not increase markedly during high rainfall periods, and do not decrease in drought conditions. Interestingly, flash flooding and lightning strikes have resulted in more giraffe deaths in the Kunene Region in recent years than most other known causes (D. Liebenberg & R. Loutit personal communication).

4.5. Methodological problems

Although the results of this study clearly show that giraffe population structures differed between the three study areas, a number of problems limited data collection. Due to the arid conditions and mountainous terrain, not all areas within the study region were accessible and movement was restricted by natural frontiers. Seasonal flood events in the ephemeral rivers prohibited access to parts of the study area during the rainy season. Furthermore, in the wilderness areas of the SCP, restricted access and limitation to the existing track infrastructure limited human, but not giraffe, movement. Therefore, some areas that giraffe might seasonally have used remained inaccessible.

4.6. Conclusion

The Kunene Region, together with Niger, has the least dense population of giraffe in Africa. The low density is likely to be the result of the arid environment in the study region. Low spatially variable rainfall, historical hunting pressures, low fecundity of giraffe and limited forage combine to restrict population growth and the study region's carrying capacity. An even sex ratio was recorded for the study region, however, different sex biases occurred within each of the three study areas. These sex biases correlated with differences in population structure and levels of association. Herd aggregations differed seasonally within each study area; solitary bulls were most commonly observed, followed by groups of two and three giraffe. Stronger inter-individual associations were observed in the smallest giraffe population, in the Khumib River study area, with fewer strong dyad associations occurring in the larger study areas. Strong bull-bull associations occurred in

the Hoarusib River population, while a matrilineal association was inferred for that in the Khumib River. Low numbers of mortalities were recorded, although the first depredation of giraffe by lion in over a decade was recorded during the study period.

Population and herd structure varied between each of the three study areas, raising questions about what causes population-level differences. Movement of giraffe between the study areas might be one of the causal factors, and this, together with home range, is considered in the next chapter.

CHAPTER 5. HOME RANGE

This chapter investigates home range and movement behaviour of the desert-dwelling giraffe in the northern Namib Desert, using both individual identification methods and GPS satellite tracking. It also investigates long distance movements and movement corridors used by giraffe between the three study areas, and the relationship between movement and temperature.

5.1. Introduction

Mammals generally range over an area that is just large enough to satisfy their ecological and biological requirements, such as food, water, mating opportunities and refugia. Home range size scales with bioenergetic needs, which increase proportionally with body size (McNab, 1963). Home range size to body mass scaling coefficients are substantially greater for mammals than other terrestrial species (e.g. McNab, 1963; Lindstedt *et al*., 1986; Swihart *et al*., 1988; du Toit, 1990a), reflecting the costs of homeothermy. In addition, much variation occurs in home range size due to sex, age and migration patterns, and environmental factors such as habitat structure, competition and resource availability (e.g. Clutton-Brock *et al*., 1989; Fischer & Linsenmair, 1999). In many mammals, food appears to be a particularly important determinant of home range, with both the dispersion of food patches (e.g. MacDonald, 1983) and quantity of food (e.g. Boutin, 1990) influencing range limits in different species.

Dispersal and home range sizes of arid-adapted mammals are larger in comparison to the same or similar species in higher rainfall environments (e.g. Viljoen, 1989a; du Toit, 1990; Dickman *et al*., 1995; Le Pendu & Ciofolo, 1999). Local rainfall, availability of food and free water are dominant factors driving mammal movements in arid environments, with individuals moving there to obtain patchy and ephemeral resources than in mesic environments where resources are often richer and more stable.

The giraffe, with a large body mass and high bioenergetic requirements, has more expansive home ranges than smaller ungulates in the same environment, such as kudu or steenbok (e.g. Cloete & Kok, 1986; du Toit, 1990a). However, large differences in giraffe home range sizes have been reported across the range of the species, as well as in different habitats and under varying management regimes (Langman, 1973; Berry, 1978; Dagg & Foster, 1982; Pratt & Anderson, 1982; Le Pendu & Ciofolo, 1999; van der Jeugd & Prins, 2000). Abiotic (e.g. climate, topography), biotic (e.g. forage availability and quality, herbivore and predator densities) and human influences (e.g. poaching, settlements, fences) are contributing factors that affect giraffe range and distribution (e.g. Dagg & Foster, 1982; Ciofolo, 1995).

Niger's desert-dwelling giraffe range individually over a substantially larger area (127 to 1,559 km^2; Le Pendu & Ciofolo, 1999) than any other giraffe in Africa; for example, 0.1 to 27 km^2 in Tanzania (van der Jeugd & Prins, 2000); 145 km^2 in Zambia (Berry, 1978); and 5 to 654 km^2 in South Africa (Langman, 1973). Increased vegetation density in savanna environments increases the available forage per area unit. This correlates, in turn, with smaller home ranges of giraffe that occur in such habitats (e.g. Langman, 1973; Pratt & Anderson, 1982; van der Jeugd & Prins, 2000). This relationship supports du Toit's (1990a) theory that food production sets the minimal home range limit in mammals.

The use of different sampling techniques and poor seasonal accessibility for researchers has often resulted in underestimation of giraffe homes (Langman, 1973; Berry, 1978; Dagg & Foster, 1982; Scheepers, 1992; van der Jeugd & Prins, 2000). Even today, most home range analyses depend on field observations of individuals. Advanced methods of animal movement and core home range analysis (Burgman & Fox, 2003; Douglas-Hamilton *et al*., In press) are providing more accurate estimates of animal ranges and movements. However, the lack of long-term studies remains the most limiting factor in understanding the home range and movements of giraffe.

Equipping animals with radio transmitter collars has aided ecological research by allowing remote collection of data on animal movements and home ranges. Radio telemetry studies have been undertaken on numerous large mammal species, including caribou (e.g. Simpson *et al.,* 1997), elk, mule and black-tailed deer (e.g. Gillingham & Bunnell, 1985; Harestad,

1985; Edge & Marcum, 1989), lions and leopards (e.g. Stander & Hansen, 2003) and grizzly bears (e.g. Hamilton & Archibald, 1985). More recently, advances in satellite technology have enabled the compaction of GPS transmitters onto collars. The ability to transmit data from an individual's collar to satellite has improved the scope and efficiency of field-based research, allowing collection of the best possible data on home ranges, seasonal movements, human-wildlife interaction zones, migration routes and speeds of migration.

Across Africa, GPS satellite tracking has become increasingly important and accessible during the past decade. Collaring is supported by most African government conservation agencies and NGOs such as the Wildlife Conservation Society, Save the Elephants, WWF, Conservation International, IUCN, National Geographic and the Born Free Foundation. The first trial of satellite collars in Africa was on desert-dwelling elephant in the Kunene Region, Namibia, in 1986 (Lindeque, 1991; Lindeque & Lindeque 1991). The reduced intensity of monitoring and large number of high-resolution locations obtained by satellite tracking provided a greater understanding of elephant movements and ranges than ever before. African countries where GPS satellite collars are currently deployed for wildlife tracking include Kenya, South Africa, Botswana, Mozambique, Namibia, Mali and Gambia.

Tracking of giraffe has historically been limited to direct field observation (e.g. Foster & Dagg, 1972; Berry, 1978; van der Jeugd & Prins, 2000), although several studies using telemetry have provided considerably more data and greater accuracy than incidental observations and monitoring (e.g. Langman, 1973; Dagg & Foster, 1982; Scheepers, 1992). Tracking studies of giraffe continue to require intensive field monitoring, although finding and following individuals is considerably easier, more reliable and time efficient than relying on chance encounters. However, no GPS satellite collaring of giraffe has previously been undertaken in Africa.

In this chapter, direct observations and GPS satellite technology were used to provide a better understanding of the home ranges and seasonal movements of giraffe. Importantly, it was anticipated that the knowledge obtained could be used to protect giraffe populations

in the communal areas of the study region and the broader Kunene, where giraffe conservation is currently limited.

5.1.1. Aims

The movements and ranges of individuals within a population provide insight into their behavioural activities and ability to track resources, as well as the area needed to sustain their ecological and biological requirements. In order to examine these issues, in this chapter I investigated:

- home range size of giraffe;
- movements (hourly, daily, monthly, seasonal and long distance); and
- movement corridors of giraffe in the three study populations (Hoanib, Hoarusib and Khumib Rivers).

Each study area was treated as a separate unit, although movements between them were observed. The investigations were intended to provide an overview of the range requirements and the dispersion of giraffe throughout the study region, and also the movement of giraffe in relation to temperature.

5.2. Methods and materials

Over a two-year period (2002 and 2003), monthly field trips were conducted in the study region and observations of giraffe were made predominantly by vehicle and sometimes on foot. The Hoanib and Hoarusib River study areas were visited more frequently than the Khumib River study area due to time, distance and logistical constraints. Once spotted, locations and co-ordinates of individual giraffe were recorded using a Garmin II *plus* Global Positioning System (GPS) which was fixed to the vehicle with an external antenna. These co-ordinates, along with relevant bio-data (see section 4.2), were transferred to a Microsoft Excel Professional 2000 database and MapInfo Professional 6.5 Geographical Information System (GIS) (MapInfo Corporation, 2001). Additional data were collected from GPS satellite collars fitted to four giraffe (see section 5.2.2). Movement corridors

were established by overlaying GPS co-ordinates for giraffe onto dedicated MapInfo maps of the study area.

5.2.1. GPS satellite collaring

The satellite system used for GPS tracking during the study was an Inmarsat 3, the first in a series of five third-generation satellites (see Appendix 8). Using spot-beam technology to supply data communication services, a navigation transponder enhanced the accuracy, availability and integrity of the GPS and Glonass satellite navigation systems.

The GPS unit (MT2000 terminal) was a lightweight (<900 g) mobile transceiver designed to utilise L-band satellite frequencies. The unit was compact with a single sealed enclosure, constructed from chemical-resistant polycarbonate, with an integral antenna subsystem and transceiver for communicating with satellites. A top antenna cover was welded to a bottom shell, while gaskets and weatherproof connectors sealed the unit. The unit was powered by an external battery pack consisting of six 'DD' batteries positioned on the opposite side of the collar to the GPS unit in a protective casing similar to that used for the GPS unit. The batteries and GPS unit were connected via insulated and protected wiring. The battery pack also served as a counter balance for the collar, enabling the GPS unit to remain upright. Each of the GPS units also had an in-built VHF telemetry transmitter that enabled tracking of individual giraffe using a hand-held antenna (frequencies ranged from 148.150 to 148.360 MHz). The GPS collars were designed and constructed by African Wildlife Tracking Services, South Africa.

Four giraffe (one cow and three bulls) in the study region were fitted with GPS satellite collars during a three-day collaring period in September 2002 (28–30/09/02) (see Appendix 9). Two collars were fitted to bulls in the Hoarusib River study area. In the Hoanib River study area collars were fitted to one bull and one cow (Figure 5.1). The collaring was undertaken in accordance with the MET research/collecting permit number 497/2001 and under the auspices of the Namibian Elephant & Giraffe Trust (NEGT). The collaring team consisted of myself, a wildlife veterinarian, a wildlife health advisor, an

MET game capture specialist, MET staff, donors, support staff and communal conservancy members.

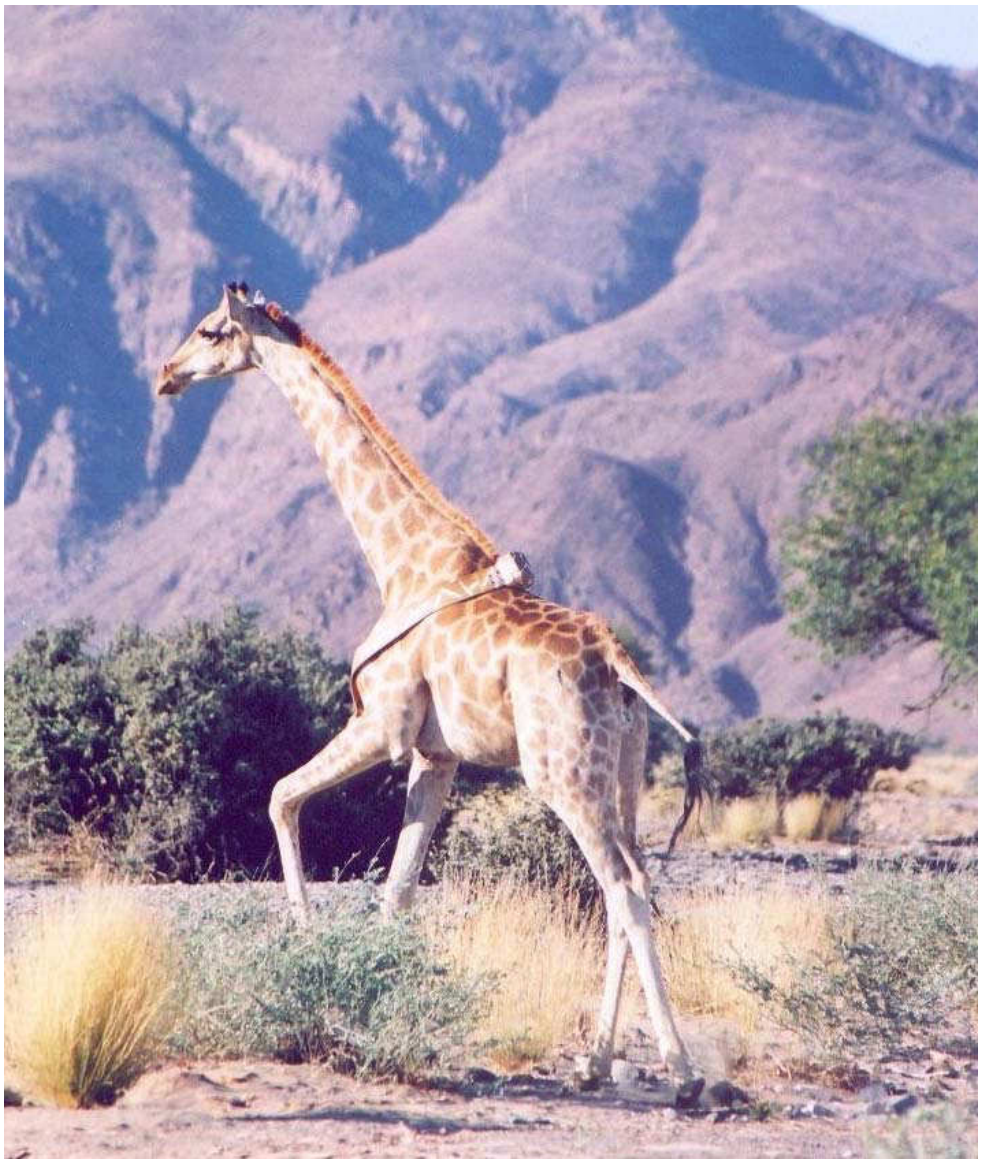


Figure 5.1. Example of GPS satellite collared giraffe in the study region: collared cow giraffe in the Hoanib River study area, September 2003 (photo courtesy of R. Caudle).

Giraffe were darted from a Bell Jet Ranger helicopter with A3080; an immobilisation drug. The dosage used to sedate the giraffe during the collaring ranged from 13 to 16 mg of A3080 dependent on the size and sex of the individual. Once the drug took effect, the giraffe were brought to the ground by the game capture specialist and support staff. Once restrained on the ground the giraffe were held down by hand and the reversal drug, M5050 (diprenorphine), injected. The giraffe were also blindfolded and ears blocked during the collaring procedure to reduce stress. Whilst the collar was fitted, blood and tissue samples

(see Chapter 3) were taken, and measurements of the giraffe were collected for other studies. The mean down time for the four collared giraffe was six minutes and no injuries or post-capture stress were observed. All giraffe were monitored intensively for a 24-hour period to ensure no lasting effects of the drug or collaring.

All GPS satellite collars were programmed to transmit at eight-hour intervals, providing three GPS readings and ambient temperatures per day. The collars were expected to transmit data for up to two years using eight-hour transmitting intervals. However, complications, such as collars twisting and breaking wiring connections, were experienced and the life span of no collars exceeded 3.5 months. In addition, three of the four collars were programmed to transmit hourly GPS readings for 4 to 5 consecutive days per month to obtain high resolution data for hourly, daily, weekly and monthly analyses.

Mean monthly and weekly ranges were estimated using 100% MCP. Mean hourly and daily movements were calculated in the MapInfo extension program Range Manager v.1 by tallying total distance travelled.

5.2.2. Home range analysis

Estimates of home range size were calculated using data from individually identified giraffe observed during field research and, where available, data from the GPS satellite collars. Home range sizes were estimated using both the 100% minimum convex polygon (MCP) and 95% or peeled MCP methods (Jenrich & Turner, 1969). These methods were used to enable comparisons with other giraffe studies in Africa. The MCP 95% method is considered to provide a better estimate of home range as it reduces outlier fixes representing forays or other potentially random movements (Broomhall *et al*., 2003).

The home range estimates were obtained using the MapInfo extension program Range Manager v.1 (Data Solutions, 1998). Range Manager was developed as shareware for the display and analysis of animal location data in the MapInfo Desktop GIS Mapping System (MapInfo Corporation, 2001).

Individual home ranges were estimated for giraffe with at least 10 observations collected over a minimum period of one year. Mean home range sizes were calculated for individuals within each of the three study areas as well as for bulls, cows and juveniles throughout the study region. Published estimates for giraffe have used fewer observations to obtain home ranges (Foster & Dagg, 1972; Berry, 1978), however, no asymptotic home range size has been reached for any population, as the numbers of fixes obtained per individual were considered too low. The results obtained during this study provide the first minimum home range size estimates for giraffe in Namibia.

Differences in home range estimates between sexes and study areas, as well as between sexes within the study areas, were tested using Kruskal-Wallis and two-tailed Mann-Whitney U tests. These non-parametric techniques were preferred to analysis of variance due to non-normality in the distribution of data, which could not be correlated by transformation. The MCP 100% and 95% home range size estimates were compared to ascertain differences between individuals and sexes when outlier fixes were removed.

5.3. Results

5.3.1. Home range

From direct observations, the largest recorded home range estimates were obtained for a giraffe bull (1 950 km^2) and the second largest for a cow (1 098 km^2) (Table 5.1). Home range estimates using the MCP 100% and 95% methods varied markedly both between and within the sexes (Table 5.1; also see Appendix 10). Data on home range sizes of juvenile giraffe were limited (n =2), but showed that juveniles occupied smaller areas than bulls or cows.

The MCP 95% home ranges of giraffe were markedly reduced when compared to the MCP 100% estimates. The reduction in home range size between the MCP 100% and 95% estimates was about 50% for cows and 70% for bulls and juveniles. Eliminating outlier fixes using the MCP 95% method appeared to provide a more accurate estimate of home range sizes and core resident areas, as it excluded areas which giraffe used infrequently,

such as gravel plains.

The mean home range sizes of giraffe bulls in the total study area (MCP 100% and 95%) were greater than those of cows (two-tailed Mann-Whitney U test, $U = 174$; $P=0.003$ and $U = 208$; $P=0.016$, respectively). In the Hoanib River study area, where sample sizes were sufficient for comparisons, home ranges of bulls (MCP 100% and 95%) were also greater than those of cows (two-tailed Mann-Whitney U test, $U = 56$; $P=0.006$ and $U = 74$; $P=0.039$, respectively).

Table 5.1. Mean annual home range size estimates (km^2) and ranges (km^2) of giraffe in the study region using the 100% and 95% MCP method (*n* = number of individuals).

		Estimates of home range size (km^2)			
		MCP 100%		MCP 95%	
Study Region	*n*	Mean (km^2)	Range (km^2)	Mean (km^2)	Range (km^2)
Bull					
Hoanib River	20	494.1	26.7-1 950	330.4	11.5-1 773
Hoarusib River	22	572.6	33.9-1 627	408.5	10.1-14.9
Khumib River	2	67.1	66.1-68.1	22.7	21.8-23.7
Study Region	44	513.9	26.7-1 950	355.5	11.5-1 773
Cow					
Hoanib River	13	219.7	12.9-1 098	119.1	8.3-702.1
Khumib River	3	117.3	34.6-158.6	23.6	23.5-23.9
Study Region	16	199.5	12.9-1098	100.0	8.33-702.1
Juvenile					
Study Region	2	20.8	10.7-30.9	14.5	10.3-18.7

The largest mean home range estimate was obtained for giraffe bulls in the Hoarusib River study area (572.6 km^2). This was marginally larger than that in the Hoanib River study area (494.1 km^2) and substantially larger than that in the Khumib River study area (67.1 km^2). However, these estimates (MCP 100% and 95%) were not significantly different between the three areas (Kruskal-Wallis: MCP 100%; $H = 1.829$; d.f.=2; $P=0.401$; and MCP 95%; $H = 1.437$; d.f.=2; $P=0.487$, respectively) because of the large variation in individual range estimates within each area. Limited numbers of individuals and poor access to the Khumib River study area may have contributed to an underestimate of home range size, making comparisons between areas unreliable.

The mean home range estimate for cows in the Hoanib River study area (219.7 km^2) was almost twice that for cows in the Khumib River study area (117.3 km^2). However, comparisons using MCP 100% and 95% were not significantly different (Kruskal-Wallis: Hoanib-Khumib; H = 0.222; d.f.=1; P=0.637 and H = 0.041; d.f.=1; P=0.84, respectively) due to the large variance in range estimates within the two study areas. Limited observations of individual cows in the Hoarusib River study area made any analysis of home range size impossible, but my observations suggested that home range size there is similar to that of cows in the Hoanib River.

5.3.2. Movements

No seasonal movements or seasonal home range partitioning was observed between the study areas. Giraffe predominantly used the main riverbeds in all the three areas, but they also foraged up the tributaries and sometimes moved into the adjacent study area (see Appendix 11). Giraffe movements between the Hoanib and Hoarusib River study areas were observed on >10 occasions, although more were apparent on analyses.

In the Khumib River study area both sexes moved year round along the main riverbed, as little vegetation was available elsewhere. In the Hoarusib River study area bulls often moved between the main riverbed and the southern tributaries, while cows resided for most of the year in the southern tributaries. During the hot-dry season cows were observed in the Gomatum River, a tributary of the Hoarusib River, for short periods before returning to the southern tributaries of the Hoarusib. In the Hoanib River study area, most adults moved along the main riverbed year-round, while increased movements by subadult bulls and cows into the northern and southern tributaries were observed in the wet and cold-dry seasons.

5.3.3. Long distance movements

Long distance movements (>50 km), often lasting between one and seven days, were most commonly undertaken by giraffe bulls, although a small number of cows also moved long

distances. No correlation between long range movements and seasons was apparent for either sex. The majority of the long distance movements were observed between the Hoanib and Hoarusib River study areas, a distance of approximately 70 km in a straight line.

Thirty individual giraffe bulls, representing approximately 42% of the bull population in the study region, moved between the Hoanib or Hoarusib River study areas, and vice-versa. However, only a third of these (n =10) were recorded in the actual Hoanib and Hoarusib riverbeds. One bull moved between the Hoanib and Hoarusib River study areas three times during the study period. Only one bull was observed in both the Hoarusib and Khumib River study areas, and would have moved approximately 35 km in a straight line to achieve this movement.

Seven cows were recorded undertaking long distance movements. One moved from the Hoarusib River to the Hoanib River study area over a period of two days before returning to the southern tributaries of the Hoarusib River. Another cow moved from the Hoanib River study area into the southern tributaries of the Hoarusib River, a movement of some 55 km. Five cows that resided predominantly in the southern tributaries of the Hoarusib River study area, moved occasionally into the Gomatum River before returning to the southern tributaries of the Hoarusib River catchment, but movements were not greater than 50 km. This indicated that cows moved substantially within the Hoarusib River study area, but avoided the Hoarusib River itself. Unfortunately, limited sightings of these five cows over the study period precluded analysis of their home ranges. During their long distance movements, two juveniles accompanied these five giraffe cows. In general, juvenile home ranges appeared substantially smaller than those of bulls or cows, but limited observations restrict the reliability of range estimates.

5.3.4. Movement corridors

A number of movement corridors were identified within and between the study areas (Figure 5.2). Movements occurred predominantly along the main riverbeds within each of the three study areas, while movements between the areas and into alternative forage areas

were undertaken via the main north-south tributaries. These movements are the first recorded movements by giraffe between the three river systems.

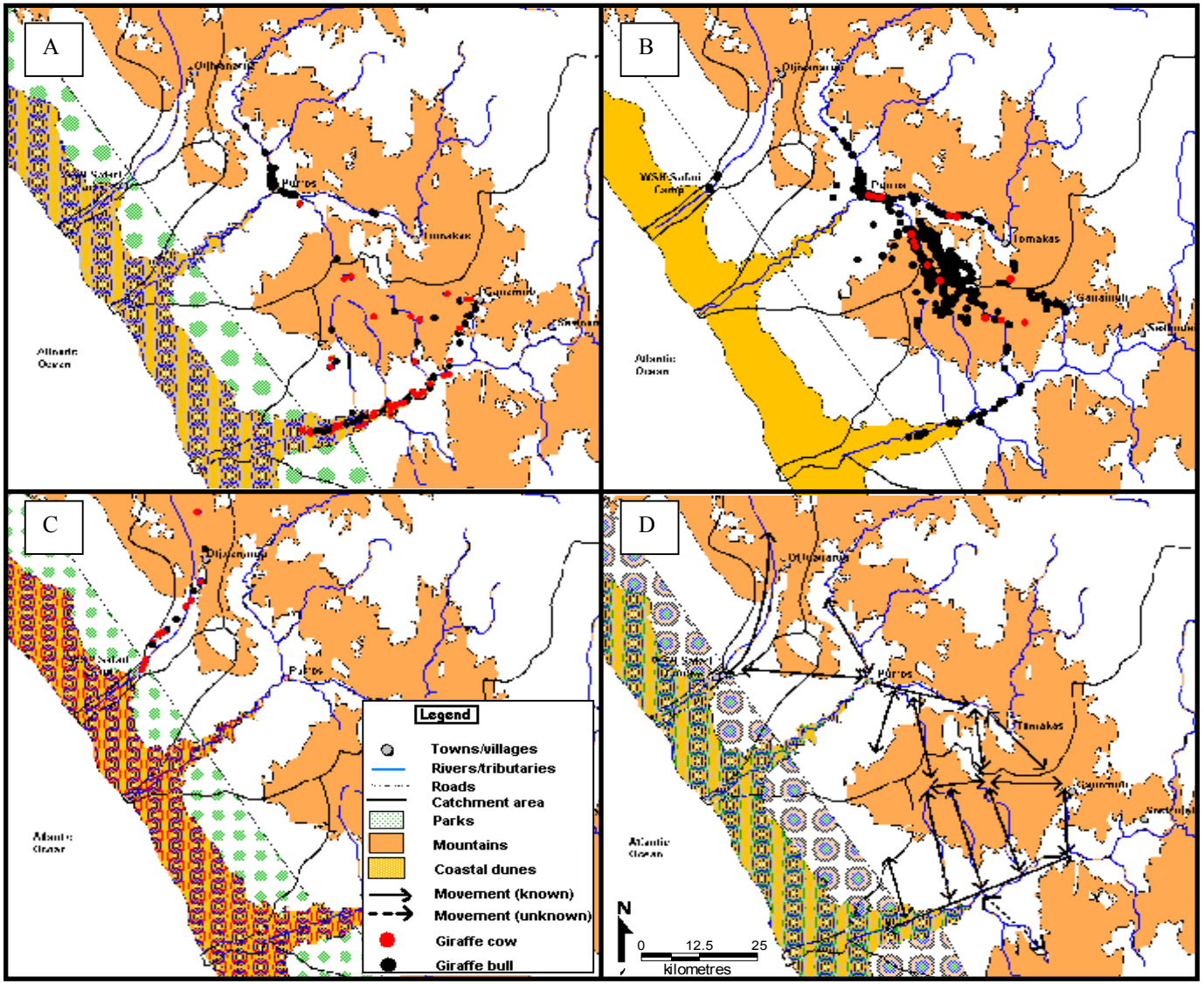


Figure 5.2. GPS locations of all giraffe sightings during the study. All giraffe were assigned to the study area of their first observation: (A) Hoanib River; (B) Hoarusib River; and (C) Khumib River. All giraffe sightings (D)—known and assumed movement corridors.

5.3.5. GPS satellite collar movements

Technical problems and up-link failures limited the success of the GPS satellite collars. None of the collars transmitted for longer than three and a half months (Table 5.3). However, for transmitted data, the numbers of non-readings and unusable fixes were low. A total of 732 readings were obtained for the three collared giraffe bulls and 46 for the one cow.

Table 5.3. Number of transmitted readings and non-readings received for four GPS satellite collared giraffe and last date of transmission (collaring dates: 28-30/09/02).

Sex	Individual	Readings	Non-readings	Last date of transmission
Adult bull	HSBM3	430	16	31/12/02
	HSBM12	301	11	12/01/03
	HNBM17	1	1	05/10/02
Adult cow	HNBF18	46	0	18/10/02

Despite the limitations, the data obtained from the satellite collars provided detailed insight into the daily, weekly, monthly and annual movements of giraffe (Table 5.4). Home range estimates were larger for the satellite collared bulls (HSBM3 & HSBM12) than the cow (HNBF18). Weekly, monthly and annual mean home ranges were larger for one bull (HSBM3) than the other (HSBM12).

Table 5.4. Weekly, monthly and annual home range estimates (km^2) using the MCP 100% method for two GPS satellite collared giraffe bulls (HSBM3 & HSBM12) and one cow (HNBF18), October 2002-January 2003. N.B. Annual home range estimates include ground observations.

	Home range estimates (km^2)		
	HSBM3[a]	HSBM12[b]	HNBF18[c]
Weekly			
Mean (km^2)	91.57	67.56	6.11
Range (km^2)	14.52-229.7	13.09-155.4	3.65-8.79
Monthly			
Mean (km^2)	414.2	300.53	17.67
Range (km^2)	352.4-480.9	116.2-505.6	*
Annual			
Total (100% MCP)	1 260	1 099	41.98
Total (95% MCP)	1 092	778.4	37.78

*insufficient data available; a – weekly (n = 12 weeks) and monthly (n = 3 months); b - weekly (n = 14 weeks) and monthly (n = 4 months); c - weekly (n = 3 weeks) and monthly (n = 1 month).

Additional GPS locations for the annual home ranges of the collared giraffe where collected using conventional radio tracking, equating to approximately 10%.

The weekly, monthly and annual (95% MCP only) home range estimates of HSBM12 were between 71.3% and 73.8% of the size of those observed for HSBM3. Furthermore, the averaged monthly range estimates for both bulls were 4.5 times their mean weekly range estimates, while the annual range estimates were 2.6 times their monthly range estimates.

Due to the limited data and sample sizes for weekly and monthly ranges, no general conclusions regarding giraffe ranges and movements can be drawn for the study region. However, the data obtained from the collared animals, in combination with the mean population home range size estimates, imply that giraffe bulls had substantially larger home ranges, as well as greater weekly and monthly ranges, than cows. Range areas increased in both sexes over time.

5.3.6. Daily movements

Data on daily movements were obtained from hourly fixes from two satellite collared bulls and one collared cow during the hot-dry season over a combined total of 180 days (Table 5.5).

The average daily movements of bulls were 5.64 km compared to 1.87 km for the cow. The difference in the daily movements of the two bulls was not in proportion to the difference in their estimated weekly, monthly and annual home ranges. This variance is a reflection of the non-linear foraging pattern of giraffe. Giraffe commonly re-use or return to an area to forage within a 24-hour period and/or over consecutive days.

Table 5.5. Daily linear movements (mean ± s.d., km) and ranges (km^2) of two GPS satellite collared giraffe bulls (HSBM3 & HSBM12) and one cow (HNBF18), October 2002-January 2003.

Month (Hot-dry season)	Mean daily movement (km ± s.d.)	Range (km^2)
HSBM12 (*n* = 83)		
October	7.51 ± 7.02	0.90-20.86
November	6.12 ± 6.25	0.29-28.81
December	4.31 ± 2.15	0.09-8.95
January	5.29 ± 2.83	2.08-9.58
HSBM3 (*n* = 82)		
October	4.99 ± 4.36	1.16-21.39
November	6.12 ± 6.52	0.40-32.24
December	5.16 ± 2.97	0.42-10.08
HNBF18 (*n* = 15)		
October	1.87 ± 2.05	0.06-7.41

N.B. although expressed as means ±s.d., the movement data are derived from repeated measurements on the same individuals and hence cannot be considered independently. In this context, means ±s.d. are presented simply as convenient summary statistics.

5.3.7. Hourly movements

While the GPS satellite collars provided co-ordinates of giraffe locations, ambient temperatures were also transmitted (Figure 5.3). When analysing the data on the two bulls, no correlation was found between daily distance travelled and the daily ambient temperature (r = 0.129, P>0.05), nor between hourly movements and hourly ambient temperatures (r = -0.345, P>0.05). However, hourly linear movements were shorter pre-dawn but increased at dawn and post-dawn in correspondence with an increase in ambient temperature. During the hottest periods of the day, giraffe travelled only short distances. Mean hourly movements increased again pre- and post-dusk, corresponding to reduced ambient temperatures.

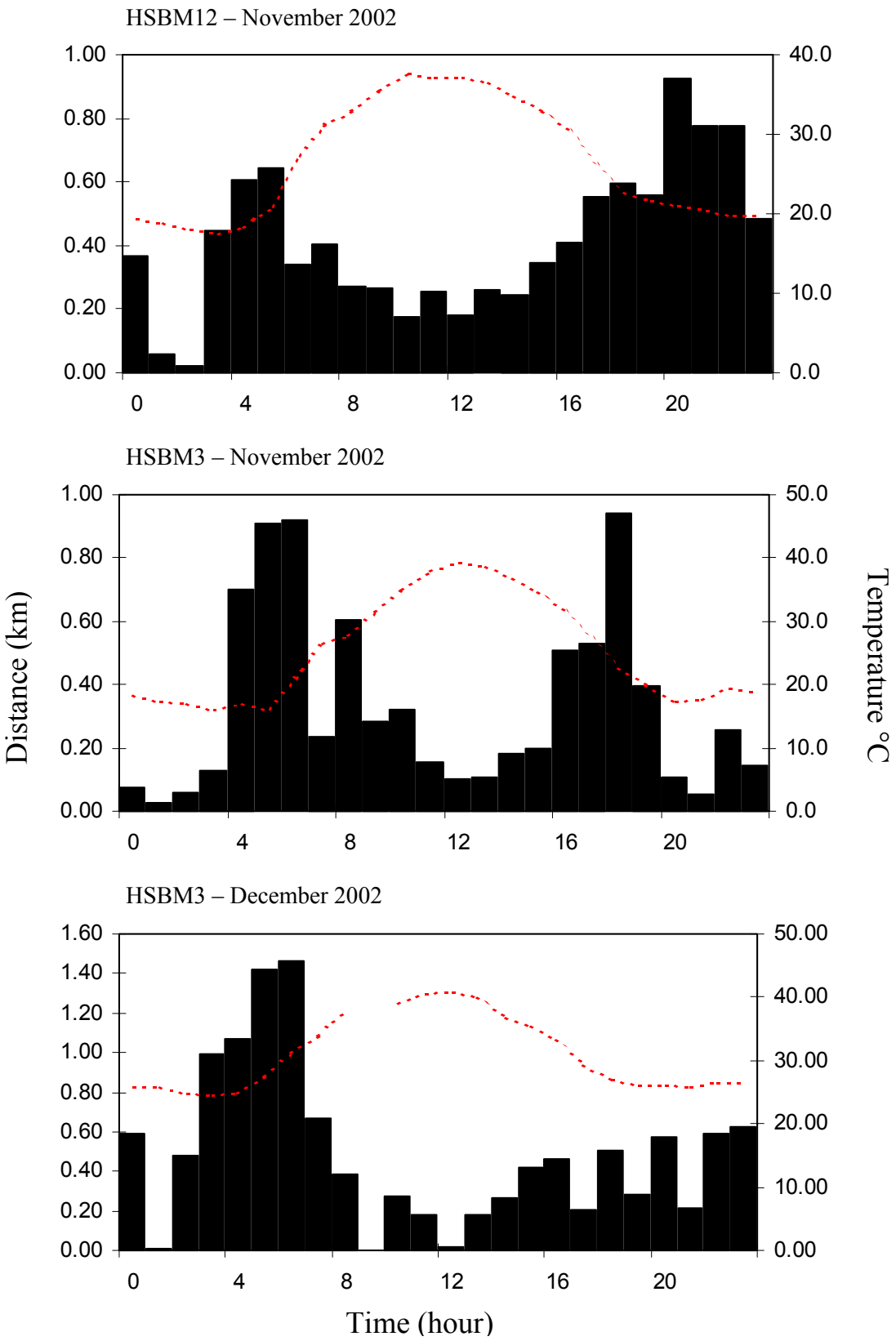


Figure 5.3. Hourly linear movements (km) (black blocks) and hourly temperature (°C) (dashed red line) of two satellite collared giraffe bulls in the hot-dry season 2002. Note different distance scales on graphs.

5.4. Discussion

5.4.1. Home range

Giraffe bulls in the study region had substantially larger home ranges than cows (>2.5 times). The two largest home ranges of bulls were 1 950 km^2 and 1 627 km^2, respectively, and represent the largest recorded home range estimates for bulls in Africa (see Appendix 12) (Foster & Dagg, 1972; Langman, 1973; Berry, 1978; Leuthold & Leuthold, 1978; Le Pendu & Ciofolo, 1999; Van der Jeugd & Prins, 2000). Previously, the largest reported home range for a bull was from the desert-dwelling giraffe population of Niger (1 559 km^2; Le Pendu & Ciofolo, 1999). The two largest bull home ranges in this study incorporated two of the main riparian woodlands in the Hoanib and Hoarusib Rivers, although both giraffe also foraged in the tributaries and the mountains between the two study areas. The large home range sizes reported in the study region presumably reflect the reduced probability of giraffe encountering potential mates in the sparsely populated northern Namib Desert. However, for both bulls, the large home ranges could represent efforts to achieve or maintain dominance in the study population, or may reflect the movements of two large animals seeking forage to maintain their energetic and nutritional requirements.

The home ranges of giraffe cows were substantially smaller than those of bulls, with only one cow occupying a range >1 000 km^2. The largest home range reported for a cow was in arid Niger (1 379 km^2; Le Pendu & Ciofolo, 1999). The giraffe in Niger migrate seasonally across communal farmland, similar to that in the northern Namib Desert, and between two distinct foraging areas (Le Pendu & Ciofolo, 1999). The similar environmental conditions experienced by giraffe in Niger and Namibia help to account for the large ranges of giraffe in both regions.

Home range sizes of juvenile giraffe were small (20.81 km^2) compared to those of both cows and bulls in the study region, however, they did correspond with their mothers' home ranges for the same periods. Although ranges of juvenile were greater than those observed elsewhere (e.g. 12.8 km^2 in South Africa, Langman, 1973; see Appendix 12), they still appeared to be underestimates of the true ranges occupied. For example, juveniles observed in the southern tributaries of the Hoarusib River ranged further than the mean

estimates reported (personal observation), but low numbers of observations restricted home range size analysis for these individuals. These juveniles were sighted at all times with their mothers who moved between the southern tributaries of the Hoarusib River study area and the Gomatum River in the hot-dry season, covering an estimated area of 200 km^2. Increased numbers of sightings would provide a better indication of the home ranges of juveniles in the northern Namib Desert.

Published estimates indicate that giraffe in arid environments have relatively large home ranges, and that bulls have larger ranges than cows (Scheepers, 1992; Le Pendu & Ciofolo, 1999). Smaller home ranges are observed for giraffe in more densely vegetated savanna environments, while sex differences in range size are not as pronounced (Foster & Dagg, 1972; Langman, 1973; Berry, 1978; Leuthold & Leuthold, 1978; van der Jeugd & Prins, 2000; see Appendix 12). Range sizes also vary between areas where giraffe have different population structures and densities, as well as between environments differing in forage availability, seasonal rainfall, predators, management regime, intensity of hunting and area size (see Appendix 12).

A negative correlation (r = -0.45; see Appendix 12) was observed between published estimates of home range size against population density in giraffe, indicating that giraffe in sparse populations generally occupy larger mean home ranges. Results from the study area support the concept that low population density and large range are correlated, as reported for arid environments generally (Scheepers, 1992; Le Pendu & Ciofolo, 1999). Decreased availability of forage and high variability in seasonal and spatial rainfall are important factors limiting density and increasing the range sizes of giraffe in arid environments (Scheepers, 1992; Le Pendu & Ciofolo, 1999).

Previous research indicates that the home ranges of giraffe also vary in shape. Along forage rich riparian environments, home ranges are often linear and elongated (Berry, 1978; Scheepers, 1992) but can be irregular in shape (Dagg & Foster, 1972; Leuthold & Leuthold, 1978; Pellew, 1984b; du Toit, 1990a; Le Pendu & Ciofolo, 1999; van der Jeugd & Prins, 2000). In the study region most home ranges of giraffe were linear because the riparian environments are the lifelines of the northern Namib Desert; there is little forage available elsewhere. Home range sizes have not been reported for giraffe in the Hoanib

River because of these linear movements (Scheepers, 1992). However, during this study, giraffe in the study region were found to be more mobile than previously assumed, thus allowing range estimates to be made. Despite some individuals moving along the northern and southern tributaries of each catchment and between the study areas, giraffe seldom used all the area in their home range. This is because much of the home range is devoid of forage and encompassed inhospitable terrain.

Home ranges of giraffe bulls and cows in the study overlapped both within and between the three study areas. In both the Hoanib and Khumib River study areas, giraffe of both sexes foraged predominantly along the riparian woodland of the main riverbeds and their tributaries. No apparent spatial or seasonal segregation in habitat use was observed for either sex in the study area. However, spatial segregation between bulls and cows did occur in the Hoarusib River study area. No cows were sighted in the Hoarusib River during the study period, and they foraged only infrequently in the Gomatum River, residing predominantly along the study area's southern tributaries. The Hoarusib River population is strongly bull-biased. The residence of bulls in the main Hoarusib and Gomatum riverbeds can be attributed to the greater availability of food along these rivers than elsewhere in the study area. Giraffe bulls need more food than cows to maintain their larger body mass, hence bioenergetic advantages would presumably accrue to bulls able to exploit the Hoarusib River.

If rich food resources were available in the Hoarusib River study area, why should bulls, but not cows, exploit them? It has been hypothesised that, in various ungulate species, cows forgo foraging benefits for environments that are more suitable for raising young (Main & Coblentz, 1990). Giraffe cows in the Hoarusib River study area foraged only seasonally in the Gomatum River during the hot-dry period when food availability was reduced elsewhere. The avoidance of the Hoarusib and, to a lesser extent, Gomatum Rivers by cows may be an attempt to reduce conflict with both bulls and communal farmers in the area, and thus protect their offspring by limiting potential interactions with bulls, people and/or villages. Similar hypotheses have been postulated for the local distribution of giraffe cows and their offspring in other parts of their range (e.g. Foster, 1966; Dagg & Foster, 1982; Pratt & Anderson, 1982; Pellew, 1984a; Young & Isbell, 1991; Ginnett & Demment, 1997). This resource-shelter trade-off may be feasible when

population numbers are low, however, if giraffe numbers increase it may begin to deplete food resources in the tributaries and mountains away from the main riverbeds. In the long-term, this may result in cows increasing their time spent in the main riverbed during periods other than the hot-dry season to supplement nutrient intake and maintain their bioenergetic needs.

Sex-dependent and geographical patterns of segregation have been reported in other giraffe populations (e.g. Foster, 1966; Pratt & Anderson, 1982; 1985; Caister *et al*., 2003). However, home ranges of individuals in these populations overlapped considerably, if only seasonally, and no permanent socio-spatial segregation or territoriality has been reported (e.g. Backhaus, 1961; Foster & Dagg, 1972; Berry, 1978; Leuthold, 1979; Le Pendu *et al*., 2000; van der Jeugd & Prins, 2000). Overlapping home ranges are common in other ungulates such as impala (Jarman, 1972; Matson, 2003) and kob (Fischer & Linsenmair, 1999), while sex-dependent segregation in habitat use has also been reported in kudu (du Toit, 1995) and red deer (Clutton-Brock *et al*., 1982). Habitat segregation can result from many factors, although it is driven predominantly by the quality of available food—cows have higher energetic and nutritional requirements during pregnancy and lactation (giraffe - Ciofolo & Le Pendu, 2002; Caister *et al.,* 2003; other ungulates - Clutton-Brock *et al*., 1982; du Toit, 1995; Fischer & Linsenmair, 1999), and will exploit the richest habitats that still provide some security for their offspring.

5.4.2. Movements and corridors

Giraffe in the study region showed the highest preference for the riparian environments, almost to the exclusion of other habitat types. Giraffe were sighted in all other habitat types at some stage throughout the study period, but their use of or residence time in these habitats was low. The strong preference of giraffe for riparian environments is similar to that reported for desert-dwelling elephants in the northern Namib Desert (Viljoen, 1988; 1989b). Giraffe and elephant spend much of their time foraging in the riparian woodlands in both the Hoanib and Hoarusib River study areas, although elephant are absent from the Khumib River study area.

Movements in each of the study areas were predominantly along the main riverbeds and their tributaries. Giraffe were observed traversing and, on occasion, opportunistically foraging in open gravel plains and dune habitats; one cow was seen foraging on a steep mountain ridge. Giraffe usually avoid rocky habitats (Bond & Loffell, 2002), but may forage there if food is scarce elsewhere. Movements of giraffe across the barren open plains were predominantly straight-line traverses between two forage sources, and usually between the riparian woodlands and the food that they contain.

During the cold-dry season and occasionally the early hot-dry season, giraffe were identified venturing into and exiting the mountains between the Hoarusib and Khumib Rivers. No designated tracks or roads exist in this remote and rocky terrain, which limits vehicular access. However, it was assumed that giraffe were using these areas away from the riverbed as alternative seasonal forage sources during this time of the year to supplement their forage requirements. Precipitation in the form of evening fog blankets the mountains and raises the average moisture content in rarely-foraged mountain plant species, such as *Commiphora, Maerua* and *Boscia* spp. (Viljoen, 1988; Scheepers, 1992). Selective browsing of these plant species is considered to be the reason giraffe venture into the mountains to forage at certain times of the year. Desert-dwelling elephant have also been observed in the mountains at the same time, foraging on the same moisture-rich plant species (Viljoen, 1988; 1989b; K. Leggett, personal communication; personal observation). While distinct seasonal movements of giraffe between areas are limited, short excursions into the seasonally forage-rich mountain areas occur. The desert-dwelling giraffe in Niger have dry season home ranges twice the size of those during the rainy season due to the seasonal movement of giraffe between two distinct forage areas (Ciofolo & Le Pendu, 2002; Caister *et al*., 2003).

In general, movements and home range sizes of giraffe have been linked strongly to seasonal browsing and/or the availability of water (Foster & Dagg, 1972; Leuthold & Leuthold, 1972; Hall-Martin, 1974; Berry, 1978; Leuthold & Leuthold, 1978; Pellew, 1984b; Scheepers, 1992; Le Pendu *et al*., 2000; van der Jeugd & Prins, 2000; Caister *et al.,* 2003). Specifically, seasonal movements of giraffe have been associated with phenological changes in preferred plant species (Hall-Martin & Basson, 1975; Leuthold & Leuthold, 1978; Scheepers, 1992; Le Pendu & Ciofolo, 1999), with shifts in preferences

for plant species leading to seasonal expansion or contraction of ranges (Leuthold & Leuthold, 1972; Hall-Martin & Basson, 1975; Scheepers, 1992; Le Pendu *et al*., 2002). The few observations of giraffe drinking in the study region (less than ten sightings in 70 years: Viljoen, 1981; Scheepers, 1992; Fennessy *et al*., 2003) suggest that surface water is not a factor influencing either seasonal or annual movements of giraffe, as they do not actively seek this resource out.

Seasonal movements of giraffe east-west and associated use of the riverbed, have been reported in the Hoanib River study area (Fennessy *et al*., 2003). During the hot-dry season giraffe aggregate there in response to the increased availability of *Faidherbia albida* pods, an essential dry-season food, and an early flush in *Colophospermum mopane* leaves. *Acacia* species, *Salvadora persica* and *Euclea pseudebenus* are also relatively abundant, but little other vegetation is available along the river. During the hot-dry season giraffe are more frequently observed in the eastern and central parts of the Hoanib River study area. This may be a response to *F. albida* podding earlier here than in the western section, raising the question of whether giraffe move in relation to forage availability, forage nutrients and moisture composition, or other additional factors. Chemical analysis of the preferred forage of giraffe along an east-west gradient in the Hoanib River is discussed in Chapter 7, with the findings posited to provide a better understanding of why subtle seasonal movements of giraffe occur along this riparian strip.

5.4.3. Long distance movements

This study recorded the first movements of giraffe between any of the three study areas. Giraffe were previously assumed to reside in only one catchment and to be restricted to the main riverbed and its tributaries (Scheepers, 1992). The large distances between study areas across the arid northern Namib Desert were assumed to inhibit any large-scale movements by giraffe (Viljoen, 1982; Tarr, 1986; Scheepers, 1992). The initial observation of giraffe movement between the study areas was recorded for a GPS satellite-collared bull giraffe (HNBM17). This specific unit transmitted only one usable reading following collar placement. The bull moved north from its collaring site in the Hoanib River into the Hoarusib River study area, a direct line distance of 70 km. However, due to

the topography of the area, the movement would more likely equate to a distance of about 80 km; this was confirmed by ground truthing of the bull's movement. This initial finding provided insight not only into the magnitude of giraffe movements and home ranges, but also population structure and gene flow in the study area. Throughout the remainder of the study, increased numbers of identified giraffe were observed traversing the Hoanib and Hoarusib River study areas.

Many giraffe bulls made long distance movements between study areas (42% of individuals), similar to bulls studied in a low-density arid area in Niger (Le Pendu & Ciofolo, 1999). Long range movements are probably the result of numerous factors such as searching for receptive cows, seeking or maintaining dominance or forage, conflict with communal farmers, tourism and local poaching. Most likely, however, long distance movements in this study were the result of searching for receptive cows and the movement by giraffe away from newly occupied communal settlements. Similar interactions have been reported in Niger, with giraffe movements in both areas synchronised with communal farmer activities (Ciofolo, 1995; Le Pendu & Ciofolo, 1999). Long range movements of giraffe have been observed elsewhere in Africa but have been attributed usually to searching for forage or bulls seeking receptive cows (Berry, 1978; Dagg & Foster, 1982).

Only one giraffe, a bull, was recorded moving between the Hoarusib River and Khumib River study areas, a distance of less than 50 km. This bull was not observed associating with any giraffe in the Khumib River before returning to the Hoarusib River study area, although it is possible it may have been in search of receptive cows. Its movement into the Khumib River area was not correlated with any known human-wildlife conflict issues and the bull spent much of its time there in close proximity to the SCP WSN camp. It remained in the Hoarusib River study area after returning from its excursion to the Khumib River. As movements between areas occur, it is possible that excess bulls migrate from the Khumib River into the Hoarusib River area to relieve pressure on forage.

It is considered that most long distance movements by giraffe cows in the study area reflected searches for seasonal forage. Movements between the southern tributaries of Hoarusib River and the Gomatum River were observed during the hot-dry season. Cows were observed in the Gomatum River only during the hot-dry season for brief periods

before returning south to the tributaries between the Hoarusib and Hoanib River study areas. Movements of cows along the Hoanib River were predominantly into its northern tributaries (Swaragab and Obias Rivers) where forage was available. Only one cow moved between both the Hoanib and Gomatum riverbeds and it was often sighted feeding along the tributaries between the Hoanib and Hoarusib River study areas. Its behaviour was similar to that of a dominant bull searching for receptive cows; it associated infrequently with any other giraffe, independent of sex or age class, and spent little time in any one location.

Research on elephants in the northern Namib Desert has correlated long-range movements with forage quality, proximity of forage to water, seasonal rainfall and flood events (Cooper, 1980; Viljoen, 1980; Tarr & Tarr, 1989; Viljoen & Bothma, 1990a). Elephants have been observed moving up to 70 km in a 24-hour period between forage and water resources in the northern Namib Desert (Viljoen & Bothma, 1990a; Leggett *et al*., 2003a) and have been recorded travelling in excess of 600 km in one season (Leggett, 2004). However, survival of giraffe in the northern Namib Desert is not dependent on free-water, as observed for elephant, and therefore their ranges were not correlated with proximity of forage to water.

5.4.4. GPS satellite collar movements

The monthly range of the collared bulls was substantially larger than that of the collared cow (more than 17 times) and greater than the average derived from direct observations. This may suggest that the extent of movement by giraffe has been systematically underestimated in observational studies, although there are no other comparable data for collared giraffe. The monthly range estimates were approximately 38% of the annual range estimates (95% MCP) for both bulls, suggesting that ranges drift across the year. This hypothesis is further supported by the weekly range estimates being approximately 22% of the monthly range estimates for both bulls. Movements of bulls were probably directed at seeking out nutrient-rich forage during the hot-dry season and conflict avoidance with communal seasonal settlements. The range estimate for the collared cow in

the hot-dry season was small and indicated that foraging was restricted to the Hoanib River riparian environment and its immediate surrounds.

Daily movements varied markedly between all collared giraffe. The giraffe cow's average daily movement and range (1.87 km) was lower than for cows elsewhere: 2.9 km in South Africa (Langman, 1973) and ≤2.3 km in Zambia (Berry, 1978). However, the cow's home range (199.51 km^2) was substantially larger than that of giraffe in South Africa (24.6 km^2: Langman, 1973) and Zambia (68 km^2: Berry, 1978). These giraffe occupy more densely vegetated habitats and use a greater portion of their seasonal range each day than giraffe in open, arid environments. Similar patterns have been reported for other species in the Artiodactyla family (Clutton-Brock *et al*., 1989; Fischer & Linsenmair, 1999).

The daily movement of the two collared bulls in the study region averaged 5.64 km, similar to or greater than that observed elsewhere in Africa: 2.6 km and 5.9 km in South Africa (Innis, 1958; and Langman, 1973, respectively) and 3 km in Zambia (Berry, 1978). The daily movement data were collected during the hot-dry season, coinciding with the highest ambient temperatures, which may have resulted in smaller movements. Giraffe were observed to browse in a non-linear fashion, although they often re-visited the same area to forage, and made intensive use of the riparian woodlands.

As a consequence of the apparently selective foraging strategy of giraffe, it has been suggested that some plants produce increased tannin levels when eaten, preventing browsers from feeding at one source for any length of time (Leuthold & Leuthold, 1972; Hall-Martin, 1974; 1975; Hall-Martin & Basson, 1975; Sauer *et al.*, 1982; Pellew, 1984a; Caister *et al*., 2003). As plant tannin concentrations usually differ between habitats (Sauer *et al.*, 1982), it is possible that plant tannin levels in the northern Namib Desert are lower than elsewhere, enabling giraffe to forage longer on individual trees and thus reduce their daily movements. However, while daily movements may be short, the weekly, monthly and annual movements of the GPS-collared giraffe were considerably larger than those observed elsewhere. The arid conditions in the study region presumably require bulls to shift as forage conditions change seasonally, as well as to spend more time searching for potential partners in the sparse desert population (du Toit, 1990a).

The mean hourly movements of the collared giraffe in the hot-dry season were strongly biphasic throughout 24 hours. Increased movements occurred post-dawn/early morning and in the period following, as well as pre-dusk/early evening. Distance travelled was least during the hottest period of the day (midday), thus reducing excess heat loads, as postulated in the 'heat-load' concept (Leuthold & Leuthold, 1978; Pellew, 1984a). Although no direct correlation was recorded between ambient temperature and distance travelled, the results suggest that giraffe rest predominantly during the middle of the day and show another reduced period of activity again in the late evening/early morning. Evaluation of giraffe activity budgets (Chapter 6) provides further insight into the biphasic movement patterns of giraffe, and their engagement in energy consuming activities at different ambient temperatures.

The GPS satellite collars collected substantial amounts of continuous data when functioning and provided high resolution data in a shorter period of time than is possible using either radio collars or individual identification methods (Langman, 1973; Dagg & Foster, 1982; Scheepers, 1992). The collars also allowed this study to record the first detailed hourly movements of giraffe over 24-hour periods.

5.5. Methodological problems

The GPS satellite collars impacted minimally on giraffe behaviour with no signs of post-capture stress. However, the longevity of the GPS units was poor, with a maximum of three and half months of data collected from what was anticipated to be a two year study. The exact reasons for the technical failure are unknown as the collars will be recovered in late 2004/early 2005. However, failure in the wiring or its connection between the battery pack and GPS unit is assumed to be the most likely reason.

In addition to the GPS units failing to transmit for the intended period, it was noted that collars shifted or moved around the neck of each giraffe. This was not anticipated. The continual shifting of the collars resulted in the GPS units not remaining in an upright position on the giraffe's backs. The battery packs, which were intended to act as counter-weights to stabilise and keep the GPS units in an upright position, often wedged

themselves behind the giraffe's front legs when shifting. The battery packs never impeded movement, but the collar shifting may have reduced the transmission quality. It was not uncommon to observe a collar in three different positions (GPS upright, right and left) over a 12-hour period. The more physical behaviour of giraffe bulls may have contributed to their collars shifting more often. Initially, the shifting of the collars was assumed to be the main reason for the lack of data transmission (D. Okuysen, personal communication), however, the two collars that remained functional the longest were those on the giraffe bulls, and both were observed shifting continuously.

When it worked, radio tracking assisted greatly in finding individuals in the rugged terrain, especially those giraffe that had moved out of the riverbeds. Furthermore, the collared individuals became 'Judas' giraffe in the sense that, when one was found, numerous other giraffe were often detected due to their gregarious nature.

It is strongly recommended that design flaws are rectified and trialing of GPS satellite collars be undertaken prior to further field use of this technology on giraffe. Testing variations of the collar and transmitter on captive or habituated individuals would improve cost effectiveness, field efficiency, reliability and longevity. Other features that should be assessed in the future include the use of a data logger that could store readings for an extended period of time before downloading to a beacon or vehicle station, hence improving data security. Furthermore, increased battery numbers or improved battery technology would allow for increased transmission time and data collection.

5.6. Conclusion

Estimates of home range size in the study population were on average larger than those in other studied populations, with the exception of the desert-dwelling giraffe in Niger. In particular, the largest individual home range of a giraffe bull was recorded during this study. The larger home range size in my study region was correlated with low population density, reduced forage density and increased searching for receptive cows by bulls. The predominant pattern of movement was linear, along the riparian environments in each of the three study areas; however, large-scale irregular movements into tributaries and other

areas were also recorded. Seasonal movements of giraffe in the study population were not as distinctive as those in other giraffe populations. Small-scale movements by bulls into the mountains above the Hoarusib River, as well as by cows into the northern tributaries of the Hoanib River, were observed. Small-scale habitat segregation was observed in the Hoarusib River study area with giraffe cows foraging only in the Gomatum River during the hot-dry season; this is considered to have limited conflict with communal farmers and tourists.

Numerous observations of giraffe, predominantly bulls, moving between the study areas were recorded, indicating that giraffe were not as restricted in range as previously assumed. This supports the idea that gene flow should occur between the riparian populations, supporting the results on genetic architecture and haplotype distribution presented in Chapter 3. Finally, use of GPS satellite collars provided some of the highest resolution data on giraffe movements to date. Strong biphasic movement behaviour of giraffe over 24-hour periods indicated that activity correlated with ambient temperatures. This behaviour is further investigated in the next chapter when assessing hourly and seasonal activity.

CHAPTER 6. BEHAVIOURAL ECOLOGY

6.1. Introduction

Giraffe occupy a wide range of environments across the African continent. However, the Namib Desert is at their ecological limit. The northern Namib Desert is characterised by extreme climatic conditions, including highly variable and patchy rainfall (<50 mm per annum) and a seasonal temperature range from 0°C to over 40°C (Seely, 1978; Scheepers, 1992). While rainfall is highly variable, precipitation in the form of fog is as much as three times more reliable and is an invaluable water source for flora and fauna (Seely, 1978; 1987). Within the Namib Desert and throughout southern Africa, the behavioural ecology and social organisation of resident ungulates has been linked closely with precipitation and, consequently, with forage quality and quantity (e.g. Underwood, 1982).

The physical challenges of an arid environment, particularly during summer, are characterised by extreme temperatures, while the scarcity or absence of water offers little opportunity for amelioration of these conditions. Smaller mammals in arid areas seek refuge underground during the hottest periods of the day and feed at night when ambient temperatures are lowest (e.g. Skinner & Smithers, 1990). Furthermore, many species have physiological adaptations, such as elaborated renal systems, which aid in heat regulation and water conservation (e.g. Cloete & Kok, 1986). Large mammals in arid areas do not have the same ability to seek out daytime refuges due to their size, but they do show many behavioural responses that aid their long-term survival. One of these is to increase energy consuming activities, such as walking and feeding, during the cooler periods of the day when water loss will be lower, while undertaking energy conserving activities, such as resting, during the hottest periods of the day (Lewis, 1975; Mitchell, 1977). Other activities, such as facing away from the sun, help to reduce heat absorption. In the central Namib, for example, Hartmann's mountain zebra orient their bodies away from the sun while resting or feeding at midday (light to dark ratio 3:1) as opposed to standing broadside at other times (light to dark ratio of the exposed body surface of 1:3) (Joubert, 1974).

Many mammals are able to regulate the rate of heat flow through 'thermal windows', e.g. sparsely haired or naked areas, such as the groin, scrotum and mammary glands. They are also able to dump excess heat by convection while lying on shaded ground, as the relatively cool ground allows for conductive heat flow between the ground and the animal (Schmidt-Nielsen, 1964; Joubert, 1974). The renal efficiency of larger mammals in arid environments is usually less than that of smaller mammals (e.g. Cloete & Kok, 1986), although water loss in faeces is greatly reduced in wild animals in comparison to ill-adapted domestic species such as cattle and sheep (Schmidt-Nielsen, 1964; Joubert, 1974). Across their range, giraffe have been reported to combine both physiological and behavioural adaptations to exploit different environments (Leuthold & Leuthold, 1978; Langman *et al*., 1979 & 1982; Dagg & Foster, 1982; Pellew, 1984a; Langman, 1982). Examples of these adaptations include biphasic activity behaviour and nasal temporal heat exchange. Investigation of physiological adaptations in giraffe was beyond the scope of this thesis.

6.1.2. Aims

Despite much published work on giraffe behaviour (Innis, 1958; Foster & Dagg, 1972; Leuthold & Leuthold, 1978; Pellew, 1984a; du Toit, 1990a; Skinner & Smithers, 1990; Estes, 1995), investigation of the behaviour of desert-dwelling giraffe in Namibia remains very limited (Scheepers, 1992; Fennessy *et al*., 2003). The studies reported in this chapter are the first to document the activity budgets of the giraffe of the northern Namib Desert, or of the Namibian giraffe population as a whole. The specific aims were to:

- categorise giraffe behaviours;
- describe overall activity budgets for these behaviours;
- test whether activity budgets vary in relation to ambient temperature;
- compare activity budgets between seasons and between different components of the giraffe population; and
- study flight behaviour and the possible effects of tourist activities.

6.2. Methods and materials

6.2.1. Activity budgets

Giraffe were observed predominantly by vehicle, although sometimes on foot, between sunrise and sunset over a two year period (2002 and 2003). Although the study focussed on the riparian woodlands, giraffe were observed also in the plains, dunes, floodplains and some mountain areas. Observations of behaviour were made in conjunction with the population structure component of the study (see Chapter 4).

Adapting methods used by Norton (1981) and Cloete & Kok (1986), observations of giraffe activity were recorded every minute by scan sampling. By scanning individuals as well as large groups, I endeavoured to obtain a detailed, yet broad, overview of giraffe activity budgets under a range of herd structures. The high intensity observation schedule (every minute) was chosen, even though many studies of giraffe (e.g. Innis, 1958; Leuthold & Leuthold, 1978; Pellew, 1984a; van der Jeugd & Prins, 2000) and other species (e.g. eland—Watson & Owen-Smith, 2000) have used five minute scan sampling (Altmann, 1974). During my preliminary research, the behaviour of giraffe in the study region often changed more frequently than every five minutes. To limit discrepancies and improve standardisation, observations were recorded at the top of every minute (±15 seconds), thus reducing recorder bias and subjective perception of the main activity over a five minute period. Due to the possibility of observing up to ten giraffe at any one time, identifying the sex and age of the giraffe prior to beginning observations was important. Once established, observers were assigned giraffe and a scribe recorded the activities and checked the time to ensure accuracy and efficiency.

The minimum number of monthly observations for giraffe bulls and cows was established at 200 observations for every hour of a 12-hour day (i.e. 7am–7pm). This frequency provided an adequate sample size for analysis. When possible, sampling was undertaken in 'block' periods of three to four hours of intensive research at a time during morning, midday and afternoon, and on 10–20 days throughout the month. Spreading observation periods throughout the month limited the potential for temporal confounding, as may happen when all observations are made over a short period. The minimum number of

observations was achieved for almost all time periods each month. However, seasonal and daily movements of giraffe, seasonal rainfall and flood events, dense fog, tourist interference and the rugged terrain in the study region, all limited observations on occasions. No systematic observations were made at night.

Activities of adults and subadults were combined for each sex as in previously published studies (Innis, 1958; Leuthold & Leuthold, 1978; Pellew, 1984a; Ginnett & Demment, 1997; van der Jeugd & Prins, 2000), and as suggested from personal observations that indicated little variation in the behaviour of different aged giraffe. Data on juveniles were collected for both sexes and combined.

Observations were recorded predominantly from a vehicle, although giraffe were also tracked on foot and studied from a high elevation vantage point when possible. Based on researcher experience, observations were always undertaken at a distance deemed to have no impact on the giraffe's 'normal' behaviour. This distance varied daily and seasonally depending on environmental factors, such as climatic conditions (wind, fog), topography, herd size, study area, vegetation cover, presence of other vehicles, tourists and other species (domestic and wild). Minolta binoculars, 10x50 and 8x40 magnification, were used to observe giraffe when the animals were too far away to clearly observe with the naked eye.

The behavioural activities of giraffe were divided into 10 distinct categories based on previously published work (Innis, 1958; Leuthold & Leuthold, 1978; Dagg & Foster, 1982; Pellew, 1984a; Le Pendu *et al.,* 2000; van der Jeugd & Prins, 2000) and personal observations of behaviour in the study region. These are listed below:

- Feeding: The giraffe was observed physically eating; this activity included the time spent chewing and swallowing.
- Resting: The giraffe stood, sat or slept in the sun or shade and was neither ruminating nor showing vigilance.
- Ruminating: The giraffe chewed its cud while standing, sitting or walking.
- Walking: The giraffe travelled between forage sources or within the study region (not ruminating).
- Grooming: The giraffe was observed scratching and rubbing itself.

- Sexual behaviour: This activity included flehmen testing, courtship and mounting attempts. Flehmen testing involves the testing of urine (to detect pheromones) to assess a giraffe's reproductive status.
- Excretion: The giraffe was observed defecating or urinating.
- Vigilance: The giraffe focussed on external stimuli such as predators, domestic stock, tourists or other wildlife.
- Interaction: This activity included neck sparring (necking) between males and rubbing or chesting other giraffe.
- Drinking: The giraffe was observed drinking. Due to the apparent independence of giraffe on water in the study region (Scheepers, 1992; Fennessy *et al*., 2003), every observation of spoor at a water source was noted.

Animals were often observed ruminating in the direct sun or shade. Although ruminating could also be perceived as resting, especially when in the shade, rumination requires energy and was recorded separately. When analysing mean monthly and mean daily activity budgets of giraffe bulls and cows, some activities i.e. interaction, sexual behaviour, excretion and drinking, were combined into 'other' activities. These behaviours comprised a minor percentage of the giraffe's activity budget.

Aside from the standardised collection of activity behaviours, incidental observations of giraffe behaviours were also recorded.

6.2.2. Flight behaviour and impacts of tourism

In the study region, tourism and hunting are two key factors affecting wildlife behaviour. The flight behaviour patterns of giraffe in the Hoanib River study area have been recorded as a potential indicator of the impacts of tourism and, to a lesser degree, hunting, on the population since the late 1980s (Scheepers, 1992).

Flight was defined in the present study as movement away from an observation point due to a direct or indirect stimulus such as vehicles, domestic stock, noise or hunting. Flight distances of giraffe were measured from the initial point of observation to the stopping

point, when the animals recommenced 'normal' activity. The flight distances were classified into five distinct categories:

Table 6.1. Flight categories and distances observed for giraffe in the study region

Flight category	Flight distance (m)	Description
1	≤ 10	no significant flight
2	> 10-25	little flight distance
3	> 25-50	medium flight distance
4	> 50-100	large flight distance
5	≥ 100	extreme flight distance

6.2.3. Statistical analysis

A common problem in analysing the results of activity budget studies is that successive observations are necessarily obtained from the same individuals, and these are often pooled before formal analyses are undertaken. The major problem with pooling is that multiple observations of the same individuals are not independent, and inflation of the true sampling size (i.e. the number of individuals observed) by pooling can lead to spuriously significant effects (Machlis *et al*., 1985).

One solution to this problem is to average repeated observations from the same individuals prior to analyses so that n = the number of individuals observed and not the number of measurements. The major disadvantage is that hourly, daily or seasonal comparisons of behaviours are still precluded if data have been collected from the same individuals. In small populations, or situations where individuals cannot be readily identified, multiple observations of the same individuals are likely to be inevitable.

A second possible solution is to use data points from the same individuals that have been shown to be 'independent' in a strictly statistical sense, such as by serial correlogram analysis (Das & Sen, 1995). In practice, this may mean discarding observations taken close together or adopting a minimum time period (one minute in this study, see section 6.2.1) during which any of a defined set of behaviours could be exhibited. Empirical and simulation studies of the effects of data discarding have yielded contradictory results, with

some suggesting that even the deletion of >90% of data points will not guarantee statistical independence (e.g. Rooney *et al*., 1998). Even if some data points are deleted, multiple observations of the same individuals will of course still be biologically dependent and compromise formal statistical comparisons between different times.

A practical resolution of the multiple observation dilemma is to recognise the limitations imposed by non-independent data and seek to employ statistical analyses in an exploratory rather than hypothesis-testing or confirmatory sense (Martin & Bateson, 1993). Here, statistical comparisons can be made of individuals between times and places simply to reveal patterns or changes in behaviours. Because of the constraints inherent in the other approaches to using data from the same individuals, and because I am concerned here with describing patterns of giraffe behaviour, the exploratory approach is preferred.

Chi-squared analyses were used to compare frequencies of each of the categories of behaviour observed and performed by the different population components of giraffe between different hours of the day and between seasons. Where the same data have been compared in more than one analysis (such as in pairwise comparisons between the three seasons), sequential Bonferroni corrections were applied to reduce the risk of committing type-1 errors (Quinn & Keough, 2002). However, probability values adjusted in this way differed little from unadjusted values, so for brevity only the latter have been reported here. Finally, the major activity behaviours of bulls, cows and juveniles were correlated against one another on a minute by minute basis to identify any associations between behaviours.

6.3. Results

In excess of 108 800 individual observations of giraffe were recorded for bulls, cows and juveniles. The activity budget research was undertaken over a total of 1 813 hours, equating to 151 12-hour days and an average of 9 066 individual observations per month. On average 50 hours of actual giraffe observation time was undertaken each month, spread out over 10–20 days per month. Often the 12-hour observations periods would be consecutive.

6.3.1. Activity budgets

A significant difference was observed overall between the diurnal activities of bulls, cows and juveniles (χ^2 =2949.09, d.f.=18, P<0.001; Table 6.2; see Appendix 13). The four dominant activities for all giraffe were feeding, walking, ruminating and resting, which comprised 95% or more of their daily time budgets (Figures 6.1 to 6.5). Differences were detected between these activities for bulls compared to cows (χ^2 =686.18, d.f.=3, P<0.001), with cows spending more of their time feeding (59% vs. 51.1%), as well as resting (14.2% vs. 13%), compared to bulls. Bulls spent more time ruminating than cows (13.1% and 9.1%, respectively), as well as walking (17.4% vs. 15%) and engaged more frequently in interactions (χ^2 =1027.51, d.f.=1, P<0.001).

Table 6.2. Diurnal activity behaviours observed for bull, cow and juvenile giraffe in the study region. Data are expressed as mean percentages of observations.

Activity	Mean (%)		
	Bull (*n*=57 049)	Cow (*n*=39 223)	Juvenile (*n*=12 532)
Feeding	51.1	59.0	51.9
Walking	17.4	15.0	12.9
Resting	13.0	14.2	24.4
Ruminating	13.1	9.1	7.0
Vigilance	1.9	1.5	2.0
Grooming	0.8	0.6	1.1
Interaction	2.1	0.1	0.5
Sexual Behaviour	0.3	<0.1	-
Drinking	0.1	0.3	<0.1
Excretion	<0.1	<0.1	<0.1

Seasonally, bulls spent different amounts of time on different activities (χ^2 =1089.93, d.f.=9, P<0.001). The four dominant activities (feeding, walking, ruminating and resting) accounted for 94–98% of the time budget of bulls in the wet season, 83–98% in the cold-dry season and 88–98% in the hot-dry season (Figure 6.3).

Significant differences were observed in the major activities of bulls between seasons: wet versus cold-dry (χ^2 =142.43, d.f.=3, P<0.001); wet versus hot-dry (χ^2 =156.99, d.f.=3,

$P<0.001$); and cold-dry versus hot-dry (χ^2 =295.78, d.f.=3, $P<0.001$) (Figure 6.3). Feeding increased from the wet to the dry seasons (48.07%, 50.13% and 53.2%, wet, cold-dry and hot-dry seasons, respectively). Ruminating was observed less in the hot-dry season (14.7%, 15.25% and 10.75% for wet, cold-dry and hot-dry seasons, respectively), while resting predominated in the wet season (15.4%, 10.56% and 13.92%, wet, cold-dry and hot-dry seasons, respectively). No seasonal difference was observed in walking by bulls. Giraffe bull interactions increased in the cold-dry season (3.41%) compared to the wet (0.79%) and hot-dry seasons (1.33%), although the time spent interacting overall was quite limited.

Giraffe cows spent different amounts of time seasonally in different activities (χ^2 =617.17, d.f.=9, $P<0.001$), with feeding, walking, resting and ruminating predominating (Figure 6.4). These latter activities accounted for 90–100% of the hourly diurnal activities of cows in the wet season, 92–99% in the cold-dry season and 91–99% in the hot-dry season (Figure 6.4). There were significant differences in the time spent by cows in these activities between seasons: wet versus cold-dry (χ^2 =245.85, d.f.=3, $P<0.001$); wet versus hot-dry (χ^2 =64.76, d.f.=3, $P<0.001$); and cold-dry versus hot-dry (χ^2 =460.22, d.f.=3, $P<0.001$). Interestingly, seasonal increases and decreases in different cow activities were different to those of bulls. Feeding increased in the cold-dry season (59.59%, 64.52% and 55.81%, wet, cold-dry and hot-dry seasons, respectively), while ruminating decreased in the wet season (7.96%, 9.23% and 9.67%, wet, cold-dry and hot-dry seasons, respectively). Resting was considerably reduced in the cold-dry season (15.27%, 8.17% and 16.88%, for wet, cold-dry and hot-dry seasons, respectively). Similar to bulls, cows exhibited no seasonal difference in walking activity.

There were significant differences in the frequency of performance of activities by juveniles (χ^2 =877.56, d.f.=9, $P<0.001$), although feeding, walking, resting and ruminating still predominated (Figure 6.5). These four activities accounted for 90–99% of the hourly diurnal activities of juveniles in the wet season, 89–100% in the cold-dry season and 86-99% in the hot-dry season (Figure 6.5). Differences also occurred in the time spent by juveniles in these different activities between seasons: wet versus cold-dry (χ^2 =293.04, d.f.=3, $P<0.001$); wet versus hot-dry (χ^2 =101.63, d.f.=3, $P<0.001$); and cold-dry versus hot-dry (χ^2 =702.13, d.f.=3, $P<0.001$). Feeding increased in the wet season (60.16%,

47.38% and 45.26%, wet, cold-dry and hot-dry seasons, respectively), while resting decreased in the wet season (14.36%, 30.99% and 25.40%, wet, cold-dry and hot-dry seasons, respectively). Little can be inferred from the resting activities due to their age. Similar to bulls and cows, juveniles exhibited no seasonal difference in walking activity.

The diurnal distribution of feeding behaviour of bulls, cows and juveniles was biphasic, with increased feeding occurring post-dawn and again pre-dusk. Fewer feeding activities were observed during the middle of the day, coinciding with increased ambient temperatures and an increase in resting. The pattern of diurnal resting was inversely correlated with feeding by bulls, cows and juveniles (r =-0.92, P<0.001; r =-0.90, P<0.001; r =-0.96, P<0.001, respectively), reaching a peak during midday and early afternoon. Furthermore, the distribution of ruminating was inversely correlated with feeding by bulls, cows and juveniles (r =-0.69, P<0.001; r =-0.72, P<0.001; r =-0.63, P<0.001, respectively), as too was resting to walking (r =-0.77, P<0.001; r =-0.67, P<0.001; r =-0.84, P<0.001, respectively). All other activities, including grooming, vigilance, sexual behaviour, excretion and drinking, were observed infrequently (Figures 6.1 to 6.5).

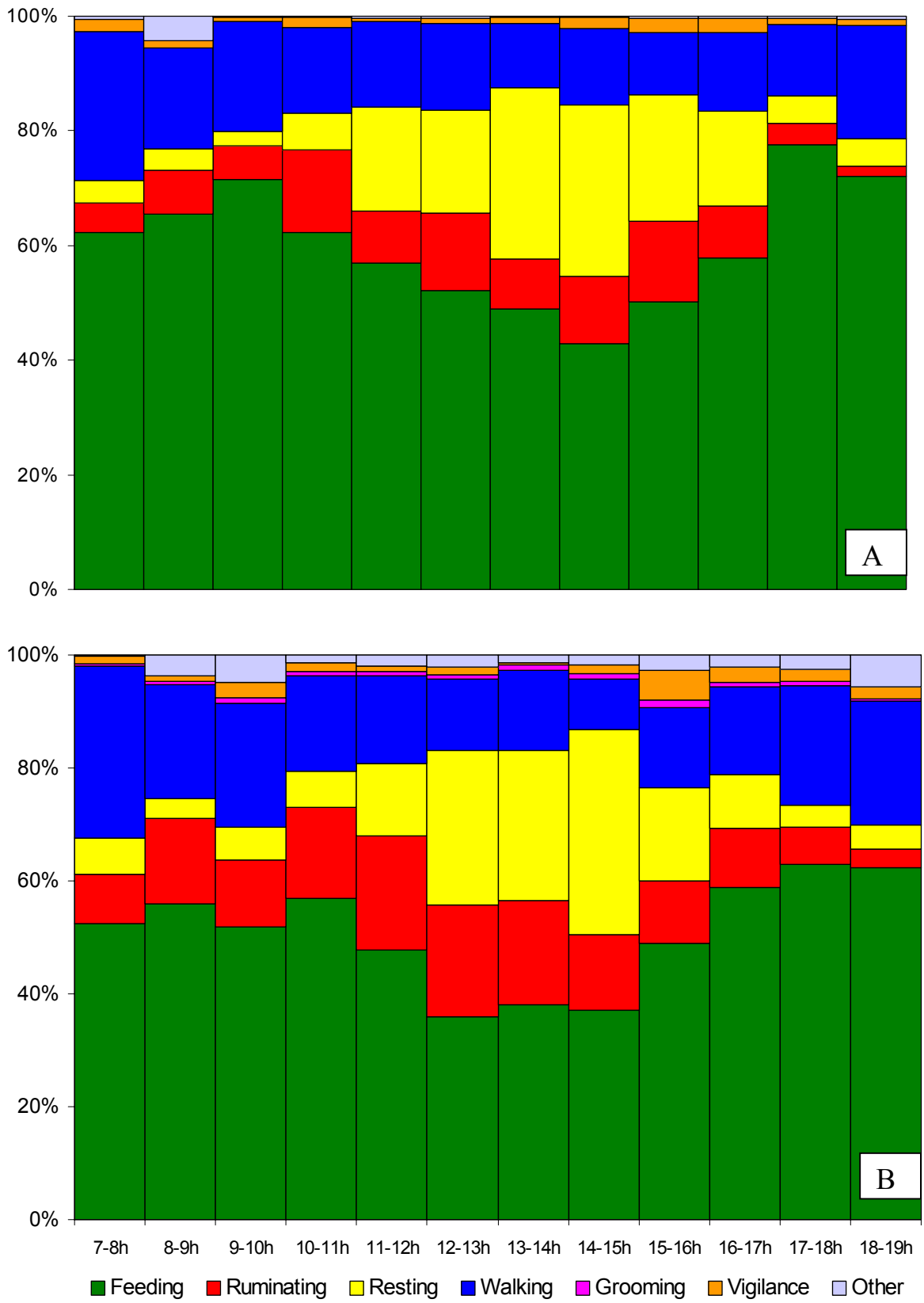


Figure 6.1. Diurnal activity budgets of giraffe expressed as hourly means: (A) cows & (B) bulls.

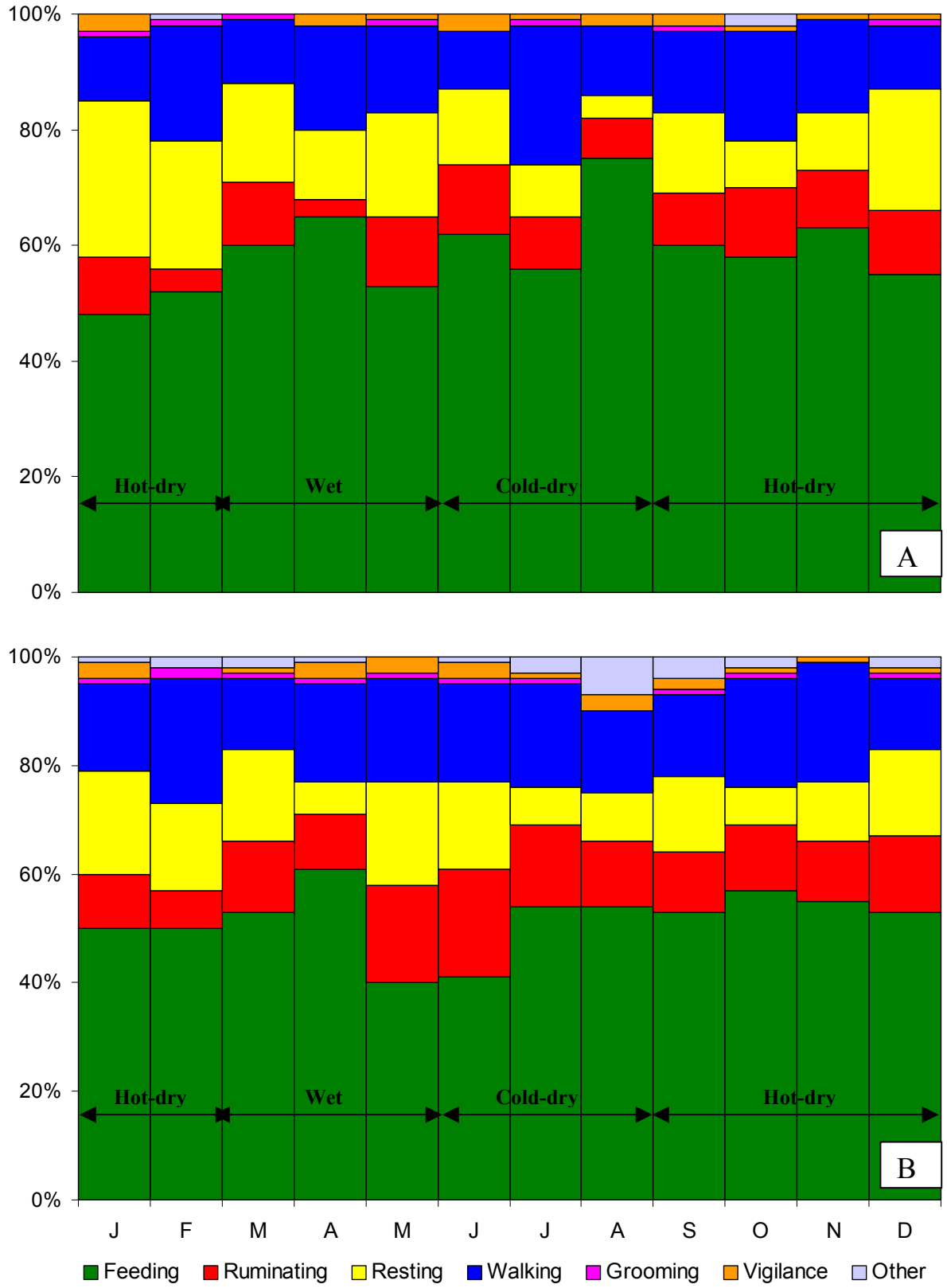


Figure 6.2. Diurnal activity budgets of giraffe expressed as monthly means (seasons highlighted): (A) cows & (B) bulls.

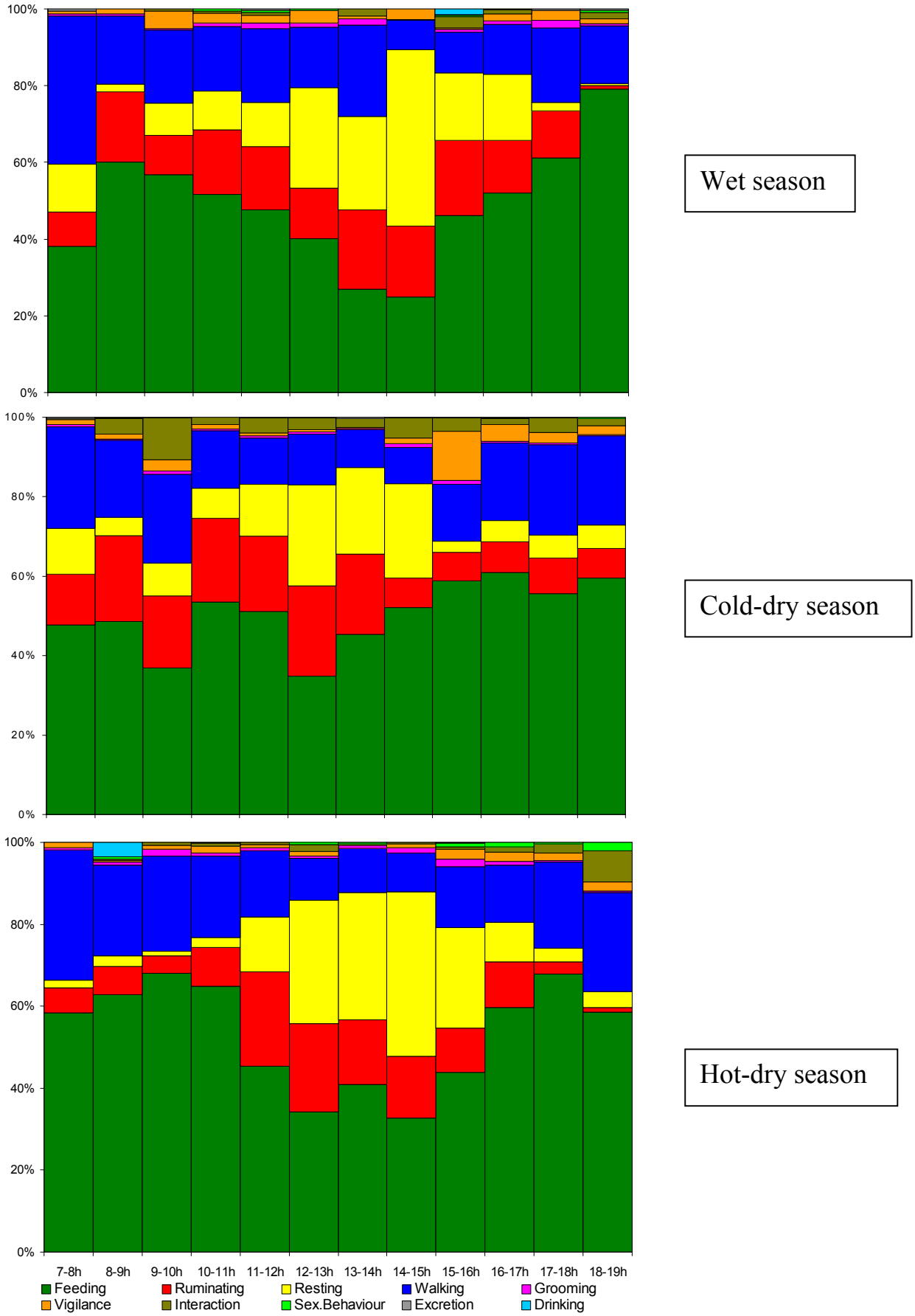


Figure 6.3. Seasonal activity budgets of giraffe bulls in the study region, expressed as hourly means.

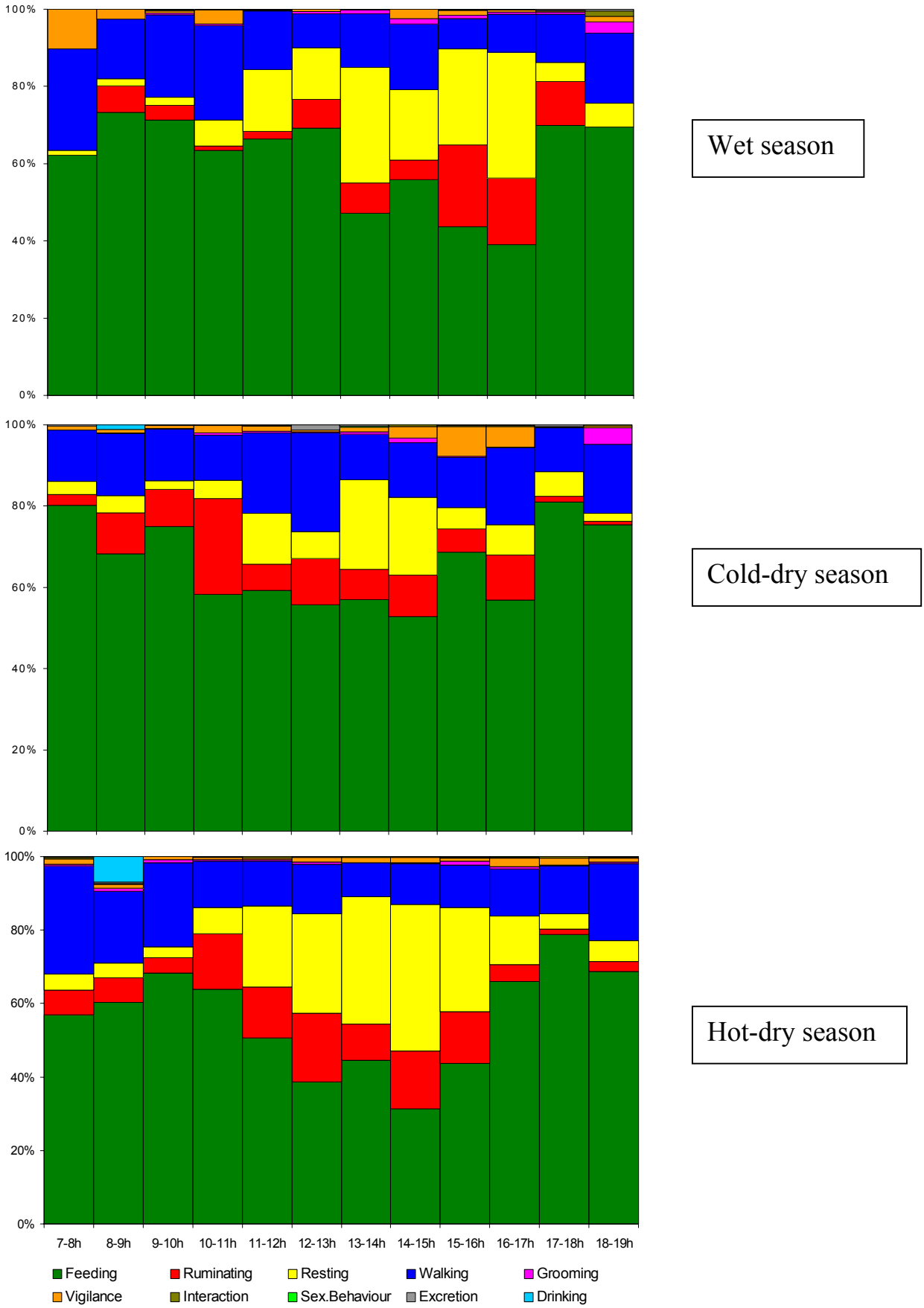


Figure 6.4. Seasonal activity budgets of giraffe cows in the study region, expressed as hourly means.

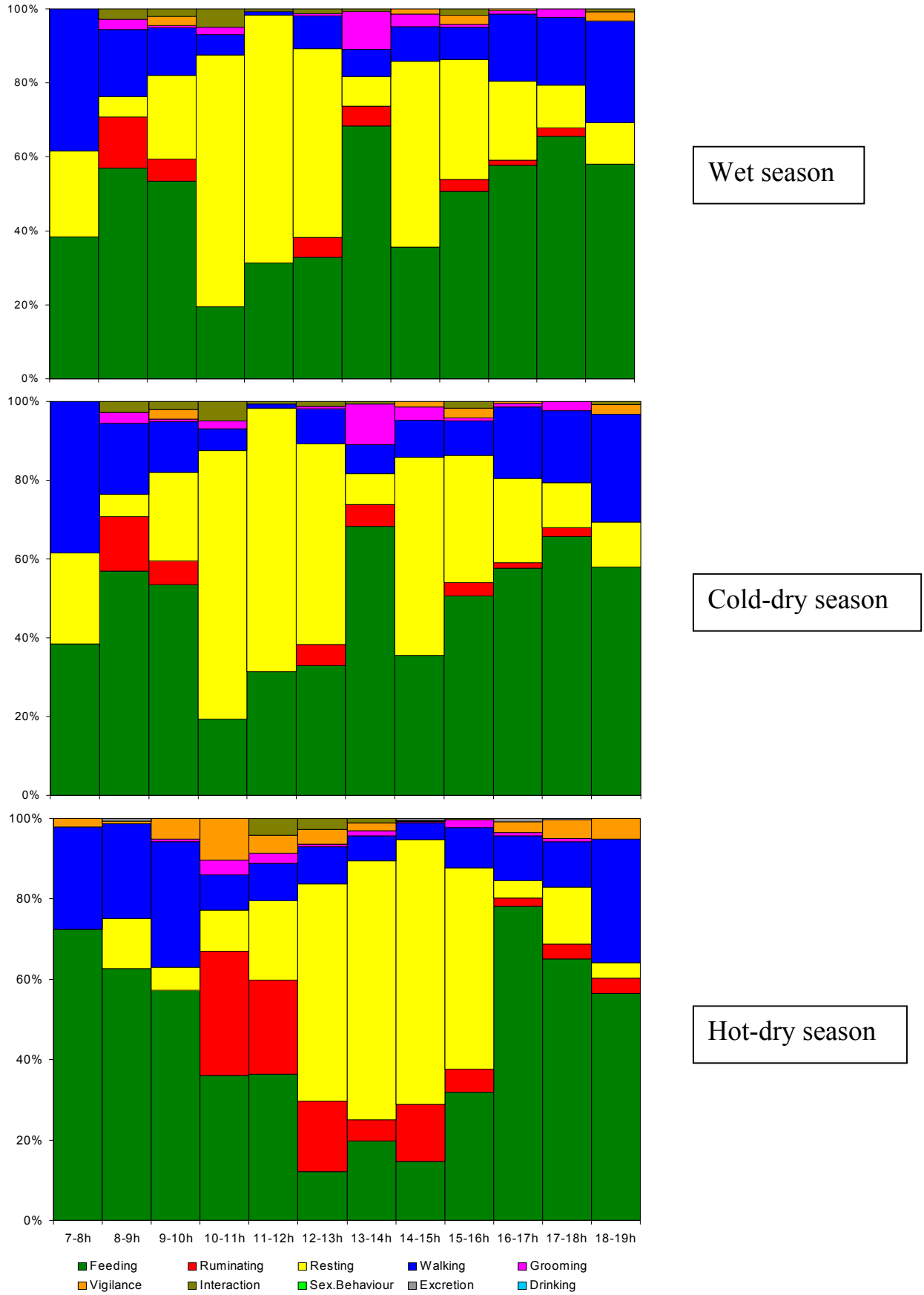


Figure 6.5. Seasonal activity budgets of juvenile giraffe in the study region, expressed as hourly means.

6.3.2. Flight behaviour and impact of tourism

The flight distances observed in this study were markedly less than those previously reported (Scheepers, 1992), averaging 6.7 m over a 12-month period, and ranging from no observed flight to ≤ 25 m (Table 6.3).

Table 6.3. Mean flight distances (m) of giraffe in the Hoanib River study area, 1986–2000.

	Season				
Year	Wet	Cold-dry	Hot-dry	Combined	Source
1986				156 m	Scheepers (1992)
1988				114 m	Scheepers (1992)
2000	6.7 m ±5.5	3.3 m ±4.0	10.0 m ±7.3	6.7 m ±6.0	This study

Seasonal variations in flight distances in this study were not great, although individual giraffe responded differently and contributed to the relatively high observed standard deviations. The marginally increased flight distances observed during the hot-dry season could be attributed to an influx of giraffe into the river systems (Fennessy *et al.,* 2003), coupled with seasonal winds that increase giraffe vigilance, but the high variance does not allow firm conclusions to be drawn.

6.4. Discussion

6.4.1. Activity budgets

Daily and longer term patterns of behaviour appear to reflect responses by giraffe to changing biotic and climatic conditions in the northern Namib Desert. These are discussed below.

6.4.1.1. Feeding

Feeding was the dominant activity of giraffe in the study region, although the proportion of time spent feeding differed significantly between the sexes and seasons. Diurnal feeding behaviour was strongly biphasic, with animals showing strong avoidance of energy

consumptive activities such as feeding and walking during the hottest period of the day. Such activities increased in the early morning and late afternoon and correlated with lower ambient temperatures. Energy conserving activities, such as resting, showed a strong inverse correlation with feeding and walking. This activity pattern conforms to the 'heat-load' concept (e.g. Lewis, 1975; Mitchell, 1977; Leuthold & Leuthold, 1978; Pellew, 1984a), where animals maximise heat loss during the day by simply shifting activity. Giraffe across their range show similar biphasic activities (e.g. Leuthold & Leuthold, 1978; Pellew, 1984a) as do other mammals (e.g. elephant—Guy, 1976a; dikdik *Madoqua kirki*—Tinley, 1969; klipspringer *Oreotragus oreotragus*—Norton, 1981; steenbok—Cloete & Kok, 1986; impala—Jarman & Jarman, 1973). Although nocturnal studies were not undertaken during this study, previous studies of giraffe suggest that feeding and walking activities are greatly reduced in the night when ambient temperatures are lowest (Pellew, 1984a).

The feeding behaviour of giraffe cows in the study region can best be explained as an 'energy maximizer' strategy (Schoener, 1971). During the cold-dry season cows increased their time spent feeding, enabling them to increase fat deposition and therefore cope better during the extended dry season. During the hot-dry season forage intake of cows was reduced. Aside from exhibiting increased time feeding during the cold-dry season, the reduction in forage intake in the hot-dry season correlated with a change in dietary intake (see Chapter 7). Seasonal changes in the phenology of woody plants eaten may have enabled cows to obtain their necessary nutrient requirements with reduced forage effort. This ability to reduce the energy consumptive activities at such a critical time of the year should increase the chance of survival.

In contrast, bulls appeared to adopt an 'energy minimizer' strategy (Schoener, 1971) in the study region. A seasonal increase in bull feeding activity was observed from the wet to the hot-dry season, although the increase was not as distinct as that observed for cows. The reduced feeding in the wet season could be attributed to an increase in the nutrient quality of forage (see Chapter 7). The increase in bull feeding activity in the hot-dry season was possibly a result of reduced availability of forage in the canopies; if so, bulls may have been feeding on a wider choice of plants at different heights to maintain their bioenergetic requirements at this time of the year. Similar observations of feeding activities have been

reported for giraffe in the Serengeti NP, Tanzania (Pellew, 1984c), Mikumi NP, Tanzania (Ginnett & Demment, 1997), and in Niger (Ciofolo & Le Pendu, 2002).

Maintenance of bioenergetic requirements is dependent on a variety of factors, including the availability, digestibility and quality of forage. Giraffe bulls obtain more nutrients and meet metabolic thresholds from reduced foraging times (e.g. Pellew, 1984c) in part from feeding higher in the canopies than cows (e.g. du Toit, 1990b; Young & Isbell, 1991; Ginnett & Demment, 1997; Woolnough & du Toit, 2001). Bulls feed selectively on new shoots and leaves with higher nutrient levels (e.g. du Toit, 1990b; Pellew, 1984c) or on plants with increased biomass (e.g. Woolnough & du Toit, 2001), which are often out of reach of cows and other herbivores. Similar feeding selection has been reported and correlates with the seasonal nutrient intake and bioenergetic requirements of bulls versus cows (e.g. Pellew, 1984a; Caister *et al*., 2003).

During the wet season, new leaf growth results in higher nutrient levels in some woody plant species (see Chapter 7). These seasonal changes altered forage selection, as well as plant-part selection, by giraffe. For example, pods of *Faidherbia albida* were eaten more often in the hot-dry season. The observed differences between the seasonal feeding pattern of bulls and cows was due to a combination of factors, not the least access to different foliar nutrients and moisture quality, and forage intake rates. Reduced seasonal feeding activity could be expected to limit other energy consuming activities such as walking. However this did not appear to be the case as there were no significant differences in walking activities observed between sexes or seasons.

Although yearly feeding activities varied between bulls (51.1%) and cows (59%), the difference was not as great as reported in other activity studies of giraffe (Leuthold & Leuthold, 1978; Pellew, 1984a; Ciofolo & Le Pendu, 2002). The differences in time spent in diurnal feeding activities between sexes and populations could be attributed to numerous factors, including differences in population structure and density, forage quantity and quality, forage intake rates, habitat use and water availability. For example, van der Jeugd & Prins (2000) postulated that reduced feeding activity by giraffe in Lake Manyara NP, Tanzania (average 35% for bulls and cows), compared to giraffe in the Serengeti NP, Tanzania (55.4% bulls and 72.4% cows: Pellew, 1984a) was due to access to higher quality

habitat and/or higher rates of food intake. In Niger, the desert-dwelling giraffe show far greater seasonal variation in feeding activity (Ciofolo & Le Pendu, 2002) than the giraffe in this study. Time spent in feeding activities of giraffe in Niger doubled in the dry season compared to the wet season (46 and 22.8%, respectively), probably due to seasonal shifts in forage quality. Niger's giraffe migrate seasonally between two main habitats, with forage quality being markedly higher in the wet season habitat compared to the dry season habitat (Ciofolo & Le Pendu, 2002; Caister *et al*., 2003).

No similar large-scale seasonal shifts in habitat use were observed during the present study. However, within the Hoanib River study area seasonal changes in the availability of preferred forage may have resulted in dietary shifts (see Chapter 7) and consequent small-scale movements along the riverbed (see Chapter 5). These movements were not as pronounced as in Niger, but are indicative of the different factors that may impact on activity patterns in different areas.

This study could not confirm or refute the suggestion that giraffe do not feed during rain (Dagg & Foster, 1982), but personal observations indicated that windy conditions reduce giraffe feeding activities and increase vigilance. During windy conditions giraffe were observed to seek out sheltered areas away from the main riverbeds. It was unclear whether these activities increased before the onset of windy or other inclement weather conditions, but a distinct decrease in feeding and an increase in vigilance were observed while wind was blowing. Scheepers (1992) observed that flight distances also increased in windy conditions. Further analysis might provide greater insight into the impacts of weather on giraffe behaviour, especially on activity budgets and energy maintenance.

6.4.1.2. Ruminating, resting and vigilance

Time spent ruminating by giraffe was inversely correlated with that spent feeding in both sexes and in juveniles, although not as strongly as the inverse correlation between feeding and resting. Time spent ruminating increased during midday and early afternoon. Giraffe bulls ruminated more often than cows (e.g. Leuthold & Leuthold, 1978; Pellew, 1984a), and less in the hot-dry than the cold-dry season. Increased rumination by bulls is possibly

related to their feeding patterns and the ability to extract more nutrients from the food source (E. Cameron personal communication). The large increase in heat-load experienced during the hot-dry season may reduce daily rumination activities (Dagg & Foster, 1982). I could not determine whether rumination increased by night during the hot-dry season, but Dagg & Foster (1982) and Pellew (1984a) reported rumination to be the dominant nocturnal behaviour.

In the Serengeti NP, giraffe ruminated more at midday and in early afternoon, showing a strong inverse correlation with feeding (e.g. Pellew, 1984a). The time spent ruminating by giraffe in my study was less than that reported elsewhere, possibly reflecting an adaptation to conserve energy in the arid environment during the most critical periods of the day. A lack of supportive studies from arid environments limits any strong inference.

Rumination was often associated with vigilance. When vigilant, giraffe focussed their attention in the direction of the stimulus, which was sometimes not obvious to the researcher. Giraffe would begin to ruminate while still being vigilant, although it is unknown whether this was a coincidental activity or nervous behaviour. Similar nervous behaviours associated with vigilance, such as ruminating and self-grooming, have been reported for other African ungulates (e.g. Siegfried, 1980; Mooring & Hart, 1995). Increased vigilance may also help to reduce interactions with predators, other giraffe or competitors, or people.

Throughout the study, giraffe showed varying degrees of vigilance, although this equated to just 1.5% to 2% of the time (bulls, cows and juveniles). Vigilance occurred in response to external stimuli, such as the activities of communal farmers, tourists, light aircraft, domestic stock, other giraffe, birds, elephant, gemsbok, springbok and/or predators. All of these potential conflicts, competitive situations or predatory distractions were common throughout the study region. It is important to note that in the daily activities of the giraffe population in the communal areas of the northern Namib Desert, people, as much as other wildlife, are potential threats, particularly in light of historical poaching activities.

The percentage of daytime activity dedicated to vigilance in the study was not mostly related to dominance, as proposed previously by Young & Isbell (1991). Increased

vigilance comes at a cost to foraging time, while conversely it reduces the risk of predation (Siegfried, 1980). Many African ungulate species aggregate in large numbers for protection against predators (e.g. Bertram, 1979; Siegfried, 1980; Underwood, 1982; FitzGibbon, 1989; Mooring & Hart, 1995); however, the giraffe's obvious height advantage reduces such a need. Furthermore, ungulates increase vigilance behaviour during seasonal breeding periods (e.g. Underwood, 1982; Jarman & Jarman, 1973). Giraffe in the study region and other populations across the range showed seasonal peaks in breeding, but these were not as defined as for other ungulates. As a consequence, little seasonal variation in vigilance activity was observed in the study region. Interestingly, time spent in vigilance in the study population was considerably less than that reported for giraffe in East Africa (e.g. Ginnett & Demment, 1997) and in comparison to other African ungulates, such as impala, which spend 22% to 27% of the day being vigilant (e.g. Hunter & Skinner, 1998; Matson, 2003). A low density of predators in the study region (Stander & Hanssen, 2003) might have reduced the need for extensive vigilance activities.

Giraffe preferred resting in the riparian woodlands rather than in open habitats (personal observation). The riparian woodland in the study region has large banks that channel wind along the rivers. Matson (2003) proposed that impala inhabiting semi-arid and desert climates may use particular slope orientations in relation to topography to optimise heat loss, whilst Hudson & White (1985) noted that the lightest of winds could reduce herbivore skin temperatures substantially. Giraffe in the study region appeared to rest in microhabitats, such as under trees within the riparian woodland, allowing shade and wind to optimise heat loss or gain. When observed resting on occasions in the open, giraffe orientated their body away from the sun. This behavioural orientation reduces water loss and is observed in other species in arid environments (e.g. Hartmann's mountain zebra; Joubert, 1974). Such behaviours assist giraffe under extreme thermal conditions.

Diurnal sleeping was not observed commonly during the study, but giraffe of all age and sex classes slept at some point by day. The limited time (<0.1%) spent in diurnal sleep was similar to that reported for giraffe elsewhere (e.g. Leuthold & Leuthold, 1978; Dagg & Foster, 1982; Pellew, 1984a). Although not quantified in the wild, giraffe sleep mostly at night (e.g. Kristal & Noonan, 1979; Dagg & Foster, 1982; Pellew, 1984a; Tobler & Schwierin, 1996). Perhaps too, in the present study, it is possible that giraffe spent some

time asleep while sitting or standing, hence resulting in an underestimation of diurnal sleep behaviour.

Giraffe usually sleep when recumbent, lying with the neck bent backwards, head under the rump, on the hind limb or on the ground (e.g. Kristal & Noonan, 1979; Dagg & Foster, 1982; Moss, 1982; Pellew, 1984a; Tobler & Schwierin, 1996). This form of sleep is referred to as 'deep sleep', and giraffe are sometimes presumed to fully rest only in this position. However, based on studies of other ruminants (e.g. Ruckebusch *et al*., 1974), it seems likely that giraffe can sleep while recumbent with their necks in an upright position (Kristal & Noonan, 1979), or even while standing (Tobler & Schwierin, 1996).

When giraffe were observed sleeping, the episodes were short and fragmented, a result of their inability to rise quickly from the ground and flee as a response to an external stimulus such as predators (e.g. Tobler & Schwierin, 1996). Such vigilance and predator avoidance may encourage giraffe to sleep in a standing position (Tobler & Schwierin, 1996). Whilst standing or sitting, giraffe were often observed motionless, not ruminating and with an upright neck. From these observations, and those of Tobler & Schwierin (1996), it could be inferred that during rest giraffe sleep more often than previously assumed. Increased periods of resting while both recumbent and standing were observed at midday and during early afternoon, and corresponded with higher ambient temperatures. Tobler & Schwierin (1996) further noted brief periods of sleep during rumination. Ruminating was often associated with both standing-resting and recumbence during this study, but no overall correlation was detected.

6.4.1.3. Grooming and social interactions

Grooming, although observed relatively infrequently, consisted of any of the following: tail swotting, shaking, biting or nibbling, scratching the neck, head, back and inside of the ear on tree trunks, branches and rocks, and scratching the underbelly and legs by straddling small bushes and shrubs. No giraffe were observed dusting, wallowing or bathing as has been reported for other mammals (e.g. Clough & Hassam, 1970; Guy, 1976a; Leuthold, 1977b). The rare behaviour of allogrooming was observed just once. The importance of

grooming activities for many African animals has been well documented (e.g. warthog *Phacochoerus aethiopicus*—Clough & Hassam, 1970; impala—Jarman & Jarman, 1973; Hart & Hart, 1992; Mooring & Hart, 1995; zebra—Joubert, 1972; waterbuck *Kobus ellipsiprymnus*—Spinage, 1968; elephant—Guy, 1976a; birds—Redpath, 1988; MacLean, 1993).

Grooming in the present study primarily aided in the removal of ectoparasites such as ticks. Giraffe regularly used small shrubs and bushes, such as *Salvadora persica, Pechuel-Loeschea leubnitziae, Tamarix usneoides* and *Colophospermum mopane,* and branches from trees such as *Faidherbia albida, Acacia erioloba* and *A. tortilis,* to scratch themselves. The use of trees and shrubs as grooming 'tools' has been reported (e.g. Dagg & Foster, 1982). It is not clear why giraffe in the study allocated so little time to grooming. It is possible that they are less affected by water-borne parasites due to their limited use of free-water (e.g. Graczyk *et al*., 1997; Wobeser, 2002), or that increased grooming occurs at night.

The need to groom in many species of African mammals has encouraged the occurrence of bird/mammal associations. Specialist ectoparasite gleaners, such as Oxpeckers (*Buphagus* spp.), occupy specific niches with mutual benefit for both bird and mammal. In regions where specialist ectoparasite gleaners do not occur, facultative ectoparasite gleaners have filled the niche in their absence. This evolutionary process is dynamic. In the study region, facultative ectoparasite gleaners, such as Palewinged Starlings (*Onychognathus nabourup*), were observed in association with giraffe (Fennessy, 2003), providing the first recorded observation of any bird/giraffe feeding association from the region (see Appendix 14 for published article on ectoparasite gleaning of giraffe in this study).

Studies of social interactions among giraffe have revealed many similarities, as well as differences, between populations and subspecies (Innis, 1958; Foster, 1966; Foster & Dagg, 1972; Leuthold & Leuthold, 1978; Dagg & Foster, 1982; Pratt & Anderson, 1982; Pellew, 1984a; Young & Isbell, 1991; Ginnett & Demment, 1997; van der Jeugd & Prins, 2000; Bashaw, 2003). Many of the social activities exhibited by giraffe are similar to those reported for other African ungulates, such as impala (Jarman & Jarman, 1973) and gerenuk (*Litocranius walleri*; Leuthold & Leuthold, 1978). In the study region many

social interactions among giraffe were observed. Some of these were age or sex dependent, while others were not. Interactions included (see Innis, 1958; Young & Isbell, 1991; Bashaw, 2003):

- greeting or contact interactions, such as naso-frontal greeting (nosing);
- rubbing, sniffing and licking;
- play interactions, such as gambolling;
- neck sparring and kicking;
- affiliative interactions, such as cow-calf bonding, suckling;
- dominance and agonistic interactions, such as neck sparring, avoidance, chesting, bumping; and
- sexual interactions including flehmen testing and mounting.

Affiliative, contact and play interactions appeared to decline in frequency with an increase in age, while agonistic and sexual interactions increased with maturity. These findings appear to reflect that observed elsewhere (e.g. Pratt & Anderson, 1982; Le Pendu *et al*., 2000).

In Chapter 4 it was inferred that strong inter-individual associations occurred among giraffe in the Khumib River study area; this population was the smallest in the study region. This population appeared to have a matrilineal structure, while strong bull associations were observed in the Hoarusib River population. Social interactions between giraffe in the study region were most conspicuous amongst bulls and cow-calves. Neck sparring (discussed below) was observed more often in the bull-biased Hoarusib River study area. Cow-calf interactions varied in type but were more frequent in the Khumib River compared to the Hoanib River study area. Juvenile giraffe rubbed their neck or head along the flanks, rump or brisket of their mothers for various reasons. Rubbing often appeared to be a precursor to suckling, but it appeared also to reflect nervous behaviour. When giraffe appeared nervous, independent of age and sex, they would often run away immediately from the stimulus, or seek solace in a nearby giraffe, rubbing or chesting them. This behaviour perhaps enticed the other giraffe to move away from the potential conflict, or simply to seek security. Younger giraffe almost always initiated this nervous contact behaviour and were usually ignored by the dominant giraffe shortly after contact.

Interactions, dominance or leadership amongst giraffe cows are little understood, with most research being focussed on bulls and their social hierarchy (Leuthold, 1979; Pratt & Anderson, 1985; Bashaw, 2003). In the published literature, only occasional observations of cow interactions, such as neck rubbing, neck sparring and chesting, have been reported. Leuthold (1979) reported that interactions among cows in the Tsavo NP, Kenya, were rare, with less than observations being made over a seven year study. In contrast, Pratt & Anderson (1985) reported many interactions among giraffe cows in various parks in Tanzania, with over 140 observations in ten months.

In the study region, interactions among cows were common, although not as lengthy or as often as observed for bulls. All forms of interactions, i.e. contact, play, affiliative, agonistic and sexual behaviour, were observed, but at different frequencies. For example, cow-calf interactions were more common than chesting, which was more common than neck sparring between cows.

Cow-calf interactions were dominant, enabling calves to suckle, while at the same time developing a stronger social bond between the two. Juvenile giraffe had the most contact and play interactions of all giraffe age classes. Juvenile giraffe also showed deliberate physical contact and play behaviour with other giraffe, particularly juveniles. Pratt & Anderson (1982) reported similar observations. Interactions such as naso-frontal greeting, rubbing, sniffing, licking, and gambolling were observed most often in the first weeks of life and decreased markedly after one year. There appeared to be no difference in interaction type or frequency by juveniles of each sex.

One interaction of particular interest was the introduction of a newborn giraffe to a herd. The juvenile was led towards the herd, with the mother initially remaining a short distance away. Immediately, one of the juveniles in the herd playfully chased the newborn. Following this, a subadult cow approached and sniffed the newborn, which caused the newborn to run again. This was followed by the first juvenile playfully chasing it again. An adult cow then approached the newborn and sniffed it. A second juvenile approached the newborn and naso-frontal greeted (touched noses) with it. This caused the newborn to run into a nearby shrub, followed by the two juveniles and two sub-adults, all jumping and running. The newborn and its mother stayed with the herd for ten minutes before slowly

moving away. Both of the juveniles then joined the newborn and its mother. Eventually, one of the juveniles returned to its initial herd while the mother, newborn and the other juvenile moved up a gorge and out of contact. The strong interest exhibited by giraffe suggests the existence of some social structure within the population, and provides evidence that giraffe have considerable social awareness of other giraffe beyond that expected.

Significantly more interactions were observed among giraffe bulls compared to either cows or juveniles, primarily due to the high frequency of neck sparring events among bulls. Differences in bull interactions between the three study areas were not assessed, however, from personal observations a marked increase in bull interactions occurred in the bull-biased Hoarusib River study area compared to the other study areas. More interactions also occurred among bulls in the cold-dry season compared to either the wet season or hot-dry season. Giraffe calving peaked during the hot-dry season in the study region (see Chapter 4) which correlates with increased conceptions in the cold-dry. Although I did not observe an increase in courting during the cold-dry season, it is expected that increased interactions among bulls in the cold-dry season were related to increased copulation attempts. These are similar observations to those reported by Dagg & Foster (1982). Since bulls do not defend a distinct territory, it may be that year round neck sparring by bulls is a social cohesion behaviour used to establish their status (dominance) in the population and as a form of play (e.g. Coe, 1967; Dagg & Foster, 1987; Simmons & Scheepers, 1996; Bashaw, 2003).

The frequency of neck sparring and dominance-related activities appears to vary between populations, often independently of population structure (e.g. Innis, 1958; Coe, 1967; Leuthold, 1979; Dagg & Foster, 1982; Pratt & Anderson, 1982 & 1985; Le Pendu *et al*., 2000). In one bull-biased giraffe population neck sparring led to bulls mounting one another, and Innis (1958) postulated that bull-bias may foster homosexual behaviour patterns. Since this initial hypothesis, mounting attempts of bulls on bulls have been observed regularly and are perceived to be associated with attaining or maintaining status in the dominance hierarchy (e.g. Geist, 1966; Coe, 1967; Dagg & Foster, 1982; Pratt & Anderson, 1982 & 1985; Simmons & Scheepers, 1996).

Neck sparring observed in the study region involved bulls almost exclusively. It has been reported that in the wild only bulls are involved in such activities (e.g. Coe, 1967; Dagg & Foster, 1982), but neck sparring by cows has been observed, although rarely (Pratt & Anderson, 1985). The two observed occurrences of neck sparring by cows in my study involved adults. One bout with a juvenile was most likely play behaviour, although distinctive necking actions by both giraffe were observed. The other neck sparring bout was with a subadult bull. During this bout both giraffe returned blows on several occasions, although the contact appeared less intense than that observed in most neck sparring between bulls.

Various age combinations were observed in neck sparring contests between bulls: adult-adult, adult-subadult, and subadult-subadult. Juveniles were also observed neck sparring on a number of occasions, both with other juveniles, subadult bulls or adults, although the latter interaction was not common. On two occasions groups of three giraffe were observed neck sparring with each other at the same time: adult-adult-subadult, and subadult-subadult-juvenile. Each of these neck sparring bouts lasted less than two minutes.

Neck sparring bouts lasted from less than one minute to intermittent bouts of over 50 minutes, each averaging approximately five minutes. During the study the neck sparring did not appear to represent serious fighting (Pratt & Anderson, 1982 & 1985), even though some bouts lasted almost an hour. On numerous occasions mounting or mounting attempts of one bull on another followed neck sparring. More often than not it appeared to be the older or dominant bull mounting the other, as might be expected from dominance hierarchy theory (e.g. Geist, 1966; Coe, 1967; Dagg & Foster, 1982). Mounting did not always involve the extension of the genitalia, although it often resulted in the mounted giraffe walking away from the immediate area. Interestingly, on one occasion a subadult bull was mounted several times by a number of adult and subadult bulls, even though he did not neck spar with them. This bull was probably relatively low in the population social structure.

On a few occasions during the study period, neck sparring bouts were associated with courting. During bouts between bulls where cows were in close proximity, the dominant bull always returned to court the cow following the bout. Dominant bulls, normally larger,

with bigger heads and necks, clearly had increased access to oestrous cows (Pratt & Anderson, 1982 & 1985; Simmons & Scheepers, 1996). Furthermore, dominant giraffe bulls within the study region appeared to court oestrous cows for longer periods. The majority of heterosexual sexual interactions were between adult or subadult bulls and adult cows. On numerous occasions older bulls were observed displacing younger bulls, which were courting or seeking the attention of an oestrous cow. On one occasion, however, an adult cow was so insistent to get the attention of the dominant bull that she isolated the bull from the rest of the herd by steering him away. Pratt & Anderson (1985) reported similar displacement behaviour. Giraffe bulls were observed chesting or chasing away other bulls from trees or shrubs on which they foraged. This behaviour was less common than neck sparring. Little correlation between flehmen testing and mating could be established, as flehmen was observed year= round in the study region, although it was more conspicuous in the cold-dry and hot-dry seasons.

Aggression by giraffe in the study region was rare overall, but when observed was due to three possible stimuli: (a) people (tourist, communal farmer or researcher); (b) other giraffe; and (c) other wildlife, including predators. Giraffe exhibited aggression mainly by stamping their front hooves, snorting or growling (see Dagg & Foster, 1982), and also by charging, necking and kicking. However, avoidance (flight) was preferred (as discussed below).

6.4.1.4. Drinking and independence of water

A unique feature of Namibia's desert-dwelling giraffe is their apparent independence of surface water, a testament to their adaptation to the desert environment (e.g. Viljoen, 1981; Scheepers, 1992; Fennessy *et al*., 2003). Permanent, slightly saline springs occur in all main riverbeds throughout the study region, while water collects temporarily in mountain pools and crevices following seasonal rainfall. Independence of water in giraffe thus appears not to be a result of lack of availability of surface water, as it is widely distributed, if only seasonally, throughout the study region. Furthermore, the desert-dwelling elephant that occupy the northern Namib Desert drink regularly.

As previously proposed (Viljoen, 1981; Hall-Martin *et al*., 1988; Scheepers, 1990), giraffe in the study region appear to obtain adequate moisture from food. However, this is only possible because of the coastal fog that sometimes blankets the region up to 60 km inland. Precipitation in the dunes and adjacent riparian woodlands is greater than at the coast due to these seasonal fogs that carry about twice as much moisture as rainfall with a third less variability (Robinson & Seely, 1980; Southgate *et al.,* 1996; MWTC, 2000). The fog envelops the trees and provides giraffe with abundant fresh water (see Chapter 7).

In the Hoanib River, fewer than ten observations have been made of giraffe drinking since 1934 (Viljoen, 1981; Scheepers, 1990; Fennessy *et al*., 2003). One observation, made in the late hot-dry season in 1978, was of a solitary giraffe in poor condition (Viljoen, 1981). In the Hoarusib River study area, giraffe were observed drinking twice and their spoor was observed at a seasonal wetland. These observations were the first of giraffe drinking in this area, although it should be noted that little focussed research had been carried out previously. In the Khumib River, spoor and sightings of a bull at the Sarusas spring, 7 km west of the population's normal range, remain the only known records of giraffe drinking in the area. Up until the installation of artificial water points in the Hoanib River study area in late 2002, no giraffe had been observed drinking during the study period. However, altered drinking behaviour was observed the year after installation; this is discussed in detail below.

Throughout Africa, giraffe have been reported to survive without water for extended periods (e.g. Taylor, 1968; Foster & Dagg, 1972; Dagg & Foster, 1982; Ciofolo & Le Pendu, 2002). Independence of water in other populations has been attributed to the moisture-rich browse on which they feed, predominantly *Acacia* spp. (e.g. Taylor, 1968; Hall-Martin & Basson, 1975; Dagg & Foster, 1982). The desert-dwelling giraffe of Niger also drink rarely, accounting for only 0.03% of all diurnal activities (Ciofolo & Le Pendu, 2002), unlike giraffe in my study population, were assumed to drink at night. Therefore, the independence of water by giraffe in the Namib appears more marked than in populations elsewhere in Africa.

To survive in the arid northern Namib Desert, giraffe and other mammal species have developed a variety of physiological and behavioural adaptations. These serve to minimise

water loss, and include selection of cool habitats, an efficient renal system and nasal heat exchange; the latter adaptation occurs in both hot (e.g. kangaroo rat *Dipodomys* spp.—Jackson & Schmidt-Nielsen, 1964; gemsbok—Joubert, 1974; camel *Camelus bactrianus*—Langman *et al*., 1978) and cold desert taxa (e.g. reindeer *Rangifer tarandus*—Langman, 1985).

Steenbok in the Namib Desert also show independence of surface water (Cloete & Kok, 1986; Seely, 1987) and have similar activity budgets and heat-load adaptations to giraffe (Cloete & Kok, 1986). As with giraffe, the renal physiology of steenbok is similar to that of mesic-dwelling relatives (Cloete & Kok, 1986; L. Scheepers & J. Patterson, personal communication), and animals also obtain moisture purely from their predominant food source, *F. albida*. In the central Namib Desert *F. albida* contains about 59% water (Cloete & Kok, 1986). *Faidherbia albida* is also the preferred forage source of giraffe in the study region and presumably contributes to water balance (see Chapter 7).

Respiratory water loss in giraffe is very small. Langman *et al*. (1979) reported that nasal counter-current heat exchange was an important mechanism for water conservation by giraffe in any arid environment. By cooling the exhaled air on the surface of the nasal mucosa, up to three litres of water per day can be conserved (Langman *et al*., 1979), only half of that exhaled at normal body temperature (Langman *et al*., 1982). The mechanism of recovering water from respired air using nasal heat exchange not only reduces water loss, but can have the added benefit of reducing metabolic heat loss, which is important during cool night conditions. Furthermore, the ability of giraffe to minimise water loss has important consequences for their food and water intake (Langman *et al*., 1982). With limited observations of giraffe drinking in the study region, moisture intake in forage and water conservation appear to be major adaptations.

Giraffe also avoid excessive evaporative cooling via panting and sweating to conserve water. Body temperatures can fluctuate between 3° and 10°C over a 24 hour period, which results in storage of large quantities of heat, while allowing for improved water conservation (Langman, 1982). Giraffe are able to heat up slowly throughout the day, allowing for passive heating and cooling for water conservation (Joubert, 1974; Langman, 1982).

In October 2002 the Namibian Ministry of Environment and Tourism (MET) built two artificial water points on the banks of the Hoanib River (one close to the confluence of the Hoanib and Ganamub Rivers, and one at the confluence of the Hoanib and Mudorib Rivers). These water points tap into the artesian water supply of the Hoanib River system and pump fresh, palatable water into purpose-built open waterholes. The water points were constructed primarily to entice elephant away from nearby Sesfontein village and so reduce human-wildlife conflict (H. Kolberg & B. Beytell personal communication). However, this was a politically driven decision and ecological impacts were not considered; no monitoring was established either pre- or post-installation of the artificial water point. In the year following their installation, use of the riparian woodland by elephant shifted away from the Dubis wetland and Sesfontein village and towards the west along the Hoanib River where the water points are located (K. Leggett, unpublished data). As a result, increased resource competition between giraffe and elephant has occurred. Furthermore, lion, leopard and cheetah numbers and residency in the Hoanib River study area have increased (personal observation).

In North America developments such as artificial water points in desert areas have often been detrimental to the long-term success of mammal populations (McQuivey, 1978; Broyles, 1995). Overpopulation, reduction in plant biomass and habitat destruction are all impacts which affect animal behaviour (Broyles, 1995). Food resources near the water points often suffer long-term damage due to increased concentrations of wildlife (e.g. Lange, 1969; Andrew, 1988; Pickup, 1994; Leggett *et al*., 2003b & c).

Since the installation of the artificial water points, particularly at the confluence of the Hoanib and Mudorib Rivers, giraffe have been observed drinking regularly, sometimes on consecutive days. In the short-term, the reliable supply of clean surface water has created a marked impact on giraffe. Giraffe are competing more often with elephant for the available forage and habitat resources surrounding these water points. In the short-term no actual displacement of giraffe has been observed and increased focal research would be required to better understand these impacts. However, a shift in elephant habitat use since the installation of the water points has resulted in short-term impacts on forage (K. Leggett, unpublished data; personal observation). Long-term monitoring of elephant movements, together with a comparative assessment of forage resources along the Hoanib River, would

provide insight into impacts on forage and habitat resources along the river. Forage impacts and population dynamics of the dominant tree in the river, *F. albida*, are discussed in Chapter 7. In light of the construction of the artificial water points, this study may also be a valuable tool in assessing the impact of elephant on the area's resources and any impact on giraffe movement and habitat use.

It is concluded that the desert-dwelling giraffe are superbly adapted to life without drinking. However, their activity, habitat use and social interactions may be affected by the installation of the permanent water points and their associated impact.

6.4.2. Flight behaviour and impact of tourism

The impacts of tourism, poaching and human development on giraffe, other wildlife and habitat have been reported (e.g. Babich, 1964; Le Pendu *et al.,* 2000; Warnken & Buckley, 2000). Flight, a reaction of wildlife to external stimuli, such as predators and tourism, can provide some insight into the degree of habituation.

The flight behaviour of giraffe in the Hoanib River study area during this study was very small (<10 m), and significantly less than that reported a decade earlier (Scheepers, 1992). Prior to the 1980s, access of tourists to the Hoanib River and the rest of the study region was limited. Scheepers (1992) commented that uncontrolled public access and increase in tourist numbers from the 1980s onwards would impact on wildlife and the riparian woodlands. Initial assessment of the impact on giraffe and their subsequent flight behaviour in the Hoanib River area in 1986 and again in 1988 suggested a marked decrease in flight distances over this short period (157m (1986) to 114m (1988): Scheepers, 1992). This reduced flight behaviour was attributed to the habituation of giraffe to tourists.

Scheepers (1992) voiced concern about the disturbance that increased tourist numbers would cause, including potential physiological costs, such as heat exhaustion from flight. The reduced flight distances observed in the Hoanib River study area indicate that such physiological costs could now be negligible. However, the time that giraffe allocate to vigilance is of concern. Vigilance reduces time spent in other activities, independent of

whether it is energy consumptive or optimising. Natural predators are an inevitable danger for giraffe and will always result in increased vigilance. However, increased tourism, light aircraft and human movement in the study region should be monitored to assess their long-term impact on giraffe and other wildlife. In the Kruger NP, South Africa, every tourist, on average, commits one or more minor offences during their visit (Babich, 1964). Studies have shown that tourism, particularly in developing areas, has the potential to have large negative impacts if not controlled (e.g. Archer & Cooper, 1994; Berle, 1990; Buckley & Pannell, 1990; Opperman & Chon, 1997). In an uncontrolled environment like the Hoanib River, the effects of tourism could be worse and potentially detrimental over time.

Throughout their range giraffe often live in close proximity to people, including communal farmers and tourists. The ability of giraffe to habituate to their changing surrounds has been reported (e.g. Ciofolo, 1995; Caister *et al*., 2003). However, in the study region and other parts of Africa where giraffe reside on communal lands, giraffe prefer areas away from people, and this reduces potential conflict. The impact on giraffe of the increasingly sedentary lifestyle of communal farmers in the study region is unknown but, with increased tourism and predation, may dramatically alter their behaviour and population status over the longer term.

6.5. Conclusion

Marked differences were observed between the diurnal activity budgets of giraffe bulls, cows and juveniles. Feeding occupied most of the time and, together with walking, resting and ruminating, accounted for at least 95% of all diurnal activities. Giraffe were strongly biphasic, with energy consuming activities such as feeding and walking being reduced during midday and early afternoon when ambient temperatures and heat load were greatest. Energy conserving activities, such as resting, increased during the same period. The dispersal of surplus metabolic heat when temperatures are lower, together with evaporative cooling and water conservation, contributes to the biphasic diurnal activity pattern. Furthermore, behavioural adaptations such as the selection of microclimates offering shade and wind, as well as body orientation, conserve energy and water.

Giraffe cows exhibited an energy 'maximizer' strategy while bulls exhibited an energy 'minimizer' strategy. Similar behavioural strategies have been reported for other giraffe populations in Africa, although in the study region differences in the activity patterns of cows and bulls were not as marked. This suite of responses is of paramount importance for the survival of giraffe in the arid northern Namib Desert.

Giraffe activities in the study area ranged from being social to solitary. The importance of understanding what giraffe do not do is as important as they do. Social interactions in giraffe are little understood and longer-term research will help to decipher their social bonds and hierarchy. Increased tourism in the study region could be detrimental to giraffe behaviour and ecology if it remains uncontrolled, but further research is required to test this hypothesis.

The independence of giraffe on water in the study region is most likely a result of their daily behavioural strategies, but even more so of their selection of forage (see Chapter 7). In the next chapter the seasonal forage preferences of the desert-dwelling giraffe and the chemical composition of their preferred forage are examined in order to better understand their independence of water intake. The impact of giraffe on forage resources and their potential role as habitat changers are also analysed.

CHAPTER 7. FORAGING ECOLOGY

This chapter investigates the feeding ecology of giraffe in the northern Namib Desert using observational methods and chemical analysis of the forage eaten. It also looks at the impact of giraffe on the dominant species of single-stemmed tree in the study region, focusing in particular on impacts in the Hoanib River study area.

7.1. Introduction

Fluctuations in primary production in the Namib Desert are primarily the result of low, unpredictable and localised rainfall events (Louw & Seely, 1982; Skinner *et al*., 1984). Mammals respond to this variability using diverse physiological and behavioural adaptations, such as nasal-temporal heat exchange, colour variation and behavioural flexibility (Louw & Seely, 1982; Skinner *et al*., 1984; Langman, 1985; see Chapter 6). However, an overriding factor in the exploitation of arid environments is the ability to obtain adequate nutrition and moisture.

Forage selection by mammals is influenced by a range of factors, including seasonal shifts in food quality and availability. The wide spectrum of plant genera eaten by giraffe throughout the African continent reflects their ability to exploit many different habitats (Dagg & Foster, 1982; Pellew, 1983a; Caister *et al*., 2003). Throughout Africa, riparian woodlands and associated habitats are essential reservoirs for giraffe during critical periods such as the dry season (Berry, 1978; Hall-Martin, 1975; Parker *et al*., 2003). In the northern Namib Desert, the riparian woodlands provide an important year-round food source and represent the only habitat that can support long-term survival of large mammals in this desert.

The dependence of large mammalian herbivores on particular habitats sometimes causes structural and compositional modifications to the habitats (Buss, 1961; Wing & Buss, 1970; Field, 1971; Field & Ross, 1976; Pellew, 1983b; Dublin *et al*., 1990; Bergstrøm, 1992; Ben-Shahar, 1996; Augustine & McNaughton, 1998; Bond & Loffell, 2001; Birkett, 2002). In particular, elephant are renowned for their role as agents of habitat change in

arid and semi-arid systems (van Wyk & Fairall, 1969; Laws *et al*., 1975; Barnes, 1983a; Ben-Shahar, 1993; du Plessis *et al*., 1998a & b). However, fire (Pellew, 1983b; Dublin & Douglas-Hamilton, 1987; Dublin *et al*., 1990; Prins & van der Jeugd, 1993; Hobbs, 1996; van de Koppel & Prins, 1998), drought, anthropogenic influences and natural seeding processes (Ringrose & Matheson, 1990; Dzwonko & Loster, 1997; Vijver *et al*., 1999; Mathooko & Kariuki, 2000; Mosugelo *et al*., 2002) also influence habitat change, and the interactions of these factors with herbivores may determine which habitats are available for use at any time. Giraffe also impact on landscape elements, including the distribution, structure and composition of plant species and communities (Foster & Dagg, 1972; Leuthold & Leuthold, 1972; Pellew, 1983b & c; Ruess & Halter, 1990; Bond & Loffell, 2001; Birkett, 2002; Parker *et al*., 2003). In particular, browsing by giraffe on *Acacia* species greatly reduces plant recruitment, and affects population structure and structural composition.

Africa's riparian woodlands are one of the major habitats to be affected by wildlife and climatic processes; impacts are particularly evident in arid and semi-arid environments where episodic rainfall events and wildlife-human aggregations are highest. The riparian woodlands are distinctive landscape features of significant conservation value, but despite this their ecology and associated wildlife-habitat dynamics are still poorly understood (Hughes, 1988; Stave *et al*., 2001). A further important issue is how plant species are selected by foragers in riparian and associated environments.

The selection of browse by mammals can be defined as the likelihood of a woody species being fed upon when encountered (Owen-Smith & Cooper, 1987). This browsing selection is influenced by six main factors (van Essen *et al*., 2002; Watson & Owen-Smith, 2002): (a) plant species composition; (b) species density; (c) availability; (d) palatability; (e) digestibility; and, (f) growth potential. The co-evolution of woody plants with browsers in Africa has resulted in the development of two major defensive traits: spines and secondary chemicals (Cooper & Owen-Smith, 1985 & 1986).

Thorns and other forms of spinescence on woody plants, such as *Acacia* species, often form a large component of plant defence (Cooper & Owen-Smith, 1986). Spines restrict bite size and intake rate of forage. Smaller trees and shrubs tend to show greater densities

of spines compared to larger and more mature trees whose canopies are out of the reach of most browsers (Dagg & Foster, 1982; Pellew, 1984a; Cooper & Owen-Smith, 1986; Milewski *et al*., 1991; Gowda, 1996). The distinct height advantage of giraffe enables them to select leaves higher in the canopy than are available to most other browsers, hence increasing access to food.

The chemical composition of plants can both attract and deter browsers. Mammals select foods generally for their moisture, energy or nutrient quality, such as protein, fat or fibre content. The chemical composition of plants appears to be an important aspect of selection for giraffe, particularly as it may affect the palatability, nutrient quality and/or digestibility of the forage. For example, plant secondary metabolites, such as condensed tannins and phenols, reduce forage digestibility and protein availability (Robbins *et al*., 1987a & b). On the other hand, some authors suggest that the primary function of condensed tannins is to protect plant cell walls against microbial and fungal penetration rather than against mammalian herbivory (Cooper & Owen-Smith, 1985). Independent of this, higher levels of secondary metabolites often reduce the nutritional value of plants, and impede intake by herbivores.

Understanding the chemical composition of browse should provide insight into why and when browsers select certain foods based on their nutrient quality and digestibility. For example, giraffe selectively eat palatable and nutrient-rich forage when it is available seasonally (e.g. Sauer *et al*., 1982). They also select young shoots and leaves, as well as flowers and fruits, which are generally more digestible and higher in protein, minerals and soluble carbohydrates than mature leaves (Hall-Martin, 1974; Short, 1975; Vangilder *et al*., 1982; Pellew, 1984a).

Browsing pressure on preferred plant resources can be expected to be greatest in areas of herbivore concentration (du Toit *et al.*, 1990b). Surprisingly, however, the impact of heavy browsing may often result in the production of higher concentrations of foliage nutrients in severely browsed trees, and reduced levels of condensed tannins (du Toit *et al.*, 1990b). This 'feedback loop' suggests that increased browsing induces a physiological response in some woody species which increases the nutritional quality and palatability of foliage (du Toit *et al.*, 1990b). Browsing by giraffe has been reported to stimulate

increased production of *Acacia* shoots (Pellew, 1983c). Browsing also increases palatability in foliage re-growth (moose and birch—Danell *et al*., 1985; Danell & Huss-Danell, 1985; giraffe and *Acacia* spp.—du Toit, 1990c). In contrast, herbivory can also increase levels of tannin and lack of palatability of foliage (Leuthold & Leuthold, 1972; Hall-Martin, 1974). However, concentrations of condensed tannin are highly variable and differ markedly between plant genera and habitats (Sauer *et al.*, 1982), making generalisations difficult.

In the Hoanib River study area, giraffe were found to concentrate year-round in the riparian woodland (see Chapters 4 & 5), potentially causing increased browsing pressure on forage resources. They also exhibited short repetitive movements between forage sources (see Chapter 5), commonly returning to the same trees to forage each day. Preliminary evidence suggests that aggregations of giraffe and other wildlife such as elephant and oryx in arid riparian woodlands, coupled with the selective foraging behaviour of giraffe, could stimulate production of *Acacia* shoots (Pellew, 1983b). Furthermore, this foraging behaviour may increase the palatability and nutrient levels of foliage, while reducing concentrations of condensed tannins (du Toit *et al.*, 1990b).

The selection of nutritious forage and specific plant parts is likely to be crucial for bioenergetic maintenance in giraffe (Pellew, 1984a), especially in the northern Namib Desert where animals are at the extreme of their habitat range (Skinner & Smithers, 1990). Historically it was believed that the giraffe and other wildlife in the study region migrated in and out of the Namib Desert in search of seasonal forage (Bigalke, 1958). However, aboriginal rock art and evidence from Chapter 5 suggests that giraffe have foraged in the region year-round for an extensive period (Owen-Smith, 1970). No prior studies have examined the dietary selection, forage nutrient quality and impacts by giraffe on their forage sources in the Namib Desert.

Faidherbia albida (Del.) A.Chev., (formerly *Acacia albida* Del.), is frequently described as one of Africa's most important tree species for conservation in arid and semi-arid regions (CTFT, 1989). Its extensive natural distribution attests to its ecological adaptability, from southern Algeria to the Gauteng Province in South Africa, and from the Atlantic to the Indian Ocean (CTFT, 1989; BOSTID, 1990; Jacobson *et al.,* 1995).

Occurring throughout two major climatic zones (the dry Mediterranean and tropical), *F. albida* extends across an altitude range from below sea level to 2 500 m, and across highly variable rainfall conditions (0–1 800 mm per annum). Throughout much of Africa, particularly Namibia, *F. albida* is important as a supplementary food source for domestic stock and wildlife (CTFT, 1989; BOSTID, 1990; Jacobson *et al.,* 1995; SDP 2, 1996; Jacobson & Jacobson, 1998). In the dry season the leaves and pods of *F. albida* can provide up to double the amount of energy and an even larger amount of digestible protein than dry grass (CTFT, 1989).

This chapter explores aspects of giraffe foraging behaviour, with a focus on the Hoanib River study area. I first describe the seasonal food preferences of giraffe across the study region, and then analyse the nutrient quality of forage from the riparian woodland of the Hoanib River with respect to season and vegetative growth phases. I also reappraise the population dynamics and impacts of giraffe on their preferred forage species, *Faidherbia albida,* in light of current and previous research conducted in the Hoanib River (Nott, 1987; Viljoen & Bothma, 1990b; Jacobson & Jacobson, 1998).

7.1.1. Aims

This chapter investigates the foraging ecology of desert-dwelling giraffe. In particular, it investigates 1) forage selection by giraffe, 2) phenological growth phases of plants selected, 3) the nutrient quality of forage, and 4) population dynamics and structural change in the preferred forage species, *Faidherbia albida*. Each study area was treated as a separate unit when collecting forage selection data (aim 1), but due to limited sampling in two of the river systems, only the Hoanib River study area could be used for detailed analyses of aims 2–4. These investigations should provide insight into whether giraffe track seasonal changes in plant phenology and nutrient quality, and provide a better understanding of population dynamics and structural change in the Hoanib River population of *F. albida* over the past three decades.

7.2. Methods and materials

7.2.1. Definitions

In much of the literature on the foraging behaviour of herbivores, particularly in the African literature, terms such as 'forage selection', 'dietary selection', 'food choice' or 'food preference' are often used interchangeably to mean the same thing (e.g. Skinner & Smithers, 1990; Owen-Smith, 1994; Fryxell, 1995; Hume 1999). However, in the broader literature there are subtle differences in the usage and meaning of these terms. Before proceeding further, it is important to provide a brief summary of some of these differences and to define the meanings of the terms used in the present study.

At the simplest level, the 'use' or 'usage' of a food resource is usually taken to mean that an animal eats the type of food in question. There is no further implication that the food is eaten in a particular way or under any particular circumstances. If a certain type of food is 'selected', or 'chosen', this is often taken in the broader literature on foraging behaviour to indicate that that food is eaten more often, or in greater quantity, compared to its availability in the environment (e.g. Pellew 1983a; Owen-Smith & Cooper, 1987; du Toit, 1990b). Selection (or choice) is often measured in a positive manner, but negative selection can be defined too. For example, if plant species *A* represents 10% of all available plants in a herbivore's environment, but is represented at 50% in the herbivore's diet, species *A* is clearly being selected for. Conversely, if species *A* forms only 1% of the herbivore's diet, it is being selected against by the herbivore. The magnitude of selection can be measured by quantifying different food types in the diet and in the environment, and by then expressing this in the form of a selection coefficient (e.g. Manly *et al*. 1993). If selection is detected, it is often possible to speculate on the processes that drive the observed pattern. However, merely showing that certain foods are selected cannot, of itself, reveal what those processes are. Detailed observations of foraging behaviour, the quality and quantity of all foods available in the environment, the herbivore's nutritional state and external forces such as competitors and predators may all be needed to understand how selection arises.

If an animal 'prefers' a certain type of food, this is usually taken to mean that it takes that food first, or in greater amount, compared to other types of food that are equally available. Types of food that are preferred will often be the same as those that are selected, but they need not be. For example, a herbivore may eat plant species *A* disproportionately more than other species in the environment because that species is preferred, but preference would be unaffected even if species *A* was eaten disproportionately less than other species and hence was selected against. This could arise if preferred food plants were difficult to access, located in dangerous places, or otherwise costly to obtain. Because preference can usually be measured only in strictly controlled situations where there are no competitors, predators or other enemies, and where different types of foods are equally abundant and available, food or dietary preference is most easily measured by observing individuals in the laboratory. Examples of preference studies include those by Murray & Dickman (1994 & 1997) on rodents or Nugent *et al*. (1990) on possums; other studies are summarised in Hughes (1993) and Krebs & Davies (1997).

In this study, it was not possible to quantify 'selection' of particular species of plants by giraffe because individuals range so far that no measure of availability could be realistically developed. Nor was it possible to study food 'preferences'; I had no way of imposing the strictly-controlled captive conditions needed to allow preferences to be identified, nor was there any retrospective means of disentangling the suite of forces likely to be affecting the dietary preferences of giraffe in the field. Hence, my descriptions of the food plants eaten by giraffe refer simply to 'use' of those plants in the strict sense noted above. Although the terms 'selection' and 'preference' have been used on occasions throughout the text, this has been in accordance with their common usage in the herbivore literature and is not intended to connote the stricter definitions used in the broader field.

7.2.2. Seasonal forage selection

The plant species eaten by giraffe were recorded incidentally each season while undertaking research on activity budgets. Observational data were collected over a two year period, predominantly from a vehicle, although sometimes on foot. Plant species selected by giraffe were mostly identified by sight, but some were collected if they could

not be identified directly. Foraging observations by giraffe were pooled across sex and age classes to ascertain seasonal shifts in use of preferred species. In hindsight, separating sex classes would have been beneficial and enabled more refined analyses.

For analysis, forage selection and nutrient content of leaves (see below) were compared seasonally. Seasonal shifts in forage selection were also compared with vegetative growth phases (phenological changes) in the selected plant species. Based on observed phenological changes, the hot-dry season was split into the early (September–December) and late (January–February) hot-dry season for part of the analysis, as observations suggested that giraffe shifted their use of plant species during this long season.

I evaluated forage selection between seasons and plant species using Chi-squared tests. Due to the variance in forage observations between the seasons, the frequency data from all seasons were combined and forage use weighted in proportion to seasonal use. When giraffe fed upon the same plant species in two or more seasons, differences in degree of use were also tested by Chi-squared.

7.2.3. Chemical analysis of giraffe forage

A variety of chemical-based analyses (Dagg, 1959; Sauer *et al.,* 1977; Pellew, 1984a; Hall-Martin, 1975; Hall-Martin & Basson, 1975; Caister *et al.,* 2003) were used to investigate the constituents of giraffe food. Due to the broad nature of the study and financial constraints, forage was not analysed for secondary chemicals. However, it should be noted that secondary chemicals may play an important role in selection of forage by giraffe (Pellew, 1984a). Collection of forage samples from the Hoanib River focused on five plant species known to be eaten by giraffe from previous work (Scheepers, 1992; Fennessy *et al.,* 2003) and from preliminary observations made during the present study (Table 7.1).

Samples of the five plant species were collected monthly over a one year period (August 2002 to July 2003) at five sites along a distance and altitude gradient in the Hoanib River (Table 7.2). Not all species were available for collection at each site, with *Cordia sinensis* being collected only at three and *Combretum wattii* at four sites. The first sample site was

at the entrance to the Hoanib River floodplain, 25 km east of the Atlantic Ocean. Sampling was then undertaken at four additional sites east (up-river) along the Hoanib River, each 10 km apart. Samples were collected at first light or soon after to retain the maximum moisture content at the time the giraffe usually fed. Determining the moisture content on collection (wet weight) was an important aspect of this study.

Table 7.1. Plant species eaten by giraffe that were analysed for moisture and nutrient content, Hoanib River study area.

Plant species		Plants sampled	
Scientific name	Common name	Leaves, shoots & inflorescence*	Pods
Faidherbia albida	Ana, Winter thorn	Yes	Yes
Acacia tortilis	Umbrella thorn	Yes	-
Salvadora persica	Mustard tree	Yes	-
Combretum wattii	Round-leaved bushwillow	Yes	-
Cordia sinensis	Grey leaved saucer-berry	Yes	-

*Inflorescences were included in the sampling in the month/s eaten by giraffe

The sampling attempted to simulate the foraging behaviour of adult giraffe, and therefore samples were collected by a combination of hand pruning and clippings. 100g of potential forage was sampled from a range of giraffe browsing heights, between ground level and six metres, and new growth, inflorescences or pods were included when present. Pods of *F. albida* were collected separately along the transect and samples pooled for analysis.

The Namibian Ministry of Agriculture laboratory in Windhoek carried out the preparation and chemical analyses of the forage samples. The analyses were undertaken in accordance with the Agri Laboratory Association of Southern Africa (ALASA) methods (Palic *et al*., 1998) to guarantee standardised results. All sample results were converted to a percentage of dry matter, with standard deviation, for comparison with other published studies.

Table 7.2. Location, GPS co-ordinates and altitude of sample sites for species of giraffe forage, Hoanib River study area.

Site	Location description	East	South	Sampled Forage	Distance (km) from coast	Altitude (m)
1	Hoanib floodplain entrance	13.04761	19.38311	*F.a, A.t, S.p*	25	221
2	SCP entrance	13.12318	19.36523	*F.a, A.t, S.p, C.w*	35	260
3	b/w Amspoort & Mudorib Rivers	13.20640	19.33690	*F.a, A.t, S.p, C.w, C.s*	45	292
4	b/w Mudorib & Obias Rivers	13.26710	19.30905	*F.a, A.t, S.p, C.w, C.s*	55	324
5	b/w Obias & Ganamub Rivers	13.32801	19.26271	*F.a, A.t, S.p, C.w, C.s*	65	367

N.B. *Faidherbia albida (F.a); Acacia tortilis (A.t); Salvadora persica (S.p); Combretum wattii (C.w); Cordia sinensis (C.s).*

7.2.3.1. Sampling and preparation methods

On collection, all plant samples were weighed (W_2) in the field using a compact precision field balance (Ohaus CS-200) with a linearity of ±0.1 g. The samples were air dried and stored in a clean labelled container or brown paper bag, away from direct sunlight, and then transported to the Namibian Ministry of Agriculture laboratory in Windhoek.

In the laboratory, the samples were placed on an open weighing vessel (W_1) and dried in a convection oven for five hours at 105ºC. After cooling, the dried sample (W_3) was then weighed while still on the weighing vessel.

The moisture content and dry matter of the samples was calculated:

$$\text{Moisture (\%)} = [(W_2 - W_3)/(W_2 - W_1)] \times 100$$

$$\text{Dry Matter (\%)} = 100 - \text{moisture (\%)}$$

where:

W1 = dish (without lid)

W2 = sample + dish

W3 = sample + dish after drying.

Representative portions of the 100g collected for each forage sample were then milled to pass through a sieve of <1 mm diameter. Additional quantities of milled samples were made in case any re-analysis was needed, however, due to unforeseen circumstances some analyses were unable to be repeated (W. Gawa!nab personal communication). All methods of chemical analysis described below were synthesised from the Agri Laboratory Association of Southern Africa (ALASA) handbook (Palic *et al*., 1998).

7.2.3.2. Crude Fibre (CF)

One gram of each dried and milled sample (m) was weighed to 0.0001 g and placed into a marked crucible. The crucible was then placed in a hot extraction unit, and cooling water turned on before 150 cm^3 of preheated (ca. 95°C) sulphuric acid solution was added. Three drops of *n*-octanol (anti-foaming agent) were then added and the heating element turned on full. After bringing to the boil, the crucible was boiled for 30 minutes. After suctioning excess water, the crucible was rinsed three times in 30 cm^3 of hot distilled water. Preheated sodium hydroxide (150 cm^3) was then added. Another three drops of *n*-octanol were added after bringing to the boil, and again boiled for 30 minutes. After filtering by vacuum, the crucible was rinsed three times in 30 cm^3 of hot distilled water. The crucible was then rinsed a further three times with 20 cm^3 acetone to remove any residual water, and placed in a crucible holder in a drying oven. Allowed to dry overnight at 105°C, the crucible was cooled in a desiccator for 30 minutes and weighed (W_1=RCD). The crucible was then placed in a cool furnace at 500°C and the sample ashed for a minimum of four hours. After cooling and placement in a desiccator for 30 minutes, the sample was again weighed (W_2=RCA). Afterwards, the amount of crude fibre was calculated:

$$\text{Crude Fibre (\%)} = [(W_1 - W_2)/m] \times 100$$

where:

W_1 = mass of residue in crucible after drying (g)

W_2 = mass of residue in crucible after ashing (g)

m = mass of original sample (g).

7.2.3.3. Crude Protein (CP)

Between 0.1 and 0.5 g of each plant sample was digested with concentrated H_2SO_4 in the presence of catalysts that increase the boiling point of sulphuric acid. During this process all nitrogen present was converted to ammonia (NH_3), which reacted with the excess of acid to form ammonium sulphate [$(NH_4)_2SO_4$]. During the nitrogen distillation, ammonia was liberated by adding sodium hydroxide (NaOH) to the digest. It was then distilled off and collected in an excess of boric acid. The quantity collected was determined by titrating the borate formed with 1 M hydrochloric acid (HCl). The crude protein in the forage sample was calculated from the nitrogen present in the protein, using the Kjeldahl procedure. Two assumptions were made in calculating the protein content: 1) all the nitrogen of the sample was present as protein, and 2) all sample protein contained 16% nitrogen. The nitrogen content was then multiplied by 6.25 to give the crude protein content.

7.2.3.4. Calcium (Ca) & Phosphorus (P)

Between 1 and 3 g of air dried sample were weighed to 0.0001 g, and placed into a porcelain crucible. The crucible was placed in a muffle furnace at 550ºC overnight and the sample ashed. The sample was then cooled, dissolved by adding 5 cm^3 of 6 M HCl and evaporated to dryness on a waterbath. After cooling, 5 cm^3 of HNO_3 was added and heated on a waterbath to boiling. Finally, the solution was washed through filter paper into a 100 cm^3 volumetric flask, cooled, and diluted to volume with deionized water and mixed well. Determination of calcium in the sample was made by atomic absorption flame spectroscopy, while phosphorus content was determined by colorimetry (Palic *et al.*, 1998).

7.2.3.5. Total Ash

A pre-dried, marked and weighed crucible (W_1) was filled with 2 g of dried and milled sample weighed to 0.0001 g (W_2). The sample was then ashed on a small flame and the

ash placed in a muffle furnace at 550ºC for four hours or until the ash was white, indicating that no carbon traces remained. After cooling, the sample in the crucible was then weighed (W_3). The amount of total ash was calculated:

$$\text{Total Ash (\%)} = [(W_3 - W_1)/(W_2 - W_1)] \times 100$$

where:

W_1 = mass of pre-dried crucible

W_2 = mass of sample + crucible

W_3 = mass of sample + crucible after ashing.

7.2.3.6. Crude Fat

Using the Soxhlet method, 2 g (±0.0001 g) of dried and milled sample (m) was first placed onto filter paper, folded, and the enclosed sample placed in an extraction thimble so that it would intermittently be totally immersed in petroleum ether. A clean and dried (at 105ºC) Soxhlet flask (MF) was then connected to the extraction apparatus filled with two-thirds petroleum ether. The thimble was placed in the extractor with a firm cotton wool plug and the temperature was adjusted to achieve the appropriate condensation of ether. Once finished, the Soxhlet flask with extracted residue (MFR) was placed in a cold, explosion-proof oven that was then heated to 105°C. The flask was left in the oven for one hour after the target temperature was reached. After cooling, the amount of crude fat per sample was calculated:

$$\text{Crude Fat (\%)} = (MFR - MF/m) \times 100$$

where:

MF = mass of flask (g)

MFR = mass of flask with extracted residue (g)

m = mass of original sample (g).

7.2.3.7. Metabolised Energy (ME)

The gas test (in vitro digestibility method) was used to measure the metabolised energy of the plant samples, following methods outlined by Menke *et al.* (1979) (*in* Palic *et al.*,

1998). Metabolised energy (ME, MJ/kg) was calculated from the gas production and the contents of crude protein and crude lipids of the sample.

7.2.4. Statistical analysis

Seasonal and site differences in sample moisture, nutrients and energy were evaluated using analyses of variance. Each of the chemical components, such as moisture, crude protein and calcium, was analysed separately from pooled samples of forage, but individual plant species were also analysed to explore seasonal or between-site differences in chemical composition.

Prior to ANOVAs, data were checked for normality and transformed if appropriate: all percentage data were transformed by arcsine. As season and site were the variables of interest, two-factor analyses of variance were used for comparisons of all the chemical constituents of food plants. *Cordia sinensis* and *Combretum wattii* were not present at all five sites along the sampling transect, reducing the degrees of freedom and hence power to detect main effects and interactions for these taxa. Post-hoc tests to identify the source of significant *F*-ratios used Tukeys HSD test (Quinn & Keough, 2002). Analyses were carried out using Systat version 9.01.

7.2.5. Population dynamics of *Faidherbia albida*

I collected bio-data on more than 1 800 *F. albida* trees along the Hoanib River, covering more than 60 km. The data collection was undertaken with the assistance of local and international volunteers and researchers over a three-month period. GPS co-ordinates were recorded for every tree using a hand-held Garmin II *plus* logger and bio-data stored in a Microsoft Excel Professional 2000 database. Following seasonal rainfall events, the transect was re-surveyed to evaluate the number of prostrate and dead *F. albida* trees.

This study also reappraised the historical population dynamics of *F. albida* in the Hoanib River. In 1982 (Viljoen & Bothma, 1990b), 1987 (Nott, 1987) and 1995 (Jacobson &

Jacobson, 1998), assessments were made of the structure, distribution, mortalities and impacts by elephant on *F. albida* in the Hoanib River, although varying survey methods were used and comparative analyses limited. No previous studies used total counts as undertaken in this study. I collected bio-data on:

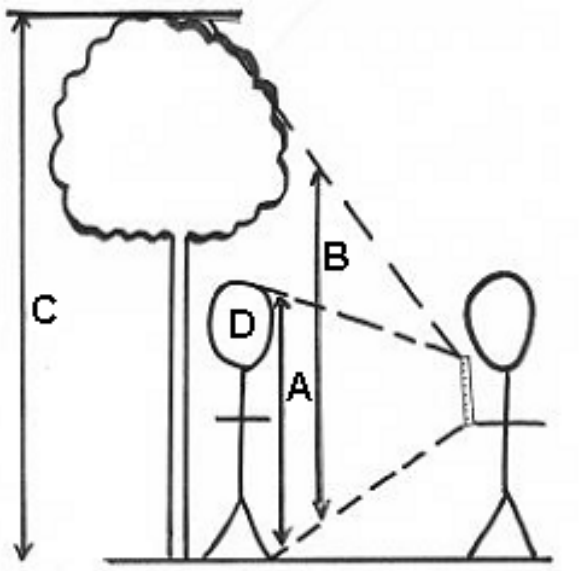
7.2.5.1. Stem number and circumference

Faidherbia albida was the predominant single-stemmed tree species along the Hoanib River, although numerous multi-stemmed *F. albida* trees were observed. When a tree was divided into separate stems at ground level or below one metre, the number of stems was recorded. The circumference of each stem was measured at one metre above the ground or above any buttress swelling. Where debris had collected around the base of the tree and measurement was not possible, the diameter was measured and later converted.

7.3.5.2. Height

Numerous methods were trialed to obtain a quick and accurate estimate of tree height. Methods included: placing a person of known height at the base of a tree and estimating how many times they 'fit' into the tree's height, and using an inclinometer. However, these methods proved either too laborious or inaccurate for large numbers of trees. As a result, the field method depicted below (Figure 7.1) was developed, and this proved to be both reliable and accurate.

The method was based on assessing the ratio of a person of known height to the top of the tree. The height of the person standing at the base of tree was established in relation to a ruler, which was held at arm's length. Using the same method, the relative height of the tree was estimated. The actual height was later calculated from the ratio of the ruler estimates and known height of the person.



Formula: (B/A) x D = C

where:

A = estimated height of person standing at base of tree with ruler at arm's length
B = estimated height of tree in relation to the ruler held at arm's length
C = estimated height of tree
D = actual height of person

Figure 7.1. Simplified stick figure diagram of method used to estimate the height and browse height of *F. albida*.

7.2.5.3. Damage

Giraffe, elephant and flood events all impact on the structure and growth of *F. albida* in the Hoanib River study area. An assessment of this damage was undertaken using the following classifications:

- Leaf stripping (LS): low level damage, probably caused by herbivores, resulting in some tree branches being stripped of some or all of their leaves.
- Branch breaking (BB): moderate level damage, again caused by herbivores, resulting in some tree branches being broken, either at the main stem or at the ends of larger branches.
- Main stem breakage (MSB): high level damage, resulting in the main stem of the tree being broken either at the base or along its stem.
- Bark stripping (BS): low to high level damage, caused by herbivores, with bark being removed from the tree stem. The following categories and percentages of damage were used:

  (1) = 0–12% (2) = 13–25% (3) = 26–50% (4) = 51–75%

  (5) = 76–86% (6) = 87–95% (7) = 96–100%

  The percentage categories refer to the overall areas of bark that were stripped.
- Uprooting (UR): tree that had been uprooted and was still alive.

- Standing dead (SD): dead tree still standing upright.
- Lying down dead (LDD): dead tree lying down; log.

An age assessment of the bark damage was categorised as either recent (less than one month), current year and >1 year. New (green) scars highlighted recent damage where herbivores had removed bark, current year damage showed no new scars or vascular cambium re-growth, and for damage greater than one year the vascular cambium was beginning to grow over the scar.

7.2.5.4. Browse heights

One structural change to trees that is caused by giraffe and other animals is the browse line. Browse line height is a good indicator of which species are present. Giraffe are able to feed higher than most other wildlife or domestic stock in the study region, aside from elephant, although only giraffe prune trees to create distinct browse lines greater than five metres. The height to which each *F. albida* tree had been browsed was estimated using the same method as described before (see Figure 7.1). Browse heights were defined as the distance from the ground to the lowest unbrowsed part of the canopy.

The results were categorised into one of three height categories:
(i) 0–1.5 m (ii) >1.5-3 m (iii) >3 m.

7.3. Results

7.3.1. Seasonal forage selection

Throughout the study, giraffe were observed feeding on a total of 29 different plant species: 23 woody species, five annual forbs and one grass species (see Appendix 15, 16 & 17 for species eaten in each of the study areas). In the Hoanib River study area giraffe fed on 19 different species of woody plants; 15 species were foraged in the Hoarusib River and 12 in the Khumib River study area. The decrease in woody plants foraged between the

Hoanib and the Khumib River study areas corresponded with increased aridity, smaller size of the study area and hence reduced availability of forage (personal observation).

Giraffe varied their diet seasonally. *Acacia tortilis, A. erioloba*, *Faidherbia albida, Salvadora persica* and *Balanites welwitschtii* (the latter species occurring only in the Hoarusib River study area) were the dominant year-round food sources (Figure 7.2; also see Appendix 16 & 17), with *Acacia tortilis, F. albida* and *S. persica* accounting for 60–70% of the diet of giraffe in both the Hoanib and Hoarusib River study areas.

Observations of foraging were limited in both the Hoarusib and Khumib River study areas, thus precluding strong inference (see Appendix 15). However, analyses indicated that selection of *F. albida, A. erioloba, S. persica, Colophospermum mopane, Maerua schinzii, B. welwitschii* and *Combretum imberbe* by giraffe did not differ markedly between seasons in the Hoarusib River study area. Selection of *Combretum wattii,* on the other hand, did differ between the seasons (χ^2=29.826, d.f.=2, P<0.001), while the selection of *E. pseudebenus* (χ^2=8.33, d.f.=1, P=0.004) was greater in the hot-dry season compared to the cold-dry season. Equivalent analysis could not be undertaken for the Khumib River study area.

In the Hoanib River study area, giraffe showed no seasonal selection of *F. albida, A. tortilis*, *C. wattii, Cordia sinensis, M. schinzii* and *Tamarix usneoides* (Table 7.3). *Faidherbia albida* formed a major part of the giraffe's year-round forage intake, accounting for 26–28% each season (Figure 7.2; also see Appendix 15). Despite this seasonal similarity, distinctive differences in giraffe selection of *F. albida* were observed on a monthly basis (Figure 7.3a). Peaks in consumption corresponded with new growth of *F. albida,* especially with flushes of leaves following local rainfall, and an increase in use of *F. albida* pods in the late hot-dry season (Table 7.4; also see Appendix 15). Preference for *F. albida* pods was higher in the hot-dry than in other seasons (χ^2=6.382, d.f.=2, P<0.041).

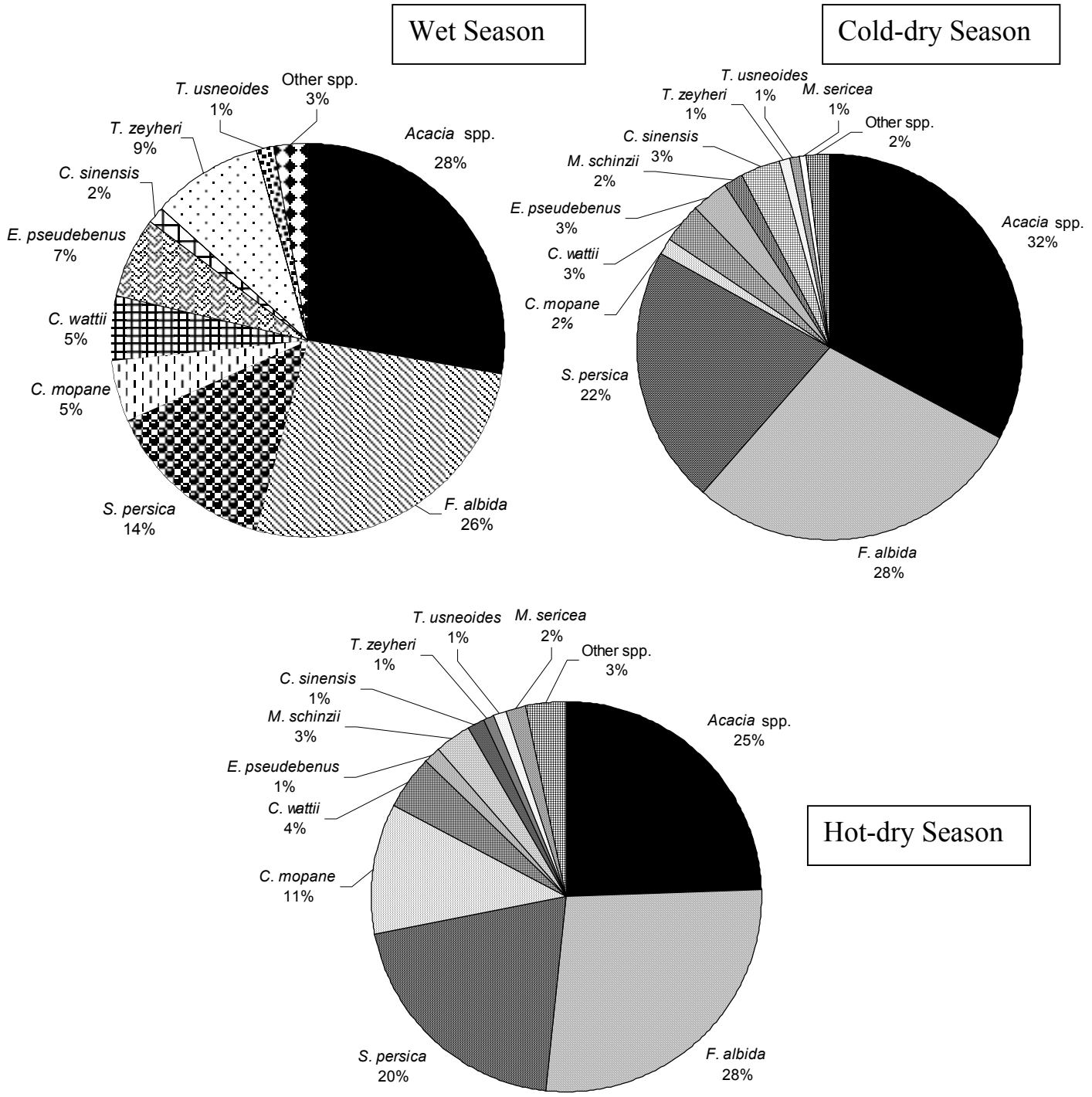


Figure 7.2. Seasonal selection of different plant species by giraffe in the Hoanib River study area, expressed as percentages of total numbers of foraging observations.

Table 7.3. Seasonal differences in selection of different plant species eaten by giraffe in the Hoanib River study area, assessed by Chi-squared tests on total numbers of foraging observations.

	d.f.	χ^2	*P*
Woody species			
Faidherbia albida	2	3.864	0.145
Faidherbia albida (pods)	2	6.382	0.041
Acacia tortilis	2	1.440	0.487
Salvadora persica	2	7.294	0.026
Combretum wattii	2	2.218	0.330
Cordia sinensis	2	4.222	0.121
Colophospermum mopane	2	31.649	<0.001
Euclea pseudebenus	2	17.783	<0.001
Tamarix usneoides	2	0.615	0.735
Maerua schinzii	1*	1.800	0.180
Forb species			
Tribulus zeyheri	2	28.488	<0.001
Mundulea sericea	1*	1.600	0.206

*wet season not included in analyses as this species was not observed to be eaten then.

Acacia spp. in the Hoanib River study area, predominantly *A. tortilis*, were equally important as year-round forage sources for giraffe as *F. albida* (comprising 25–32% of the seasonal diet) (Figure 7.2; also see Appendix 15). However, as with *F. albida,* selection of *A. tortilis* fluctuated strongly on a monthly basis, corresponding with flushes of new leaves in the wet season and inflorescences and pods in the cold-dry season (Table 7.4; Figure 7.3a).

Colophospermum mopane was eaten mostly in the hot-dry season (χ^2=31.649, d.f.=2, *P*<0.001) (Table 7.3; Figure 7.2). The leaf flush in the early hot-dry season (Table 7.4), and another in the wet season corresponded with increased consumption by giraffe.

Selection of *S. persica* by giraffe also differed significantly between seasons (Table 7.3), increasing in use from the wet to the dry seasons (Figure 7.2 & 7.3a). Similarly, another evergreen species, *E. pseudebenus,* was selected predominantly in the late hot-dry and

early wet season (χ^2=17.783, d.f.=2, P<0.001) (Figure 7.2 & 7.3b). This seasonal selection of *E. pseudebenus* was probably due to its increased palatability in the late hot-dry period.

Mundulea sericea, a fibrous perennial forb, was eaten by giraffe only in the late cold and early hot-dry seasons when flowering (Figure 7.2 & 7.3b). The selection of *T. zeyheri,* another forb, during the wet season could be attributed to its new growth following seasonal rainfall and consequently increased moisture content. Grasses were eaten only in the wet season (Figure 7.2 & 7.3b) when their moisture content is high and silica content lowest (Field & Ross, 1976). In general, grass formed a small part of the year-round diet of giraffe (<1.0%). While giraffe were observed foraging on several species of forbs in the Hoanib River study area throughout the year, including herb and vine species, non-woody species comprised a small percentage of their year-round diet.

In the Hoanib River study area, giraffe browsed more plant species in the dry seasons (19 in the cold-dry and 18 in the hot-dry), compared to the wet season (14). The increase in plant species diversity in the diet in the dry seasons was possibly due to a general reduction in the availability of deciduous and semi-deciduous species. Giraffe then needed to forage more broadly to maintain their energy and nutrient requirements.

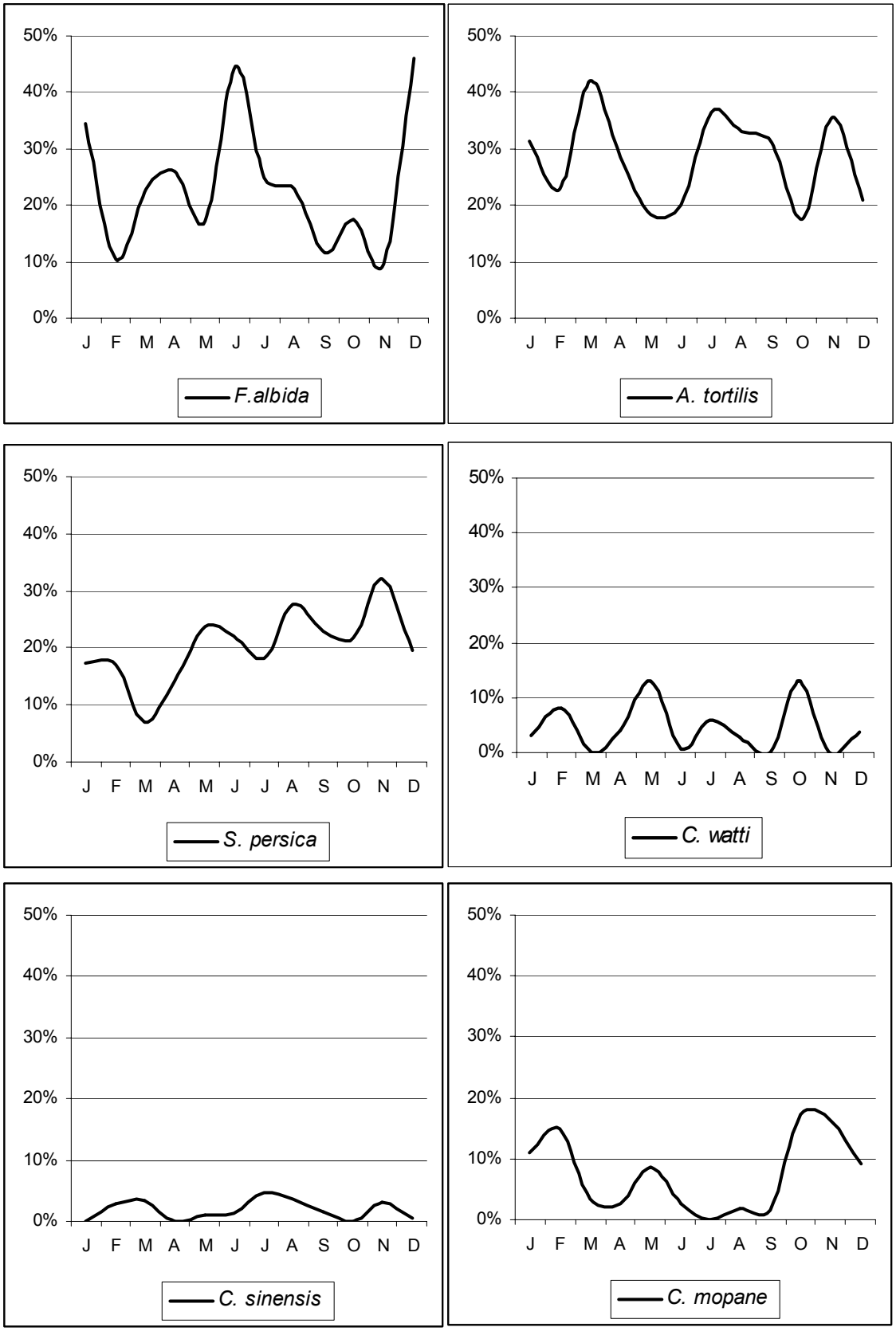


Figure 7.3a. Monthly selection of different plant species by giraffe in the Hoanib River study area, expressed as percentages of total numbers of foraging observations. Note seasons: wet (Mar to May); cold-dry (June to Aug); hot-dry (Sept to Feb).

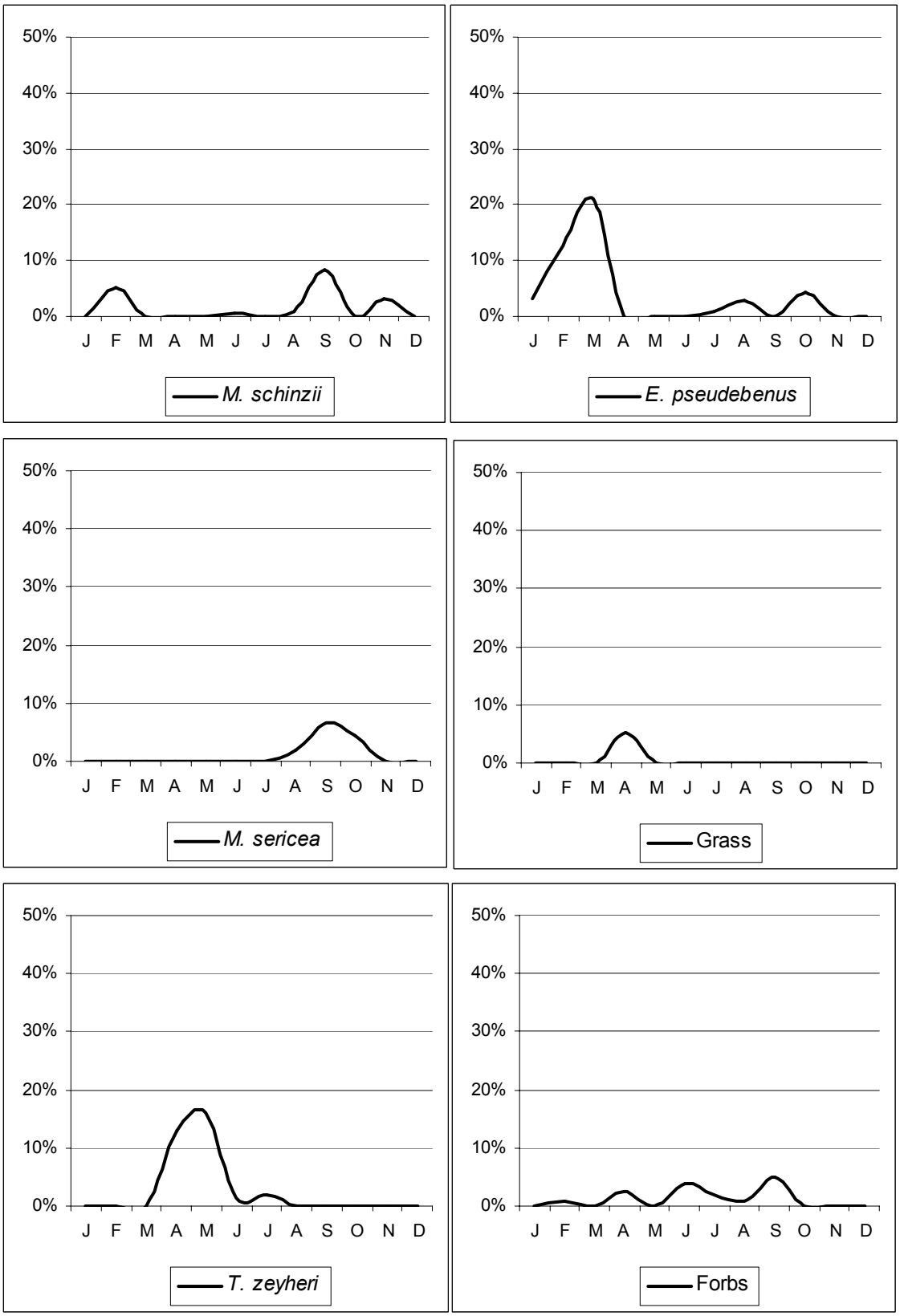


Figure 7.3b. Monthly selection of different plant species by giraffe in the Hoanib River study area, expressed as percentages of total numbers of foraging observations. Note seasons: wet (Mar to May); cold-dry (June to Aug); hot-dry (Sept to Feb).

Table 7.4. Phenological changes in woody plant species eaten by giraffe in the Hoanib River study area, 2001–2003 (adapted from Scheepers, 1992).

Season		New/active growth	Inflorescence	Podding
Wet		*F. albida*	*A. erioloba*	*A. erioloba*
		A. tortilis	*A. tortilis*	*A. tortilis*
		C. wattii		
		C. sinensis		
		C. imberbe		
		C. mopane		
		E. pseudebenus		
Cold-dry		*F. albida*	*F. albida*	*A. erioloba*
		A. tortilis	*A. erioloba*	*A. tortilis*
		C. wattii	*A. tortilis*	
		M. schinzii		
		Commiphora species		
Hot-dry	(early)	F. *albida*	*F. albida*	*F. albida*
		A. tortilis	*A. tortilis*	*C. wattii*
		S. persica	*S. persica*	
		C. wattii	*C. wattii*	
		C. sinensis	*C. sinensis*	
		C. mopane	*M. schinzii*	
	(late)	*F. albida*	*C. mopane*	*F. albida*
		A. tortilis		*C. wattii*
		A. erioloba		
		C. sinensis		
		C. mopane		
		E. pseudebenus		

7.3.2. Chemical composition of giraffe forage: pooled samples

After pooling of the five plant species chosen for detailed study, seasonal differences were found in moisture and phosphorus content, while site differences were found in crude protein and fibre (Table 7.5). No interactions were found between season and site. In general, the moisture content of plants increased in the hot-dry season in the Hoanib River

study area due to seasonal fog events, while the phosphorus levels were lower in the hot-dry compared to both the cold-dry and wet seasons. Similar shifts in phosphorus levels in giraffe forage were reported by Pellew (1984a).

Table 7.5. Statistical analyses of the chemical composition of giraffe forage sampled from the Hoanib River study area. Samples from five plant species were combined.

	Season			Site			Season*Site		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Moisture	2	18.548	<0.001	4	0.417	0.797	8	0.370	0.936
Crude Protein	2	1.165	0.314	4	5.189	<0.001	8	0.413	0.912
Crude Fibre	2	0.848	0.429	4	4.032	0.003	8	0.232	0.985
Calcium	2	2.028	0.134	4	0.500	0.736	8	0.243	0.982
Phosphorus	2	16.580	<0.001	4	0.665	0.617	8	1.111	0.356
Total Ash	2	0.463	0.630	4	1.450	0.218	8	0.086	0.999
Fat	2	0.312	0.733	4	1.633	0.166	8	0.519	0.842
ME†	2	1.411	0.246	4	0.221	0.927	8	0.266	0.976

†ME=metabolised energy

For all other chemical components, little seasonal variation was observed. Inspection of the site-based differences in crude protein and crude fibre failed to reveal any general trends in either component with distance or altitude along the gradient, as Tukeys HSD tests showed that adjacent sites differed as much from each other as did distant ones.

7.3.2.1. Chemical composition of giraffe forage: individual plant species

Seasonal differences were found in the chemical components of each plant species analysed (Tables 7.6 & 7.7), with the largest and most consistent differences observed for moisture content. Site differences between plant species were not as marked, with only crude protein, crude fibre, total ash, fat and metabolised energy showing differences in chemical components among some plant species (Table 7.6 & 7.7). *C. sinensis* showed no difference between sites for any of the chemical components, while *C. wattii* showed more difference between sites than seasons. Interactions between season and site were found only for the total ash and fat contents of *F. albida*, and indicated differences both between

sites in the same season, and between sites in different seasons. These interactions were not gradient- related.

Except for *S. persica*, the moisture contents of the sampled plant species were highest in the hot-dry season, followed by the wet season, and then the cold-dry (Table 7.6). *S. persica* held marginally more moisture in the cold-dry than in the wet season. The increase in moisture content in the hot-dry season contrasts with results from previously published studies (e.g. Hall-Martin, 1975). No significant differences in moisture contents between sites were observed.

Crude protein contents of *A. tortilis, C. wattii* and *C. sinensis* increased during the wet season and were lowest in the cold-dry (Table 7.6). The crude protein contents of *F. albida* and *S. persica* were highest in the cold-dry season, and least in the wet and hot-dry seasons respectively. Crude protein content differed between sites for *S. persica* and *C. wattii*, with results showing a trend for *S. persica* to become protein-rich from west to east.

Crude fibre contents differed markedly between the plant species sampled, and did not always correlate with shifts in crude protein. For example, the crude fibre content of *A. tortilis* increased in the hot-dry season and decreased in the wet season, while its seasonal crude protein content increased in the wet season and reduced in cold-dry (Table 7.6).

In contrast, the crude fibre and protein contents of *F. albida* increased in the cold-dry season and decreased in the wet (Table 7.6). Marked seasonal difference in the fibre contents of *F. albida* and *S. persica* were observed, due largely to increased levels in the cold-dry versus the wet season (Table 7.6). Crude fibre content differed between sites for *A. tortilis* and *C. wattii*, with *A. tortilis* showing a general trend in increasing crude fibre content from west to east along the transect (Table 7.6). No general trend can be inferred for *C. wattii*.

Table 7.6. Chemical composition of five plant species eaten by giraffe in the Hoanib River study area across three seasons. Data presented as percentages of dry matter contents (± standard deviation).

Species	Season	Moisture	Crude Protein	Calcium	Phosphorus	Crude Fibre	Fat	Total Ash	Metabolised Energy
F. albida									
	Wet	42.63±10.06	17.88±3.36	1.31±0.94	0.09±0.05	20.00±2.89	3.07±1.12	8.13±1.12	7.02±0.87
	Cold-dry	42.13±5.38	22.28±6.64	1.29±0.56	0.17±0.13	22.77±3.84	2.02±0.51	8.75±2.15	6.78±1.47
	Hot-dry	51.83±15.50	18.34±2.35	1.68±0.77	0.07±0.03	20.90±2.48	2.46±0.71	8.90±1.54	6.20±0.93
	Mean	47.03±13.30	19.22±4.45	1.49±0.85	0.10±0.08	21.15±3.00	2.51±0.93	8.65±1.66	6.57±1.11
A. tortilis									
	Wet	40.84±10.20	19.70±2.80	0.84±0.88	0.13±0.06	21.61±8.13	2.18±1.22	6.53±1.90	5.68±0.68
	Cold-dry	36.77±6.33	17.12±3.63	1.49±1.22	0.13±0.04	24.03±8.33	2.92±1.24	8.92±3.55	5.29±0.80
	Hot-dry	48.031±6.16	19.65±2.79	1.32±1.04	0.10±0.04	24.38±8.26	2.71±1.80	8.58±2.83	5.38±1.03
	Mean	43.62±13.70	18.64±3.06	1.21±1.16	0.11±0.05	23.17±8.17	2.62±1.45	7.98±3.03	5.42±0.95
S. persica									
	Wet	49.12±6.54	16.31±5.40	4.33±2.31	0.08±0.04	9.14±1.24	0.91±0.30	35.47±4.30	8.90±0.98
	Cold-dry	50.46±2.93	17.61±4.04	5.07±1.34	0.12±0.10	11.10±1.37	0.97±0.61	35.63±4.70	8.80±1.77
	Hot-dry	59.91±15.75	14.26±4.59	5.60±2.39	0.05±0.03	9.35±1.56	0.84±0.34	37.29±3.64	8.98±0.94
	Mean	54.68±12.65	15.97±4.92	5.14±2.04	0.07±0.06	9.74±1.53	0.89±0.41	36.41±4.06	8.91±1.18
C. wattii									
	Wet	45.46±9.60	15.44±2.42	0.71±0.23	0.15±0.09	31.29±3.29	1.64±0.64	12.10±4.65	5.93±0.88
	Cold-dry	37.90±5.11	14.00±2.62	1.79±0.82	0.17±0.12	30.70±4.22	1.99±1.51	16.36±4.62	5.93±1.18
	Hot-dry	54.79±14.82	14.59±2.86	1.13±0.71	0.11±0.03	29.15±3.18	1.73±0.85	13.33±4.16	5.68±0.91
	Mean	48.61±13.45	14.65±2.69	1.19±0.75	0.14±0.08	30.07±3.55	1.77±1.00	13.78±4.58	5.84±0.97
C. sinensis									
	Wet	49.40±7.68	19.24±3.98	1.35±0.51	0.23±0.11	17.04±2.95	1.68±0.47	12.83±1.28	7.35±1.26
	Cold-dry	42.62±2.40	15.69±3.66	2.15±1.03	0.17±0.06	18.23±1.33	2.51±1.02	14.83±2.94	6.60±1.12
	Hot-dry	59.15±14.91	18.50±3.10	1.99±1.51	0.16±0.05	16.43±2.15	1.69±0.74	15.40±2.44	6.66±1.26
	Mean	53.04±13.19	17.98±3.58	1.87±1.27	0.18±0.08	17.04±2.29	1.89±0.82	14.61±2.63	6.80±1.21

For both calcium and phosphorus, no significant differences were observed between sites (Table 7.7). However, the calcium content of *C. wattii* increased markedly between seasons, while phosphorus contents differed significantly between seasons for *F. albida, A. tortilis* and *S. persica* (Table 7.7). The calcium content of *S. persica* was considerably larger than that for any other of the sampled plant species (Table 7.6). Increased calcium contents were observed in both the cold-dry and hot-dry seasons, but did not appear to correlate with any of the other seasonal chemical fractions. The phosphorous content of *C. sinensis* was on average higher than for all other species, and also increased in the wet season. Although significant differences were observed in seasonal phosphorus contents of *A. tortilis, F. albida* and *S. persica*, little can be reliably inferred as the standard deviation for each of these sampled plant species was high (table 7.6).

The ash content of *S. persica* was markedly higher than that of any other species, while that of *F. albida* and *A. tortilis* were the lowest (Table 7.6). Ash contents for all plant species were lowest in the wet season when new vegetative growth was greatest, and higher during the dry seasons; this trend was most significant for *C. sinensis* (Table 7.7). Ash content differed between sites for *F. albida*, *A. tortilis* and *C. wattii,* each showing a general trend in increased ash content from west to east (Table 7.7).

A negative relationship between fat and ash content was found. *F. albida* and *A. tortilis* had the lowest ash and highest fat contents, while *S. persica* had the highest ash and lowest fat contents (Table 7.6). With the exception of *F. albida*, the fat contents of all sampled plant species were highest in the cold-dry season (Table 7.6). Marked seasonal differences in fat content were observed for *F. albida* and *C. sinensis* (Table 7.7), while differences between sites were found for *F. albida* and *C. wattii* fat contents. Few obvious trends were detected in the fat contents of the study plants, making it difficult to infer much from the analyses.

In general, metabolised energy (MJ/kg) increased in the wet season, correlating with new growth, and decreased in the dry seasons (Table 7.6). Significant differences between seasons and sites were found in the metabolised energy contents of *F. albida* foliage, but failure of post-hoc tests to discriminate among seasonal means and no clear trend among sites makes these differences difficult to interpret (Table 7.7).

Table 7.7. Statistical analysis of the chemical composition of five plant species eaten by giraffe by season and site (* $P<0.05$).

	Seasons			Site			Season*Site		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Moisture									
F. albida	2	3.383	0.043	4	0.561	0.692	8	0.254	0.976
A. tortilis	2	3.030	0.058	4	0.107	0.980	8	0.324	0.951
S. persica	2	4.679	0.014	4	0.534	0.534	8	0.099	0.999
C. wattii	2	5.849	0.006	3	0.454	0.716	6	0.322	0.920
C. sinensis	2	4.816	0.017	2	0.436	0.651	4	0.255	0.903
Crude Protein									
F. albida	2	5.586	0.006	4	0.941	0.448	8	1.429	0.211
A. tortilis	2	3.004	0.058	4	1.549	0.201	8	0.998	0.451
S. persica	2	3.010	0.057	4	8.228	<0.001	8	0.781	0.622
C. wattii	2	0.868	0.427	3	10.694	<0.001	6	0.296	0.935
C. sinensis	2	2.912	0.068	2	0.218	0.806	4	0.442	0.777
Crude Fibre									
F. albida	2	3.682	0.031	4	2.326	0.068	8	1.323	0.257
A. tortilis	2	0.375	0.689	4	27.890	<0.001	8	1.184	0.330
S. persica	2	10.713	<0.001	4	1.544	0.203	8	0.525	0.832
C. wattii	2	1.769	0.182	3	6.662	0.001	6	0.990	0.446
C. sinensis	2	2.099	0.139	2	0.683	0.512	4	0.580	0.679
Calcium									
F. albida	2	1.244	0.296	4	0.598	0.672	8	0.065	0.552
A. tortilis	2	1.237	0.298	4	1.266	0.294	8	0.679	0.707
S. persica	2	2.010	0.143	4	0.225	0.923	8	0.597	0.775
C. wattii	2	8.372	0.001	3	0.959	0.421	6	0.703	0.649
C. sinensis	2	1.135	0.334	2	0.230	0.796	4	0.807	0.532
Phosphorus									
F. albida	2	10.914	<0.001	4	0.621	0.650	8	0.346	0.942
A. tortilis	2	4.117	0.021	4	1.196	0.323	8	0.252	0.978
S. persica	2	7.576	0.001	4	2.273	0.073	8	0.867	0.551
C. wattii	2	3.037	0.058	3	1.825	0.157	6	1.890	0.109
C. sinensis	2	2.654	0.085	2	0.058	0.943	4	0.158	0.958
Total Ash									
F. albida	2	0.998	0.375	4	3.752	0.009	8	2.678	0.017
A. tortilis	2	2.701	0.076	4	5.636	0.001	8	0.706	0.684
S. persica	2	1.376	0.261	4	1.515	0.211	8	1.193	0.325
C. wattii	2	3.067	0.056	3	8.306	<0.001	6	0.503	0.802
C. sinensis	2	3.608	0.038	2	0.097	0.908	4	1.216	0.327
Fat									
F. albida	2	5.669	0.006	4	4.420	0.004	8	3.787	0.002
A. tortilis	2	1.056	0.355	4	0.224	0.924	8	0.609	0.766
S. persica	2	0.528	0.593	4	0.808	0.525	8	0.638	0.742
C. wattii	2	0.418	0.661	3	7.585	<0.001	6	1.838	0.119
C. sinensis	2	3.860	0.031	2	0.922	0.408	4	0.334	0.853
ME									
F. albida	2	3.580	0.034	4	3.434	0.014	8	0.412	0.908
A. tortilis	2	0.773	0.467	4	1.540	0.204	8	0.306	0.960
S. persica	2	0.026	0.974	4	0.262	0.901	8	0.488	0.858
C. wattii	2	0.772	0.468	3	2.350	0.085	6	0.543	0.722
C. sinensis	2	1.077	0.353	2	0.729	0.490	4	0.400	0.807

7.3.2.2. Chemical composition of *Faidherbia albida* pods

Giraffe increased their use of *F. albida* pods in the hot-dry season, in correspondence with the production of new pods with high moisture and protein content (Table 7.4 & 7.8; also see Appendix 15).

Table 7.8. Chemical composition of *F. albida* pods in the Hoanib River. Data presented as percentage of dry matter for new, mature and old pods.

	New pods*	Old (new) pods†	Old pods∞
Moisture	72.51	31.79	11.72
Crude Protein	14.53	13.95	11.92
Calcium	0.41	0.31	0.53
Phosphorus	0.08	0.07	0.10
Crude Fibre	27.48	23.90	26.76
Fat	0.78	1.37	0.59
Total Ash	5.75	4.57	4.27
ME	8.1	4.5	8.9

*ripened, on tree; †brown, newly fallen; ∞fallen, last season; ME=metabolised energy

7.3.3. Population dynamics of *Faidherbia albida*

The population structure and dynamics of *F. albida* varied along the length of the Hoanib River. *Faidherbia albida* was the dominant, single-stemmed species of large tree, and also the preferred forage source (with *Acacia* spp.) of giraffe in the study region (Figure 7.2; also refer to Appendix 15).

7.3.3.1. Numbers of *Faidherbia albida*

A total of 1 833 *F. albida* trees was counted along the length of the Hoanib River (Table 7.9). The number of trees per 5 km ranged from 45 to 350 individuals, with a mean of 203.7±100.8 s.d. trees per 5 km. The highest abundance of *F. albida*, 70 trees/km, was recorded near the Hoanib floodplain. An increase in tree numbers was strongly correlated

with distance from east (Dubis wetland) to west (Hoanib floodplain) (r = 0.982, P<0.001). Lower abundance of *F. albida* near the Dubis wetlands could be attributed to the higher water table, hence lowering the soil suitability and recruitment of *F. albida*, as well as increased numbers of domestic stock and grazing pressure around the wetland.

Table 7.9. Numbers of *F. albida* trees per 5 km along the Hoanib River (n=1 833).

	Dubis wetland						Hoanib floodplain		
	5 km	10 km	15 km	20 km	25 km	30 km	35 km	40 km	>45 km
n	45	121	98	181	234	284	295	350	225
% of total *F. albida*	2.45	6.60	5.35	9.87	12.77	15.49	16.09	19.09	12.27

Approximately 43% (n = 679) of trees with a diameter less than 0.5 m were single-stemmed. Multi-stemmed trees were prevalent along the river as a result of coppicing, which resulted in stands of 'bush' *F. albida* being formed. The number of stems per tree ranged from one to 34, with a mean of 2.75±2.8 s.d. (Table 7.10). A strong negative correlation (r =-0.827, P<0.001) was observed between stem numbers per tree and total number of trees.

Table 7.10. Number and percentage of *F. albida* categorised by stem number per tree in the Hoanib River (n = 1 576).

	Stems per tree							
	1	2	3	4	5	6	7	>8
n	679	299	197	146	86	61	39	69
% of stems	43.1	19	12.5	9.2	5.5	3.9	2.5	4.3

7.3.3.2. Heights of *Faidherbia albida*

Heights of *F. albida* in the Hoanib River ranged from seedlings (<0.1 m) to 38 m, with a mean of 14.88 m ±5.7 s.d. (Table 7.11). Mean heights were lower near the Hoanib floodplain, the area with most *F. albida*. Heights also differed at intervals along the Hoanib River (F=16.158, d.f.=8, P<0.001), but no clear correlation with distance was observed (r =-0.335, P<0.05).

Table 7.11. Mean heights (m) ± s.d. of *F. albida* trees per 5 km along the Hoanib River (*n* = 1 578).

	Dubis wetland								Hoanib floodplain
	5 km	10 km	15 km	20 km	25 km	30 km	35 km	40 km	>45 km
n	5	113	98	174	220	280	139	350	199
Mean height	13.53	12.60	16.76	15.17	15.81	12.39	14.29	13.94	11.19
± s.d.	±4.50	±4.62	±4.58	±4.68	±3.75	±6.45	±6.88	±6.93	±5.42

7.3.3.3. Size class distribution of *Faidherbia albida*

The size class distribution of *F. albida* was relatively even (Figure 7.4). Excluding dead trees and those less than 0.5 m tall, the recruitment observed during the study, measured as the number of trees with a diameter ≤ 20 cm was 9.2% (*n* = 139) of the population. The 21–40 cm size distribution class represented a further 7.1% (*n* = 106), while the largest age class structure (>120 cm) represented only 16% (*n* = 241) of the population.

Strong differences were observed between the size class distribution in this study and those previously reported (χ^2=272.62, df=12, P<0.001; Viljoen & Bothma, 1990b; Jacobson & Jacobson, 1998). The percentage of trees with diameters ≤ 20cm reported by Jacobson & Jacobson (1998) was 0.2% (*n* = 2), more than two orders of magnitude below the 30.1% reported by Viljoen & Bothma (1990b) and one order of magnitude below the 9.2% observed during this study. The 21–40 cm (*n* = 52) size class distribution in this study (7.1%, *n* = 106) was smaller than that reported by either Viljoen & Bothma (1990b) or Jacobson & Jacobson (1998).

This study found more *F. albida* in the three largest size classes [81–100 cm, 101–120 cm and >120 cm: 15.7% (*n* = 236), 11.5% (*n* = 173) and 16% (*n* = 241), respectively] compared to previous studies (Viljoen & Bothma, 1990b; Jacobson & Jacobson, 1998).

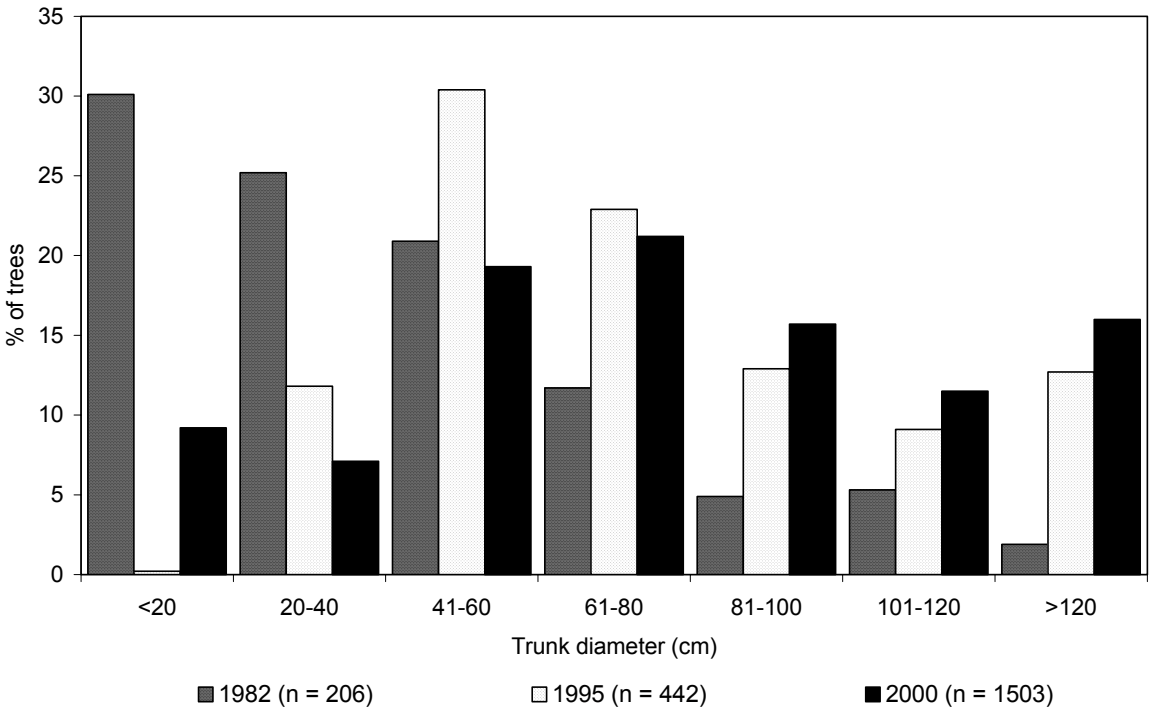


Figure 7.4. Historical and current size class distribution of *F. albida* in the Hoanib River, 1982–2000. Data presented as percentage of the surveyed population. Note 1982—Viljoen & Bothma (1990b); 1995—Jacobson & Jacobson (1998) and 2000—this study.

7.3.3.4. Damage, impact and mortalities

Leaf stripping and branch breaking were the most common categories of impact on *F. albida* in the Hoanib River, affecting 84.7% and 84.4% of trees respectively (Table 7.12). Of these trees, almost 100% had suffered both types of damage. Breakage of the main stem was observed on 14.8% of all trees, while only 0.4% was uprooted prior to the seasonal flood event.

Table 7.12. Impacts and status of *F. albida* in the Hoanib River (*n* = 1 678).

	Impacts and status categories (%)						
	LS	BB	BS	MSB	UR	LDD	SD
Hoanib River	84.7	84.4	57.8	14.8	0.4	3.3	1.7

N.B. LS – Leaf Stripping; BB – Branch Breaking; BS – Bark Stripping; MSB – Main Stem Breakage; UR – Uprooting; LDD – Lying Down Dead; SD – Standing Dead. Percentages add to> 100% because trees had often suffered more than one type of impact.

I found that 57.8% (n = 847) of *F. albida* displayed some degree of bark damage; 60.7% (n = 514) of these trees had less than 25% of their bark removed. In 89.3% of trees the damage was older than one year, in 41.6% damage had occurred within the last year; only 5.6% of trees had been damaged within the last month (Table 7.13).

Table 7.13. Age of bark damage of *F. albida* (as percentage) in the Hoanib River (n = 880).

	Age of Bark Damage		
	Recent*	Current Year	> 1 Year
% of bark damage	5.6	41.6	89.3

*within last month. Percentages add to> 100% because trees often exhibited bark damage at two or more different times.

The mean amount of bark damage on *F. albida* per 5 km ranged from three to 59% (Table 7.14). Most damage was observed close to the Dubis wetland, with a marked reduction 20 to 25 km downstream. Although the degree of bark use increased marginally near the Hoanib floodplain, a strong negative correlation between bark damage and distance along the Hoanib River was evident (r =-0.886, P<0.001).

Table 7.14. Bark damage on *F. albida*, expressed as means (%) on trees in 5 km sections along the Hoanib River (n = 880).

	Dubis wetland								Hoanib floodplain
	5 km	10 km	15 km	20 km	25 km	30 km	35 km	40 km	>45 km
% of bark damage	59	46	32	26	19	5	3	8	14

Few mortalities of *F. albida* were observed during my initial survey, with prostrate and dead trees comprising only 3.3% (n = 55) of the population and standing dead only 1.7% (n = 23). Less than five trees were ring-barked, which indicated a low impact of elephant. Following the exceptional wet season in 1999/2000, in which the Hoanib River flowed through the dunes and into the Atlantic Ocean, a re-survey of the population recorded 100 (6%) trees prostrate and dead *F. albida*. Seasonal flood events resulted in lateral channel erosion and mass wasting of the banks of the Hoanib River, which subsequently caused the uprooting of fifteen times as many trees as observed during the original survey.

7.3.3.5. Browse heights

The browse heights of *F. albida* were greater than 3 m for 81.03% (n = 1 465) of the population (Table 7.15), and resulted from the feeding of giraffe, and to a lesser extent, elephant. Along the river, seedlings and coppices of *F. albida* had been pruned by wildlife to form low 'bushes'; the majority of these plants had a browse height ≤ 1.5 m.

Table 7.15. Browse heights (m) of *F. albida* in the Hoanib River (n = 1 808).

	Browse height of trees (m)		
	≤ 1.5	>1.5-3	>3
n	341	2	1465
% of *F. albida*	18.86	0.11	81.03

High-level browsing, categorised as browse height greater than three metres, decreased close to the Hoanib Floodplain (r =-0.89, n=1808, df=8, P<0.001) (Table 7.16).

Table 7.16. Mean browse heights (m) (as percentage) of *F. albida* per 5 km along the Hoanib River (n = 1 808).

	Percentage (%) browsed								
	Dubis wetland								Hoanib floodplain
Browse height	5 km	10 km	15 km	20 km	25 km	30 km	35 km	40 km	>45 km
n	1	8	3	20	9	76	27	130	69
≤ 3 m (%)	5	6.61	3.06	11.05	3.86	26.67	22.50	24.81	30.53
n	19	113	95	161	224	209	93	394	157
>3 m (%)	95	93.39	96.94	88.95	96.14	73.33	77.50	75.19	69.47

7.4. Discussion

7.4.1. Forage selection and preference

The diet of giraffe varied between seasons and across the study region. Giraffe were observed feeding on 29 different plant species, 23 of which were woody plants. This is one of the least diverse diets reported for the species (Oates, 1973; Hall-Martin, 1975; Sauer *et al*., 1977; Berry, 1978; Pellew, 1984a; Ciofolo & Le Pendu, 2000) and can be attributed to the low diversity of woody plants in the northern Namib Desert; only 33 species occur in the study region (Viljoen, 1988 & 1989b). In spite of their restricted diet, giraffe clearly used a high proportion of the woody species available. Fewer observations were made in the Hoarusib and Khumib River study areas compared to the Hoanib, but the more restricted diets of giraffe in the former areas are likely to reflect, again, the low diversity of woody plant species available there.

Woody species generally comprise about 95% of the diet of giraffe (Field & Ross, 1976; Pellew, 1984a; Hansen *et al*., 1985; Caister *et al*., 2003). Across their range, giraffe eat some 45–50 different plant species per population (Oates, 1973; Hall-Martin, 1975; Berry, 1978; Pellew, 1984a; Ciofolo & Le Pendu, 2000). In Niger, the desert-dwelling giraffe forages on at least 45 different plant species, 35 of which are woody (Ciofolo & Le Pendu, 2000). The increased dietary diversity of these giraffe compared with the desert-dwelling giraffe of Namibia is partly a result of their seasonal movements between different habitats, which increased encounters with a broader range of plant taxa. Small-scale seasonal shifts in habitat use and selection of plant species were observed in the study region. However, as giraffe foraged predominantly in the riparian woodlands, their year-round dietary diversity was limited compared to giraffe in other populations.

In the Hoanib River study area, dietary diversity increased slightly in the dry seasons. Similar seasonal shifts in giraffe (e.g. Oates, 1973; Pellew, 1984a; Ciofolo & Le Pendu, 2000) and other ungulates (e.g. Casebeer & Koss, 1970) have been reported. New growth and increased availability of food in the wet season probably enabled giraffe to be more selective and, as a result, reduced the diversity of plant species foraged upon. During the dry seasons, evergreen species featured more prominently in their diet, perhaps because

they increased in palatability at these times compared to deciduous species (Ego *et al*., 2003), or simply because these are relatively more available. Some deciduous tree and shrub species, such as *Faidherbia albida, Acacia tortilis* and *A. erioloba*, grow more rapidly than evergreen species, are more successful in competitive situations (Coley, 1983), and appear to be eaten in preference when available (Hall-Martin, 1975; Sauer, 1983; Pellew, 1984a; Caister *et al*., 2003).

Some plant species, such as *Maerua schinzii* and *Commiphora* species, were eaten avidly when available but comprised a small fraction of the giraffe's year-round diet. In contrast, *Colophospermum mopane* was the dominant woody species in the study region and, although eaten year-round, it formed only a small component of the giraffe's yearly diet. The apparent avoidance of *C. mopane* by giraffe has been reported (Oates, 1973; Dagg, 1959) and has been attributed to this species' lack of palatability (Hall-Martin, 1974 & 1975; Sauer *et al*., 1982; Styles & Skinner, 1997). *Faidherbia albida,* by comparison, was abundant throughout the riparian woodlands, and it formed the largest percentage of the giraffe's year-round diet. Forage selection by giraffe in the northern Namib Desert clearly does not show a consistent link to plant species abundance, and may vary due to chemical composition or other factors. Observations from other giraffe populations indicate a similarly tenuous link between diet and the relative abundance of woody species (Oates, 1973, Hall-Martin, 1974 & 1975).

Shifts in the diet of giraffe in the northern Namib Desert, as reflected by the Hoanib River results, corresponded with seasonal growth of the selected forage. New shoots, leaves, inflorescences and/or pods, usually have reduced chemical defences and increased palatability (Oates, 1973; Hall-Martin, 1974 & 1975; Hall-Martin & Basson, 1975; Sauer *et al*., 1982; Sauer, 1983; Pellew, 1984a; Cooper & Owen-Smith, 1985; Cooper *et al*., 1988; Styles & Skinner, 1997; Caister *et al*., 2003). As expected, plant phenological changes often correlated with seasonal fog and rainfall. In the Hoanib River study area, higher moisture and nutrient levels (particularly crude protein) in the sampled forage species correlated with new growth and subsequent selection by giraffe. Giraffe continually modify their foraging behaviour, feeding on plant species with the densest clusters of new shoots, leaves, inflorescences and/or pods, and hence, effectively track moisture and protein content in their food (Pellew, 1984a). Both constituents have

previously been reported as the main influences on forage selection by giraffe (Hall-Martin, 1975; Hall-Martin & Basson, 1975; Sauer *et al*., 1982; Sauer, 1983; Pellew, 1984a).

Large variations in other chemical constituents have been reported between woody plants within and between habitats (Dagg, 1959; Hall-Martin, 1975; Hall-Martin & Basson, 1975; Sauer *et al*., 1977; Sauer *et al*., 1982), confounding attempts to interpret them. In this study, patterns of variation in fat, total ash and metabolised energy were difficult to evaluate. Furthermore, although seasonal increases in the calcium and phosphorus content of plant species were observed, it was not clear that giraffe responded to these in any way. Similarly, patterns of crude fibre ingestion were inconsistent, and may have impacted little on seasonal plant selection by giraffe (see section 7.4.4.1). Selection or avoidance of foods with crude fibre has been reported in giraffe (e.g. Field & Ross, 1976; McNaughton *et al*., 1985), while arid adapted eland *Tragelaphus oryx* seem to prefer forage with lower total fibre content (Watson & Owen-Smith, 2000; Watson & Owen-Smith, 2002). Fibre is regarded as a dietary deterrent for ruminants as it reduces forage digestibility (van Soest, 1967; Demment & van Soest, 1985). Increased crude fibre content also correlates with increased levels of secondary compounds, which further impede digestibility (Coley, 1983; van Essen *et al*., 2002). The inconsistent results for crude fibre in the present study may indicate that it is of less importance to foraging giraffe than other components of their food.

Overall, giraffe appear to track seasonal phenological changes in preferred plant species. This was measured by correlating preferred seasonal forage selection with nutrient quality and plant phenology. In the Hoanib river study area, giraffe selected different parts of *F. albida* and *A. tortilis* depending on seasonal growth. *A. tortilis* appeared to be selected for its new leaves in the wet season, and for pods in the cold-dry season. However, giraffe selected new leaves of *F. albida* in the wet/cold-dry season and inflorescences and pods in the hot-dry season. Seasonal shifts in selection of forage species were also observed. *Maurea schinzii* and *Mundulea sericea* were selected when available in the hot-dry season, and grass and *Tribulus zeyheri* in the wet season, in correspondence with new vegetative growth (shoots, leaves, florescence and/or pods). At no other time of the year were these plant species foraged in such large amounts.

7.4.2. Small-scale movements, habitat and diet

The majority of woody plant species in the Hoanib River exhibited new growth, flower and pod production along an east-west gradient. Small-scale movements by giraffe along the river correlated with shifts in phenology of these woody species and with subsequent shifts in diet. These movements also coincided with increased selection of *C. wattii* and *F. albida* during the early hot-dry season. Subsequently, giraffe moved east up-river in the early hot-dry season and then west down-river in the late hot-dry. The leaf flush of *C. mopane* in the early hot-dry season also corresponded with its increased inclusion in the diet of giraffe. As *C. mopane* was abundant in the middle to eastern section of the Hoanib River study area (personal observation), its availability, as well as leaf flush, most likely contributed to the observed movements of giraffe to exploit it.

Although giraffe were observed year-round along the Hoanib river riparian woodland, they aggregated in greater numbers there during the dry seasons (see Chapter 4). Increased use of the riparian woodland enables giraffe to maintain a high rate of energy, moisture and nutrient intake, particularly during the critical dry seasons when sustained production of new shoots with high moisture and protein content occurs relative to other habitats (Pellew, 1984a & c). Increased use of the river system in the hot-dry season by elephant (Viljoen, 1988 & 1989b; Leggett *et al*., 2001a & 2003a) may also increase resource competition, although minimal availability of free-water (before the construction of the artificial water points) has limited elephant movements along the length of the riverbed. Perhaps as a consequence, giraffe densities were greater in areas west of the mean daily range of elephant (Leggett *et al*., 2003a).

Although the riparian woodlands are the dominant foraging habitat for giraffe in the study region, seasonal use of mountain habitats also occurred. Thus, small-scale movements by giraffe were recorded in and out of the mountains in the Hoarusib River study area (see Chapter 5), as well as into the mountains and along the tributaries between the Hoanib and Hoarusib Rivers. It appeared that these movements coincided with seasonal fog (personal observation). This is not surprising, as the free moisture could make rarely utilised plants seasonally more abundant, palatable, moisture and nutrient-rich (Viljoen, 1988; Scheepers, 1992). Small-scale movements and selection of seasonal forage by giraffe would be

selectively advantageous; similar movements by elephant support the idea that this is an adaptive strategy (Viljoen, 1988; Leggett, 2004; personal observation).

7.4.3. Impact of fog precipitation in the northern Namib Desert

The moisture contents of the forage samples from the Hoanib River study area showed a marked increase during the hot-dry season. Following this, there was a general reduction in the moisture content of forage during the wet season, and then again in the cold-dry. During the hot-dry season, increased moisture content correlated with increased fog precipitation (personal observation). Similar peaks in fog have been reported in the central Namib Desert at the same time of year (Henschel *et al*., 1998).

In the central Namib Desert, fog peaks occur between August and January (hot-dry season), with fog recorded on 45% of days and yield an average of greater than two litres/m^2/day (Henschel *et al*., 1998). Hence, fog as a water source, was up to five times more prevalent than rainfall, with 30–180 mm of fog water being deposited per annum, occurring on 60–200 days per year (Pietruszka & Seely, 1985; Henschel *et al*., 1998; Seely & Henschel, 1998). Lancaster *et al*. (1984) reported that in the central Namib Desert there was an increase in fog-day frequency and precipitation 20–60 km inland, as well as at altitudes 200–500 m above mean sea level. The sample sites for giraffe food plants along the Hoanib River were at similar altitudes and distances from the Atlantic Coast to those reported for fog peaks in the central Namib Desert.

Based on the findings in the central Namib Desert, it is likely that the increased levels of moisture found in plant samples during the hot-dry season in this study correlated with increased seasonal fog. These increases would stimulate active vegetative growth and production of inflorescences as was observed in the five sampled species in the Hoanib River study area. Giraffe strongly prefer new shoots and leaves (Sauer *et al*., 1977; Sauer *et al*., 1982; Pellew, 1984a; Caister *et al*., 2003) and would benefit from exploiting them. Interestingly, the increase in moisture content of the sampled forage in the hot-dry season differs from that reported elsewhere; moisture content and associated chemical fractions are generally lowest in the hot-dry season (Oates, 1973; Hall-Martin, 1974 & 1975; Hall-

Martin & Basson, 1975; Sauer *et al*., 1977; Sauer *et al*., 1982; Pellew, 1984a). This presumably reflects the absence of fog in areas beyond the Namib Desert, and highlights the importance of this seasonal source of water in the study region.

The moisture content of the preferred plant parts of giraffe also differ markedly throughout the day (e.g. Sauer *et al*., 1982), with moisture levels rising from early evening, throughout the night and peaking in early morning when fogs occur and ambient temperatures are least. As giraffe concentrated their feeding during the early morning (see Chapter 6), they would maximise ingestion of water—this may be critical for maintenance of water balance.

Giraffe are not the only mammals to obtain necessary moisture from their forage in the arid Namib Desert. Despite their great differences in body size and energy requirements, giraffe and steenbok share similar preferences for *F. albida, Acacia* species and *S. persica* (Cloete & Kok, 1986; Scheepers, 1992; Fennessy *et al*., 2003) and, as their main source of moisture is dietary, both can live independently of surface water (Wyatt, 1969; Cloete & Kok, 1986; Seely, 1987). Moisture intake is supplemented by the incidental ingestion of precipitated fog whilst feeding. Neither their ability to concentrate urine, nor kidney morphology, suggest special renal adaptation in either species (Cloete & Kok, 1986; Scheepers, 1990), but common thermoregulatory behaviours, such as limiting energy consuming activities in the heat of the day, play a major role in their water conservation (Cloete & Kok, 1986; see Chapter 6).

7.4.4. Use of individual forage species

7.4.4.1. *Faidherbia albida*

Faidherbia albida is a leguminous tree species, widely distributed throughout Africa, that can flourish in areas by affected by a long, dry season (Roupsard *et al*., 1999). Its well-documented reverse phenology (see Dunham, 1991; CTFT, 1989; BOSTID, 1990 for reviews) enables it to be in leaf almost year-round, while growth and fruiting phases occur during the dry season, when most non-evergreen species offer little forage. *Faidherbia albida* acts like a facultative phreatophyte in the study region, enabling dry season growth

by the uptake of water from underground aquifers or deep soil layers (Ward & Breen, 1983; CTFT, 1989; Roupsard *et al*., 1999).

During this study, consumption of *F. albida* by giraffe peaked in the wet and again in the hot-dry season, in correspondence with different growth stages. Leaves were partially shed following the first rains and growth resumed only towards the end of the wet season. Giraffe increased their use of *F. albida* towards the end of the wet season when this new growth was most abundant. Although the nutrient quality of *F. albida* in the wet season was minimal, the moisture and crude protein contents were high compared to other forage species in the study area and, importantly, the crude fibre content was at its lowest. The crude fibre content was less than that of *A. tortilis,* and its reduced level in the wet season presumably correlated with an increase in plant use and digestibility. The high moisture content of *F. albida* in the hot-dry season has already been noted.

The seasonal use of *F. albida* pods by giraffe reflects their high seasonal abundance, moisture content and nutritional value. However, when available, the pods were used by giraffe year-round. The indehiscent pods of *F. albida,* as those of *Acacia* species, are an important forage source for giraffe, particularly in the dry season when they can comprise up to 65% of animals' dry weight intake (Gwynne, 1969; McNaughton & Georgiadis, 1986; Coe & Coe, 1987; CTFT, 1989; BOSTID, 1990; Dunham, 1991; Miller, 1994; Caister *et al*., 2003). The selection of pods in the hot-dry season correlated with new pod production as many old pods were still on the trees while others had begun to drop or had been shaken down by elephant. It should be noted that *F. albida* was not only an important year-round forage source for giraffe, but also a valuable shade tree. The trees' large size, reaching a height of up to 38 m with a similarly broad canopy, enabled giraffe to rest in their shade during the hottest periods of the day, thus increasing their aggregation in the riparian woodlands.

7.4.4.2. *Acacia* species

Throughout the study region *Acacia* species (*A. tortilis* and *A. erioloba*) formed one of the major forage resources for giraffe. *Acacia* species were relatively abundant along the

riparian woodlands and to a lesser extent on the adjacent plains. Without *Acacia* species (including *F. albida*) in the study region, it is unlikely that giraffe would be able to reside year-round at this extreme edge of their range.

As with *F. albida*, giraffe show a strong dependence on *Acacia* species as a valuable forage source, not only in the study region, but Africa wide (Dagg, 1959; Leuthold & Leuthold, 1972; Oates, 1973; Hall-Martin, 1974 & 1975; Hall-Martin & Basson, 1975; Field & Ross, 1976; Sauer *et al*., 1977; Dagg & Foster, 1982; Sauer *et al*., 1982; Sauer, 1983; Pellew, 1984a; Bond & Loffell, 2001; Ciofolo & Le Pendu, 2002; Birkett, 2002). The importance of *Acacia* species in giraffe diet has been attributed to many factors, such as the abundance and diversity of *Acacia* trees (Midgley & Bond, 2001), their high moisture and protein contents (Hall-Martin, 1974; Hall-Martin & Basson, 1975; Sauer *et al*., 1982), relatively low levels of secondary chemical compounds (Cooper *et al*., 1988), and increased shoot production stimulated by giraffe browsing (Pellew, 1983c).

Within the Hoanib River study area, giraffe showed focused foraging on *Acacia* species, seasonally selecting new growth when available to exploit its high moisture and crude protein contents (e.g. Hall-Martin, 1974 & 1975; Pellew, 1984a; Ciofolo & Le Pendu, 2002). A reduction in *A. tortilis* in the diet in the late wet season correlated with reduced levels of crude protein and a concomitant increase in the availability of other species, such as *F. albida*.

The nutrient quality of *A. tortilis* in the Hoanib River study area was relatively constant year-round, although there was an increase in crude protein content during the wet season. The increased use of *A. tortilis* by giraffe in the cold-dry season correlated with relatively high levels of crude protein, phosphorus and ash, as well as with continued leaf growth, production of flowers and, subsequently, pods. *Acacia tortilis* pods are rich in crude fibre and protein (Sauer *et al*., 1982). The nutrient composition of *A. tortilis* in the Hoanib River study area, particularly of moisture, crude protein and crude fibre, was generally similar to that reported elsewhere (Sauer, 1983; Pellew, 1984c).

Although giraffe browsed on *A. tortilis* year-round, the largest impact likely occurred during the dry seasons when new production rates are lowest. Even though browsing on *A.*

tortilis might have been more intense during the early wet season, the rapid accumulation of leaf biomass during this season would have limited browsing pressure on plant growth. It has been reported that the growth rates of *Acacia* species in arid habitats are slower generally than in other environments (Rohner & Ward, 1999), and that herbivory of *Acacia* seedlings is one of the factors impacting on their growth and survival (Dublin *et al*., 1990). On the other hand, browsers, and periodic flood events, are the main dispersal agents of *Acacia* seeds. Understanding the co-evolution of African herbivores and *Acacia* species is an important challenge for the future (Coe & Coe, 1987).

7.4.4.3. *Combretum* species

Giraffe ate *Combretum wattii* and *C. imberbe* year-round with a shift in preference between seasons and study areas. In general, I found that use of *Combretum* foliage was limited, in contrast to other studies which show that the genus forms a major food resource for giraffe elsewhere in their range (Sauer *et al*., 1982; Pellew, 1984a). The relatively low density of *C. imberbe* in the Hoanib River study area may account for its limited use. *Combretum wattii* appeared to be used in proportion to its abundance, although this did not influence seasonal selection. Elephant show a strong preference for *Combretum* species in the Hoanib River—this may reduce the availability of it as a forage source due to inter-specific competition, particularly when new growth emerges in the wet season (Viljoen, 1988).

Although *Combretum* species were not as abundant throughout the study region as other woody plants, such as *C. mopane*, *F. albida* and *Acacia* species, they serve as a valuable seasonal supplement for giraffe. Use of *C. wattii* increased with new growth, which occurred intermittently after rains, and resulted in increased availability of moisture and crude protein. Increased use of *C. wattii* was also observed in the early hot-dry season, again corresponding with increased moisture content of the foliage, but also the production of inflorescences and pods. Reduction in use of *C. wattii* by giraffe during the cold-dry season correlated with reduced moisture content and increased ash content of the leaves.

7.4.4.4. *Cordia sinensis*

Relative to the other forage species, *Cordia sinensis* formed a small percentage of the diet of giraffe in the Hoanib River study area. Analysis of the nutrient composition of *C. sinensis* showed high year-round moisture and crude protein contents, but lower crude fibre content compared to the all other species, aside from *S. persica*. Nutritionally, *C. sinensis* could be expected to be a valuable forage source for giraffe; however, elephant eat most individual plants in the Hoanib River (personal observation), making it difficult to obtain adequate sample sizes for analysis. The relatively low density of *C. sinensis* along the Hoanib River added to its low use by giraffe. Viljoen (1988 & 1989b) reported that *Cordia gharaf*, which is synomonous with *C. sinensis* in this study, was one of the preferred forage species for elephant in the study region. Therefore, although the nutrient composition of *C. sinensis* in the Hoanib River study area appears to be favourable for giraffe, reduced selection of this species probably resulted from its depletion by elephant. It may also contain high levels of secondary chemicals that were not tested for, such as tannins or phenols, although no data exist to evaluate this possibility. Giraffe, however, appear to select *C. sinensis* in proportion to its availability year-round (personal observation).

7.4.4.5. *Salvadora persica* and *Euclea pseudebenus*

The density of *Salvadora persica* along the riparian woodlands of the study region was high. Extremely well adapted to arid conditions, this evergreen species provides year-round forage for giraffe, with animals making increased use of it in the Hoanib River study area from the wet to the hot-dry season. Seasonal selection of *S. persica* was associated with diminishing resource availability and/or nutrient content of other preferred forage. During the dry seasons, *S. persica* was often more palatable and accessible than other forage resources (Parker *et al*., 2003) and hence was the preferred forage source during these periods (Leuthold & Leuthold, 1972).

The crude protein content of *S. persica* was higher in the cold-dry and lowest in the late hot-dry season, while moisture content peaked in the hot-dry season. Although an

important year-round forage source, the distinct reduction in intake of *S. persica* in the late hot-dry season may be correlated with its reduced crude protein and moisture contents at this time and with increased selection of *Euclea pseudebenus*, another evergreen woody species. Therefore, use of *S. persica* can be attributed generally to its high abundance, but its increased selection in the early hot-dry season corresponds with new growth and high moisture content. *Euclea pseudebenus* is specialised for dry conditions, relying on deep rooting and moderate growth rates (Coley, 1983); thus it was seasonally abundant, palatable and digestible during the dry seasons when compared to other deciduous plants. Giraffe readily browsed *E. pseudebenus* in the late hot-dry season when new growth was available.

7.4.4.6. *Colophospermum mopane*

Colophospermum mopane was fed upon year-round but was most important during the hot-dry season. As for most woody species, increased use of *C. mopane* could be attributed to leaf flushes in the hot-dry and wet seasons, increasing its abundance and availability. Increased foraging on *C. mopane* also coincided with reduced utilisation of *A. tortilis* in the early hot-dry season. The importance of *C. mopane* as dry season forage has been documented (e.g. Sauer *et al*., 1982; Styles & Skinner, 1997; Owen-Smith & Cooper, 1989). The leaves of *C. mopane* are most palatable in the dry season, when availability of other forage sources is often limited (Styles & Skinner, 1997), although the crude protein content of *C. mopane* is relatively constant year-round (Sauer *et al*., 1982).

Dagg (1959) reported that giraffe avoid *C. mopane*, while others (e.g. Oates, 1973; Hall-Martin, 1974 & 1975; Sauer *et al*., 1982; Styles & Skinner, 1997) have postulated that giraffe eat it reluctantly due to its high content of secondary chemicals such as turpentine and condensed tannins. These findings are surprising, as browsers often show high acceptance of otherwise unpalatable species during periods of new leaf production when protein levels rise relative to those of condensed tannin (Cooper *et al*., 1988). The limited diversity of woody species in the northern Namib Desert may result in *C. mopane* being eaten more readily by giraffe, particularly when leaves are most palatable and nutrient-rich.

7.4.4.7. Grasses and forbs

While giraffe were observed foraging on grass during the wet season, this formed only a small percentage of the year-round diet. During the wet season the moisture content of grass is highest and fibre content lowest as a result of new growth (Young, 1992). In other studies, giraffe have been reported to eat grass accidentally (Pellew, 1984a), and it comprises only a small percentage of their diet (e.g. Oates, 1973; Hall-Martin, 1974a; Field & Ross, 1976; Sauer *et al*., 1977; Ciofolo & Le Pendu, 2000). Preference by giraffe for moisture-rich browse, which has 50% more moisture than dry grass (Young, 1992), enables large ruminants to be mostly independent of free-water (e.g. Taylor, 1969; Western, 1975; Hall-Martin, 1984).

Tribulus zeyheri, an annual forb, constitutes a moderately important forage source for giraffe during the wet season (9% of diet), when it is most abundant and nutritious. Across their range, giraffe will eat forbs seasonally, however, they form a low percentage of the total year-round diet (e.g. Leuthold & Leuthold, 1972; Pellew, 1984a). In addition to being available only during limited periods, grasses and forbs may be more costly for giraffe to obtain because they have to be grazed at ground level, exposing animals to increased risks of predation and energy consumptive activities.

7.4.4.8. Incidental foraging observations

The three study areas have similar habitats with little variation in plant species diversity. !Nara *Acanthosicyos horrida,* an endemic plant species that inhabits the lower reaches of the westerly flowing ephemeral rivers and associated dunes in the Namib Desert, and *Salsola aphylla*, one of the most prevalent plant species throughout the study region (see Appendices 15, 16 & 17), both occur readily in each of the study areas, but giraffe were observed feeding on them only in the Khumib River.

While giraffe ate the leaves and stems of *A. horrida*, they preferred the large (15 cm diameter), moisture-rich melons. The marginally increased aridity and reduced forage availability in the Khumib River study area may also have resulted in giraffe utilising the

melons in the hot-dry season to supplement their diet and moisture requirements. Gemsbok and jackals in the Namib Desert have been observed to seasonally feed on the melons to supplement their dietary moisture intake (Seely, 1987; personal observation), but this is the first recorded observation of giraffe utilising this plant in the Northern Namib Desert.

Salsola aphylla has low nutrient content compared to other plant species in the study region, but still forms a valuable forage source for many other animals in the Namib Desert, such as springbok, gemsbok and ostrich (Seely, 1987; personal observation). Giraffe were observed foraging on *S. aphylla* only in the cold-dry season when it was fruiting.

7.4.5. Population dynamics of *Faidherbia albida*

7.4.5.1. Population structure

Faidherbia albida increased in numbers along the Hoanib River from east (Dubis wetland) to west (Hoanib floodplain), but decreased in mean heights along the same gradient. Several factors could have contributed to this, from competition for resources (mainly water), impacts of foraging giraffe and elephant, to climatic events.

Although the area nearer the Hoanib floodplain is marginally more arid, the increase in tree numbers could be caused by seasonal flood events depositing alluvium and nutrients downstream, enabling increased vegetation growth and higher plant densities (Seely *et al*., 1980). The accumulation of nutrient-rich sediments, combined with organic debris, provides food and shelter for seedling establishment and growth (Jacobson *et al.,* 1995), while shortage of water may still limit growth of large trees.

Giraffe and elephant feed selectively on *F. albida* seedlings, favouring seedlings, immature trees and coppices (Feely, 1965; CTFT, 1989), and thus reducing recruitment and distribution along the Hoanib River (Jacobson & Jacobson, 1998). However, as both species do not frequent areas of the Hoanib equally, their impact on the population

structure of *F. albida* is varied. Towards the floodplain both species numbers are fewer than up-river (Viljoen & Bothma, 1990b: Jacobson & Jacobson, 1998; personal observation), thus potentially enabling a greater number of seedlings to establish as a result of lower browsing pressure. Previous studies of the *F. albida* population in the Hoanib River have also suggested that wildlife browsing pressure has created strongly skewed age (= size) class distributions (Viljoen & Bothma, 1990b: Jacobson & Jacobson, 1998), but my research indicates that the population has a relatively even size distribution, indicative of a dis-equilibrium population. Other studies in Africa (Laws, 1970; Barnes, 1983b) have reported similarly skewed age class distributions in *F. albida* and *Acacia* spp., mostly attributing this to impacts from elephant. It is likely that the expansion of elephant range throughout the north-west (Viljoen, 1988; Leggett *et al*., 2003a; Leggett, 2004; personal observation) has reduced browsing pressure on the *F. albida* population in the Hoanib River in the past decade. As *F. albida* is the preferred forage source of giraffe in the Hoanib River, it is likely that they also have had a long-term effect on seedling recruitment and structural change of maturing *F. albida* trees, as observed in other populations (Pellew, 1983b; Ruess & Halter, 1990; Bond & Loffell, 2001; Birkett, 2002; Parker *et al*., 2003).

Current recruitment (seedlings <20 cm) equated to approximately 10% of the total *F. albida* population, more than one order of magnitude greater than that reported by Jacobson & Jacobson (1998). This increase in recruitment could be attributed to reduced foraging pressure by elephant as they spend less time resident in the Hoanib River than a decade earlier (Viljoen, 1988; Leggett *et al*., 2003a; Leggett, 2004), coupled with favourable rainfall years and flood events. Similar recruitment rates of *F. albida* to those in this study were reported from the central Namib Desert (Ward & Breen, 1983), where domestic stock posed the major browsing pressure, resulting in similar shifts in the population structure of *F. albida*.

Localised elephant pressure closer to the Dubis wetland in the Hoanib River has caused a localised decrease in numbers and recruitment rates of *F. albida* (Nott, 1987; Viljoen, 1988; Viljoen & Bothma, 1990b; Leggett *et al*., 2001a). However, it is feasible that the relative scarcity of *F. albida* close to the wetland may also be due to the plant's intolerance of salinity, which is caused by increased evaporation around the seasonal wetlands (Western & van Praet, 1973; Leggett *et al*., 2001b). Furthermore, a strong correlation

between tree density, salinity and tree mortalities has been reported previously, with an associated increase in *Suaeda* species abundance, a conspicuous saline indicator (Western & van Praet, 1973). Around the Dubis wetland *Suaeda* spp. is dominant, reducing in number further west. Therefore, it can be inferred that although elephant pressure has affected the population structure of *F. albida* nearer the Dubis wetland, increased salinity may also be a contributing factor.

The high variability of rainfall in the north-west could also have an impact on *F. albida* abundance and populations structure. The severe drought in the 1980s resulted in pressure on *F. albida* populations and a shift in the population dynamics of *F. albida* in the Hoanib River was reported (Jacobson & Jacobson, 1998). Long-term impacts of rainfall and other climatic events are expected, while short-term erosion of banks due to seasonal flood events resulted in relatively large numbers of mortalities (6% of mature trees). Similar findings have been published (e.g. Laws, 1970; Ward & Breen, 1983; Jacobson & Jacobson, 1998).

A shift in forage selection or degree of browsing pressure can be caused by a variety of factors, such as change in numbers of mammals, a shift in vegetation population structure, periods of high aridity and/or severe annual flooding events (e.g. Laws, 1970; Ward & Breen, 1983; Jacobson & Jacobson, 1998). Only long-term monitoring of the *F. albida* population and associated wildlife numbers in the Hoanib River can ultimately assess the dynamics and impact of wildlife on the *F. albida* population.

7.4.5.2. Structural impacts

7.4.5.2.1. Browsing

Intensive browsing by giraffe in the Hoanib River has resulted in large structural changes to the vegetation. Distinct browse lines were observed on mature trees of *F. albida*, *A. tortilis, A. erioloba* and *M. schinzii*, while a topiary or hedging effect was observed on immature and coppiced *F. albida*, *A. tortilis, A. erioloba*, *S. persica*, *C. sinensis* and *C. wattii.* Similar structural changes caused by giraffe have been reported Africa-wide (e.g.

Foster, 1966; Leuthold & Leuthold, 1972; Sauer *et al*., 1977; Dagg & Foster, 1982; Pellew, 1984a; Coe & Coe, 1987).

More general impacts on tree growth and structure from intensive wildlife browsing have been recorded throughout Africa (e.g. Laws, 1970; Barnes, 1983; Dublin & Douglas-Hamilton, 1987; Dublin *et al*., 1990; Prins & van der Jeugd, 1993; Vijver *et al*., 1999). The role of giraffe as habitat changers has not been documented to the same extent as that of elephant, but they can decrease species diversity and richness, as well as suppress growth and cause structural changes to trees (e.g. Field & Ross, 1976; Pellew, 1983b; van de Koppel & Prins, 1998; Birkett, 2002). In areas of South Africa, giraffe only cause selective mortality to *Acacia* species (Bond & Lofell, 2001).

The impact of giraffe on *F. albida* is most marked. In the Hoanib River more than 80% of all mature *F. albida* trees had browse lines at about 5 m—the maximum feeding height of giraffe. Elephant also feed high into the canopy of *F. albida* but are often not able to reach as high as giraffe; if they do, by standing on their hind legs, they break off branches rather than prune a distinct browse line. A few *F. albida* trees (<20 %) had browse heights ≤1.5 m, the majority of which were 'bushes'. Giraffe, elephant and other wildlife, selectively browse *F. albida* seedlings, coppices and immature trees, often pruning stands of *F. albida* into 'bushes'. Fortunately, *F. albida*, as indeed *Acacia* species, are well adapted to high browsing pressure and are able to withstand increased foraging pressure by giraffe (e.g. Field, 1971; Guy, 1981; Barnes, 1983; Lewis, 1991).

Increased movements by giraffe and elephant into other areas of the study region or into other catchment systems (Leggett *et al*., 2003a; Leggett, 2004), would help reduce potential competition for and impact on available forage resources. However, such an expansion would cause other problems, such as human-wildlife conflicts and competition with domestic stock. These social and human impacts could have far wider implications.

7.4.5.2.2. Bark use

Giraffe were not observed stripping bark from *F. albida* or other plant species in the study region. In the northern Namib Desert, where water and available nutrients are limited, bark is a seasonally important dietary supplement for elephant (Viljoen, 1988 & 1989b; personal observation). Few observations of giraffe feeding on bark have been reported in Africa (e.g. Birkett, 2002), and these have inferred a correlation between seasonal bark consumption, forage availability and bark mineral content, energy and water content. The observation that giraffe do not remove bark in the northern Namib Desert may simply indicate adaptation to life in an arid environment, with an ability to maintain year-round moisture and nutrient requirements from foliage resources, or that bark provides few resources that giraffe need.

Bark damage on *F. albida* trees in the Hoanib River was the result of foraging by elephant. Little more than half of the mature *F. albida* trees showed signs of bark damage, most of which was older than a year. Viljoen & Bothma (1990b) reported a much greater degree of bark damage: 71.8% of trees affected, compared to only 57.8% observed during this study, which was attributed to aggregating elephant in the river (Viljoen, 1988). Since Viljoen's study, elephant have increased their residence periods away from the Hoanib River resulting in reduced browsing pressure on the *F. albida* population (Leggett *et al*., 2001a; Leggett, 2004).

7.4.5.2.3. Mortalities

Adult *F. albida* face lethal threats throughout, in particular from large mammals (e.g. Laws, 1970; Caughley, 1976; Foster & Dagg, 1982; Bond & Loffell, 2001), climatic events (CTFT, 1989; Gerhardt, 1993; Stave *et al*., 2001), flood events (e.g. Jacobson & Jacobson, 1998; Stave *et al*., 2003) and groundwater extraction (e.g. Ward & Breen, 1983; BOSTID, 1990; Jobst, 1996; Le Maitre *et al*., 1999; van de Vijver *et al*., 1999). In the Hoanib River study area, a few mortalities of *F. albida* were caused by elephant, even though drought and poaching pressure resulted in the compression of the elephant population during the 1980s (Viljoen, 1988).

Both seedlings and mature *F. albida* appear to have a limited capacity to handle water stress and are susceptible to shifts in the water table and flood regime (e.g. Ward & Breen, 1983; Jobst 1996; Le Maitre *et al.*, 1999). However, immature trees can develop deeper roots when the underground aquifer depth lowers. Mathooko & Kariuki (2000) postulated that seasonal flooding as experienced in arid associated riparian woodlands regulates vegetation growth and survival. Following the 1999/2000 wet-season, the *F. albida* population in the Hoanib River study area was re-surveyed and approximately 6% of trees were uprooted–all were mature. This was a marked increase in mortality rates compared to the initial survey. Seasonal flood events have been reported to cause the mass wasting of banks and scouring of bed sediments in the Hoanib River, resulting in 2.8% of the *F. albida* population being uprooted (Jacobson & Jacobson, 1998). Although these uprooted trees no longer produce forage, they play an important role by providing organically rich microhabitats under which future seedlings can establish (Jacobson *et al.,* 1995). Other factors such as wood-borer insects, which have been reported to negatively impact *F. albida* populations in the Hoanib River (Jacobson & Jacobson, 1998) and elsewhere (e.g. Eltringham, 1980), were not observed to have an impact during this study.

Potentially, one of the largest impacts on the *F. albida* population, as well as on other plant species, is hydrological projects. Two artificial watering points were erected in the Hoanib River study area in October 2002. These were erected to help reduce wildlife damage in neighbouring villages by attracting elephant west along the Hoanib River and away from people and their crops. In the short-term this has proven effective, but the long-term impacts on the habitat and wildlife are unknown. No ecological study was undertaken to assess the impact of water abstraction before the establishment of the water points. Small shifts in wildlife movements have already been observed. Elephant have shifted their preferred foraging area further west along the Hoanib River, and this has resulted in increased competition between elephant and giraffe (K. Leggett, unpublished data; personal observation). With increased use of the river downstream from the Dubis wetland by elephant, shifts in the population dynamics of *F. albida* are likely to occur in the future. The observed impacts around the Dubis wetland might be replicated around the new water points, which in the long-term will reduce the availability of forage for wildlife. Additionally, continuous extraction of water at these new water points due to poor maintenance may result in a lowering of the water table and, in the long-term, tree

mortalities downstream. The knock-on effect from such a project may lead to irreversible habitat and wildlife changes (e.g. Rohner & Ward, 1999; Ngana, 2002; Mills *et al*., 2003).

7.5. Conclusion

Forage selection by giraffe varied markedly between seasons and study areas. In general, giraffe aggregated along the riparian woodlands where food availability was high, but they also moved seasonally into the mountain habitats to exploit available forage. Furthermore, elephant, people or forage proximity to villages may have influenced forage selection by giraffe. Further studies would be required to test this hypothesis. Small-scale movements along the Hoanib River appeared to be driven not by the search for moisture, but most likely by the tracking of seasonal sources of food. Giraffe exploited forage with higher levels of moisture and crude protein, which were in turn influenced by rain and fog precipitation. They also tracked phenological changes in food plants, such as seed pods and new leaves, preferring some species such as *F. albida* and *Acacia's* over others.

Assessments of the population dynamics of *F. albida* in the Hoanib River over the past two decades provided valuable insight into the changing nature of the riparian woodland and its potential use by giraffe or other wildlife. Since the early 1980s, a shift in the population structure of *F. albida* can be inferred, possibly correlated with wildlife impacts and/or hydrological occurrences. The current size class distribution of *F. albida* is indicative of a non-equilibrium population; it correlates positively with the results of Jacobson & Jacobson (1998), but has a more even size class distribution when compared to Viljoen & Bothma (1990b).

It appears likely that both giraffe and elephant have had a visual impact on the *F. albida* population in the Hoanib River, with browse heights in excess of three metres observed for approximately 80% of the population. Furthermore, elephant damage to *F. albida* bark was high, with the greatest impact close to sources of permanent or seasonal water. Increased residence periods by elephant away from the Hoanib River have reduced the pressure on forage in the riparian environments. During this study, hydrological and

climatic variations appeared to be the major influences on the population dynamics of *F. albida* in the Hoanib River.

Chapter 8. General Discussion

In this chapter, I begin by recapping some of the key findings of my research, and then discuss the history of wildlife conservation and management in the Kunene Region where the work was carried out. This provides the background needed to discuss current issues in wildlife management and sustainable use, before suggestions are made for future research.

8.1. Major findings of the thesis

The desert-dwelling giraffe of the northern Namib Desert survive at the edge of the species range. They are genetically distinct and behaviourally and ecologically different from other giraffe throughout Africa.

Genetic evidence indicates that Namibian giraffe are distinct and that they differ, in particular, from Cape giraffe *Giraffa camelopardalis giraffa* Lydekker 1904,; their taxonomic classification for the last century. The five unique haplotypes observed in the desert-dwelling and Etosha NP populations of giraffe indicate that the Namibian taxon has not interbred with other giraffe subspecies for an extended period. The genetic differences, coupled with geographical isolation of the population, warrant further investigation into the appropriate taxonomic classification of Namibia's giraffe. Unfortunately, the recent extinction of Angola's giraffe population limits genetic comparisons. However, there is evidence that the populations of Namibia and Angola overlapped historically. Upon further genetic investigation, appropriate morphological and ecological research, the Namibian giraffe may be formally reclassified as *G. c. angolensis*. The weight of evidence for this reclassification is strong, and Namibian giraffe have been considered to be *G. c. angolensis* in this chapter.

In Namibia, limited gene flow was evident between giraffe in the desert and those in Etosha NP, despite their close geographical proximity. Indeed, the only gene flow appeared to have resulted from recent translocations of giraffe from Etosha into the northern Namib Desert. Large-scale movements of giraffe in the northern Namib Desert suggest that inter-mixing occurs between populations within the study region. However,

increasing growth of human populations in this marginal farming environment may limit giraffe movements in future if access to forage areas is restricted or if direct conflicts arise.

The arid conditions of the northern Namib Desert shape aspects of the population dynamics of giraffe, such as the very low population density. However, aridity is not the only factor, as historical poaching pressures, low fecundity, limited food and low, spatially variable rainfall combine to reduce the rate of population growth. Individual associations and population structure also varied greatly within the subpopulations of the study region. For example, more associations were observed among bulls in the Hoarusib River study area, where bulls predominated; while cows preferred the areas away from the Hoarusib River. Limited food in the tributaries restricts the year-round presence of giraffe so that cows move to the broader riparian woodlands to forage in the hot-dry season, and risk the closer proximity to the communal farmers. In the small, cow-biased population of giraffe in the Khumib River, by contrast, cows associated more strongly and a matrilineal social structure was observed. In general, my observations showed that giraffe in the northern Namib Desert depend critically on the riparian woodlands of the ephemeral rivers for year-round forage and shade resources.

Direct observations and tracking showed that giraffe in the study region have large home ranges, with some individual bulls showing the largest home ranges of any giraffe yet recorded. The large home ranges were associated with low population density, but also with sparse food resources and increased searching for receptive cows. This study confirmed the occurrence of extensive movements between study areas.

The activity budgets of the desert-dwelling giraffe are strongly biphasic. Energy consuming activities such as feeding and walking were reduced at midday and during early afternoon when ambient temperatures were greatest, whilst energy conserving activities such as resting increased during the same period. Dispersal of surplus metabolic heat when temperatures are lower, evaporative cooling and adaptations for water conservation contribute to the biphasic pattern of diurnal activity. Behavioural responses such as the selection of microclimates (shade, wind and body orientation), also help to conserve energy and water.

The activity budgets of Namibia's desert-dwelling giraffe differed markedly between sexes, as observed in other giraffe populations (Leuthold & Leuthold, 1972; Pellew, 1984a; van der Jeugd & Prins, 2000), but the time spent in different activities differed between this and other studies. All giraffe in the study region spent most of the day feeding. Cows spent more time feeding and resting, while bulls walked and ruminated more often, and juveniles mostly fed and rested. Feeding, combined with walking, resting and ruminating, occupied more than 95% of the activity time of giraffe.

Giraffe cows exhibited an energy 'maximizer' strategy characterised by increased feeding during the cold-dry season; this would increase fat deposition and reduce energy consumptive activities for better survival during the long hot-dry season. In contrast, bulls exhibited an energy 'minimizer' strategy; here, feeding increased in the hot-dry season as available forage in the canopies became limited. Similar strategies have been reported in other giraffe populations in Africa, but are not as marked as in the study region. Social interactions observed during this study provided valuable insight into the bonds and hierarchy of giraffe society, although longer-term research would help to better understand such dynamics.

Selection of food plants by giraffe was driven by a combination of factors, such as chemical content, seasonal abundance and phenology. Giraffe seasonally selected forage with increased levels of moisture and crude protein, which in turn was influenced by rain and fog precipitation. Although the study area is arid and has a limited diversity and richness of plant species, selection of forage by giraffe did not always correlate with plant abundance, but did correlate with phenological changes and the seasonal availability of fresh leaves.

Giraffe foraged predominantly in the riparian woodlands, but also moved seasonally into other habitats to exploit alternative sources of food; the mountains were used mostly in the cold-dry season. I hypothesised originally that, in the Hoanib River, the moisture content of food would influence seasonal small-scale movement. However, giraffe were shown not to need free-water, and evidence suggests instead that seasonal nutrient quality and abundance of forage most influence giraffe movements.

Giraffe have caused distinct structural changes in plant species in the study region, in particular *Faidherbia albida*. Approximately 80% of *F. albida* trees in the Hoanib River have browse heights in excess of 3 m—a direct impact of giraffe. Aside from structural changes to individual trees, 20 years of assessment of the *F. albida* population indicates a marked shift in size class distribution, indicative of a non-equilibrium population (Nott, 1987; Viljoen & Bothma, 1990b; Jacobson & Jacobson, 1998). Increased residence periods by elephant away from the Hoanib River has probably reduced the pressure on forage in the riparian woodland since the 1980s and contributed to the observed shift in dynamics of *F. albida*. However, hydrological and climatic events, as opposed to wildlife impacts, have been the major influences on the population dynamics of *F. albida* in the Hoanib River.

In summary, there is a small but persistent population of desert-dwelling giraffe in north-western Namibia that has, until now, not been studied in detail. Limited historical evidence suggests that it may be vulnerable to disturbance in the riparian refugia of the Hoanib, Hoarusib and Khumib catchments and throughout the broader Kunene Region. In the next section, I discuss the conservation history of this region and evaluate some potential threats to giraffe and other wildlife as the region becomes more developed.

8.2. Conservation history, management and future of giraffe in Namibia's northwest

North-western Namibia has undergone significant political, economic, social and ecological changes over the past century (e.g. Schoeman, 1984; Dreyer, 1994; Kreike *et al*., 2004). From the first European settlements through the turbulent times of apartheid, poaching and drought, and more recently, the resurgence of wildlife, a progression of conservation methods and management techniques has affected the environment and its inhabitants.

At the turn of the 20th century, the German colonial administration of the former South West Africa (Namibia) exercised no control in the Kaokoveld (Owen-Smith, 1986). In 1915 the South African forces overran the German administration and the country was proclaimed under their rule. The barren and wild land of north-west Namibia was

proclaimed by the new administration as a reserved area for the traditional Ova-Himba and Otji-Herero tribes. Although stark, it was reported that the Kaokoveld abounded with big game (Owen-Smith, 1986). In 1928 the Kaokoveld was proclaimed by the South African administration as a protected game conservation area and, together with the Etosha NP, became known as Game Reserve No. 2 (Owen-Smith, 1970). This was then the largest conservation area in Africa, approximately five million hectares in size, and 2.5 times the area of the Kruger NP (Owen-Smith, 1970 & 1986; Gibson, 2001). At the time, and throughout the decades to follow, the wildlife of the Kaokoveld was abundant and widespread throughout the region (Viljoen, 1982).

The Kaokoveld was declared a separate magisterial district in 1939. This encompassed the majority of Game Reserve No. 2 and the existing boundaries remained similar until the Odendaal Plan was implemented in the 1960s (Owen-Smith, 1970 & 1986). In 1962, the South African Prime Minister established a commission enquiring into the welfare and future development of Namibia and its inhabitants. As a result large tracts of the Kaokoveld were de-proclaimed as part of Game Reserve No.2 to create 'ethnic homelands' for the indigenous peoples (Owen-Smith, 1970 & 1986; Reardon, 1986). Approximately 1.5 million ha of the western section of the reserve were redistributed to form the newly established homelands of Kaokoland and Damaraland. Conservationists across the region deplored this decision (Owen-Smith, 1970; Reardon, 1986; Hall-Martin *et al*., 1988). Once declared, these tribal homelands became inaccessible to the general public without a valid permit. This law did not change until 1977 when another redistribution of land was implemented under the Odendaal Plan (Owen-Smith, 1986; Reardon, 1986; Hall-Martin *et al*., 1988). However, fuelled by the construction of artificial water points and the introduction of veterinary services and other major development infrastructure, increased human populations and large numbers of domestic stock competed with wildlife for natural resources, resulting in large declines in game numbers (Viljoen, 1981; Owen-Smith, 1986; DEA, 1996; Gibson, 2001).

During the mid-1970s, poaching became a substantial problem in the Kaokoveld, with Angolan and Portuguese poachers and soldiers venturing south into Namibia. This period coincided with the beginning of the people's struggle for Independence of Namibia. Before the end of the decade, illegal hunting became a popular distraction for high-ranking

members of the South African Defence Force and the former South African government (Viljoen, 1982; Owen-Smith, 1986; Hall-Martin *et al*., 1988; Lindeque, 1991).

Also in the mid-1970s a double fence was erected from east to west across Namibia, separating the northern domestic stock-diseased area from the disease-free south. The veterinary cordon fence, or 'red line', was erected as part of the Odendaal Plan to comply with European Economic Community requirements for the export of cattle from Namibia (Owen-Smith, 1986; Loutit & Lindeque, 1988). The fence limited the seasonal movement of wildlife, which resulted in high numbers of wildlife deaths in the fragile environment of the arid north-west.

In 1977, concerned nature conservators from the adjacent Skeleton Coast Park began to undertake anti-poaching patrols inland into Kaokoland and Damaraland, which continued until the late 1980s (Owen-Smith, 1970). Prior to the mid to late 1970s, the Directorate of Nature Conservation had little infrastructure to stop poaching activities, while jurisdiction in the area was unclear. It was not until 1981 that the first nature conservator was officially stationed in the Kaokoveld. Based in Damaraland the responsible officer initially patrolled an area of approximately 95 000 km^2 (Owen-Smith, 1986).

Devastating droughts in the early 1980s further accelerated a decline in wildlife numbers, with an estimated 60% of the large mammals and some 90% of the region's domestic stock dying off (D. Gilchrist & R. Loutit, personal communication). With such impacts, local farmers turned to hunting for survival, using weapons and ammunition supplied during the independence struggle. Wildlife numbers were now markedly reduced over Namibia's north-west and few animals remained, concentrating in isolated and remote pockets, such as the arid areas south of the Hoanib River. At this time, bans on hunting, increased scientific research and conservation of the area's rare and endangered wildlife were proposed, but to no avail (Hall-Martin *et al*., 1988).

In 1982, a group of concerned conservationists and like-minded business people established the Namibia Wildlife Trust (NWT) to help fight poaching (Owen-Smith, 1986). The NWT, in conjunction with the appointed local conservator, worked closely with local tribal authorities through appropriate programs of conservation education, and extension

work. Over time the relationship yielded the respect and authority of the traditional elders, who placed their own local hunting embargo on the area's wildlife (Owen-Smith, 1986). This was a large step forward and one that would lead to the eventual creation of the current Community-based Natural Resource Management (CBNRM) program. During 1983 the NWT established the 'auxiliary game guard' system, again in close collaboration with the traditional elders, continuing the efforts to reduce poaching. This success saw the way forward for the local people to take ownership over the region's wildlife for their future. A localised resurgence in poaching occurred briefly in the late 1980s, but the combined efforts of NGOs, government, safari operators and communal authorities limited the impact (Reardon, 1986).

Prior to Namibia's Independence in 1990, communal residents were subjected to an array of dis-empowering processes and legislation (apartheid). These affected almost every facet of life, including education, health, agriculture and natural resource management practices. Wildlife belonged to the State and there was no incentive for people to manage local wildlife resources. Following Namibia's Independence in 1990, the newly-formed Ministry of Environment and Tourism (MET), in collaboration with the existing work of NGOs, embarked upon a process of changing the environmental legislation. This used a consultative approach, drawing on the ideals, wishes and needs of communal residents. The Namibian Government subsequently developed and introduced modern legislation in 1996, paving the way for the establishment of communal area conservancies (Jones & Murphree, 2001; NACSO, 2003). This legislation makes provision for communal area residents to obtain legal rights and responsibilities over the natural resources and tourism in their region. Furthermore, it provides legal and social mechanisms through which communal area residents can engage in natural resource management.

In a communally-owned and managed area, rural people have pooled their resources in order to manage, utilise and benefit from wildlife and other natural resources. Communal area conservancies allow people to diversify their livelihoods beyond normal farming practices and provide a greater incentive for sound natural resource management (Barrow & Murphree, 2001; Jones, 2001). However, conflicts and inter-communal conservancy disagreements between the conservancy boundaries and tribal groupings have hampered this process significantly (NACSO, 2003). In addition, support from the government,

although one of the initial driving forces behind the CBNRM program and associated legislation changes, was perceived to be indifferent at times (Jones, 1997; NACSO, 2003).

In addition to CBNRM, numerous conservation and management plans have been proposed since the mid-1990s, from the extension of the Etosha NP into the communal Kunene Region, to a Tourism Master Plan for the Region (e.g. Urban Dynamics Africa, 1999). Although all efforts were considered commendable and attempted to increase conservation and natural resource management, most did not leave the initial planning as legislation or general consent.

8.3. CBNRM and conservation in the Kunene Region

Almost a century of expansion and reduction of protected land in the Kunene Region, coupled with a range of management approaches, has set the framework for CBNRM in Namibia's north-west. The CBNRM program is a government initiative, actively promoting the sustainable utilisation of communal land that is economically viable and ecologically sustainable, while also being a sound mechanism driving local development, sustainable livelihoods and wildlife conservation (Long, 2004). The program is a collaborative approach that benefits communal conservancy members (predominantly subsistence farmers), and is supported by NGOs, donors and various government sectors.

The success of the Namibian CBNRM program has been largely wildlife- and tourism-based, but the depth of the program is far greater and the concept far broader. CBNRM is providing rural communities with the skills and tools to be involved in a wide range of social, economic and environment-empowering processes. From improving livelihoods, personal enrichment, capacity building, communication and management to preserving their country's natural endowments, the program has established a range of methodologies and lessons learnt in order to formulate a progressive legislative framework as a backbone for the success of the program. Importantly, the CBNRM program is not a silver bullet or panacea for any particular economic, social or ecological issue, but is part of a broader objective with a triple-bottom line approach.

CBNRM was initiated in Namibia in the 1980s and today more than five million hectares of communal land are under protective management by registered and emerging conservancies (NACSO, 2003). An increasing number of conservancies are becoming self-funded from locally-generated revenues, while direct benefits to the conservancy members include the building of local schools, distribution of cash revenue and creation of jobs. However, it would be ignorant to assume that the CBNRM program has been all things to all people. Inevitably, some components of the program are stronger than others, much of which has been dependent on NGO and donor support, the skill base and resources available (NACSO, 2003). On the whole, the program is moving in the right direction, although it is important to note that its continued success will require ongoing support. In the sections below I briefly outline and discuss some aspects of the CBNRM program with relation to long-term wildlife conservation and management in the Kunene Region.

8.3.1. Wildlife management and sustainable use

The Namibian government actively promotes sustainable use of wildlife as a management approach, and as an economically viable and ecologically sustainable tool on communal land such as in the Kunene Region. Benefits from wildlife use (consumptive and non-consumptive) on communal land are increasing annually since its recognition as an operational management tool within the CBNRM program. Economic benefits exceed N$10 million a year, while the social benefits are considerable (Ashley & Barnes, 1996). Studies indicate that sustainable use of wildlife on commercial land is currently greater than five times that on communal land, although evidence suggests that the CBNRM program will allow for far greater revenue on communal land in the long-term than currently observed for the commercial sector (Ashley & Barnes, 1996).

Community-based wildlife management in the Kunene Region has facilitated many positive offshoots, such as increased wildlife populations, financial gains, and distribution of trophy meat, but also negatives, such as human-wildlife and domestic stock-wildlife conflict. Some of the questions that are now arising from the successful conservation and

management undertaken over the past 20 years which has seen the numbers of wildlife increase in the region are:

- how sustainable is the use of wildlife in an arid environment?
- Will conservancies have the skill, resources or capital to self-administer wildlife management or seek expert advice on these issues?

Although these are critical questions, what I perceive to be most important is finding the correct methods and tools that will help understand wildlife management in the future. An important tool for sustainable use of wildlife and conservation is long-term wildlife monitoring by the conservancy. Local-level wildlife monitoring offers a broad range of benefits, such as increased wildlife populations, local empowerment, skills and job creation (e.g. conservancy game guard system). The quality and continuity of monitoring are keys for obtaining long-term, standardised data for appropriate conservation and management (e.g. Taylor, 2001). However, community lethargy has found its way into local level monitoring (personal observation) and as a result monitoring has been substandard and not continuous in some conservancies. Partly, this is due to a lack of vehicles or unclear division of responsibilities in the CBNRM program (e.g. Sullivan, 2002; Sullivan & Homewood, 2004; personal observation). This has the potential to have marked short- and long-term impacts on wildlife management, as well as a knock-on effect for the economic and ecological sustainability issues facing conservancies.

With respect to giraffe, community-based wildlife management may need to take only a guardian approach in which conservancies undertake long-term monitoring of numbers and distribution, limit poaching and, if possible, restrict consumptive use of giraffe until long-term population data have been obtained. Within the conservancies of the study region, my recommendations would include that giraffe hunting should not be undertaken as the population is too low and giraffe move regularly between two or more conservancies. Until further monitoring and research are undertaken, conflict may arise over assigning ownership and benefits (financial, meat or material) to conservancies due to the large-scale movement of giraffe. However, in proposing this, budgetary constraints within individual conservancies and the CBNRM program, coupled with the assumption that biological management of giraffe is sustainable, it appears likely that trophy hunting of giraffe in the northern Namib Desert may occur.

As outlined by Long (2004), it is important that any government revenue derived from sustainable use should go towards promoting the conservation objectives of the country, which would include diverting revenue directly back to conservancies. Recommendations for establishing guiding principles and criteria for hunting black rhinoceros were recently proposed (Leader-Williams *et al*., 2004). Many of these principles could be transferable for hunting of giraffe in the Kunene Region and support the community-based wildlife management approach (Leader-Williams *et al*., 2004):

- ensuring that any offtake is biologically sustainable and based on good monitoring;
- ensuring that incentives from hunting opportunities are maximised, without discriminating between state agencies, private and communal sector;
- rewarding good biological management and long-term commitment to wildlife conservation; and,
- ensuring that appropriate internal and external controls are in place.

In advocating these principles, it is important that rural communities understand sustainable wildlife use and show awareness that economic benefits from wildlife outweigh land use options that exclude wildlife (du Toit, 2002). In an arid environment this includes establishing population estimates and setting carrying limits on consumptive use, while taking into account stochastic abiotic factors (Mentis, 1971; Bell, 1986; du Toit, 2002). One of the problems of sustainable consumptive use in an arid environment is that offtake may vary annually, and therefore lower offtake would result in a reduction in benefits. Importantly, education is the key to conservancies understanding this process, and this would in turn support their own survival as well as that of wildlife over the longer-term in the region (e.g. Hachileka & Kokwe, 2000; Shackleton & Campbell, 2000).

Further emphasis needs to be placed on highlighting the desert-dwelling giraffe as an ecologically distinct species, as has been done for the desert-dwelling elephant and rhinoceros. Preliminary studies indicate that non-consumptive wildlife-tourism is a valuable revenue earner for conservancies in the Kunene Region provided that appropriate management, training and guidelines are provided (M. Sibalatani & M. Hearn, unpublished data). For long-term success, wildlife management needs to extend across sectors, including tourism, as well as provide support for legislative changes to devolve more responsibility and control to the conservancies.

8.3.2. Tourism

Tourism in the northern Namib Desert has been emphasised as an industry that may be able to provide socio-economic and ecological development for people in the Kunene Region (Urban Dynamics Africa, 1999). Tourist numbers and facilities are mushrooming, but largely without control or formalisation, while the benefits of tourism to conservancies in the region are increasing. Some conservancies are fortunate to have a greater abundance of charismatic megafauna than others, thus enticing tourists and joint-venture operators, and in turn revenue and job creation, into their areas. Uncontrolled tourism in the Kunene Region impacts on wildlife behaviour, causes damage to the environment, and spoils the tourism experience. (Urban Dynamics Africa, 1999; SRT & NACOBTA, unpublished data; personal observation). Similar social and environmental impacts have been reported elsewhere (e.g. Chenje & Johnson, 1994; Reid, 2000; Terkenli, 2001)

Some of the key components of a formalised wildlife-tourism market are control, safety, socio-economic benefits and sustainability. In the Kunene Region, tourist numbers have increased markedly since the mid-1990s (Urban Dynamics Africa, 1999; NACOBTA, unpublished data). These trends indicate a greater demand and potential for sustainable tourism in the region. However, some consequences of increased tourism have included photographers harassing wildlife, motorbikes circling elephant, elephant charging vehicles and injuring or trampling tourists (Urban Dynamics Africa, 1999; SRT & NACOBTA, unpublished data; D. van Smeerdijk, personal communication; personal observation). With escalating and uncontrolled tourism, the impact on wildlife and the environment becomes difficult to predict.

A key strategy for long-term wildlife-tourism and its sustainability is low-impact community-based tourism. This would be beneficial for the environment, conservancies and their members, and potentially the private sector, which establishes joint-venture tourism agreements. Importantly, and particularly in light of increased tourist numbers and the unknown impacts of tourism on giraffe and other wildlife populations, an integrated tourist control or monitoring program is required for long-term conservation and tourist management in the study region.

Two methods proposed specifically for the Kunene Region include setting limits for the maximum use of an area, essentially estimating an area's carrying capacity, and establishing Limits of Acceptable Change (LAC) (Urban Dynamics Africa, 1999). The latter is more quantifiable and is an appropriate measure of the impacts of tourism in the study region. LAC defines management actions that would be triggered in response to defined signs of tourist pressure, established by local CBNRM planning and monitoring. Wildlife is the focus for tourism in the region and appropriate monitoring of the population behaviour should be a priority. However, other factors which should be assessed are road condition, vegetation or soil condition, litter and other pollution, the impact of visitors on local communities and visitor satisfaction levels (Urban Dynamics Africa, 1999). This would require regular and consistent, qualitative and quantitative data being obtained for the factors mentioned, and it is critical that long-term monitoring is undertaken so that guidelines for conservation and management of the resources can be established.

In addition to wildlife-tourism and control, one of the most effective measures to support wildlife conservation in the Kunene Region is to proclaim certain areas within and across conservancies as protected land. This would then afford increased protection to wildlife and the environment, as well as help control tourism. However, this may be legally difficult due to the proclamation of the communal area at Independence that allows free access to all people. Long-term planning and collaboration between all parties involved in the CBNRM program may lead to greater protection of land in communal areas.

8.3.3. Water development programs

It has been well documented that wildlife abundance in Africa has a negative relationship with human density (e.g. Eltringham, 1990; Happold, 1995). Human settlements tend to develop around water sources, both permanent and seasonal. The increase in use of these areas, particularly in arid environments, often results in irreversible environmental damage such as severe degradation, erosion and overgrazing. Furthermore, human settlements restrict access and increase competition for wildlife that use these water sources. In the arid Kalahari of Botswana, throughout the Sahel and elsewhere, permanent settlements have had a marked impact on wildlife movements (development), wildlife numbers

(hunting) and habitat use (competition for forage with domestic stock) (e.g. Parris & Child, 1973; Leisinger & Schmitt, 1995; Ngana, 2002; Biswas, 2004). Similar processes are currently operating and have occurred historically in the study region, to the detriment of the wildlife.

Increased numbers of water points in the study region have already had an affect on wildlife (K. Leggett, personal communication; personal observation.). For example, the foraging range of elephant has increased along the Hoanib River, and so too have predator numbers. This development has put severe stress on giraffe in the study region and resulted in the first known giraffe mortalities by predators in the Hoanib River in the past decade (personal observation). Permanent water also encourages communal farmers and their domestic stock to use areas for extended periods that have historically been only seasonally accessible. While this has not yet been observed for the new water point installations in the Hoanib River, historical knowledge indicates that communal farmers have used these areas seasonally in the past, and this may encourage their use in the future to the potential detriment of wildlife (J. Patterson, personal communication; observation). As the long-term impacts of water installations in the study region are unknown, it is important to undertake ecological monitoring to assess any resulting changes, whether they be human or wildlife-induced.

8.3.4. Poaching

Poaching of wildlife in the Kunene Region has been markedly reduced since the onslaughts of the 1960s to the 1980s. There was no evidence of giraffe poaching during this study, but small-scale poaching of smaller wildlife does occur (Katjiua *et al*., 2002; K. Vaughan personal conmmunication). This low intensity poaching may be sustainable in the sense that it is subsistence hunting for the family pot, although the localised impacts on wildlife is unknown.

A real concern is the potential for an increased demand of wildlife products, as this could result in large-scale losses of wildlife (e.g. Viljoen, 1989; Leader-Williams *et al.,* 1990; Milliken *et al*., 1993; Caughley & Sinclair, 1994). Poaching of giraffe has never been an

issue that has drawn significant conservation or management attention, but recent reports indicate that giraffe poaching has risen markedly in Tanzania where local authorities believe that giraffe meat is a potential cure for HIV/Aids (Anon, 2004a). The HIV/Aids pandemic has caused many deaths and debilitation to families and economies across Africa. Appropriate education is necessary to dispel such irrational myths as soon as possible before widescale deaths of wildlife ensue.

8.4. Future research

No long-term monitoring of giraffe has ever been undertaken in Africa. This study provides useful baseline research that could form a solid grounding for long-term research and monitoring. I believe that without long-term research our understanding of giraffe will remain too limited to achieve effective conservation, and our attempts at management will continue to provide only short-term solutions.

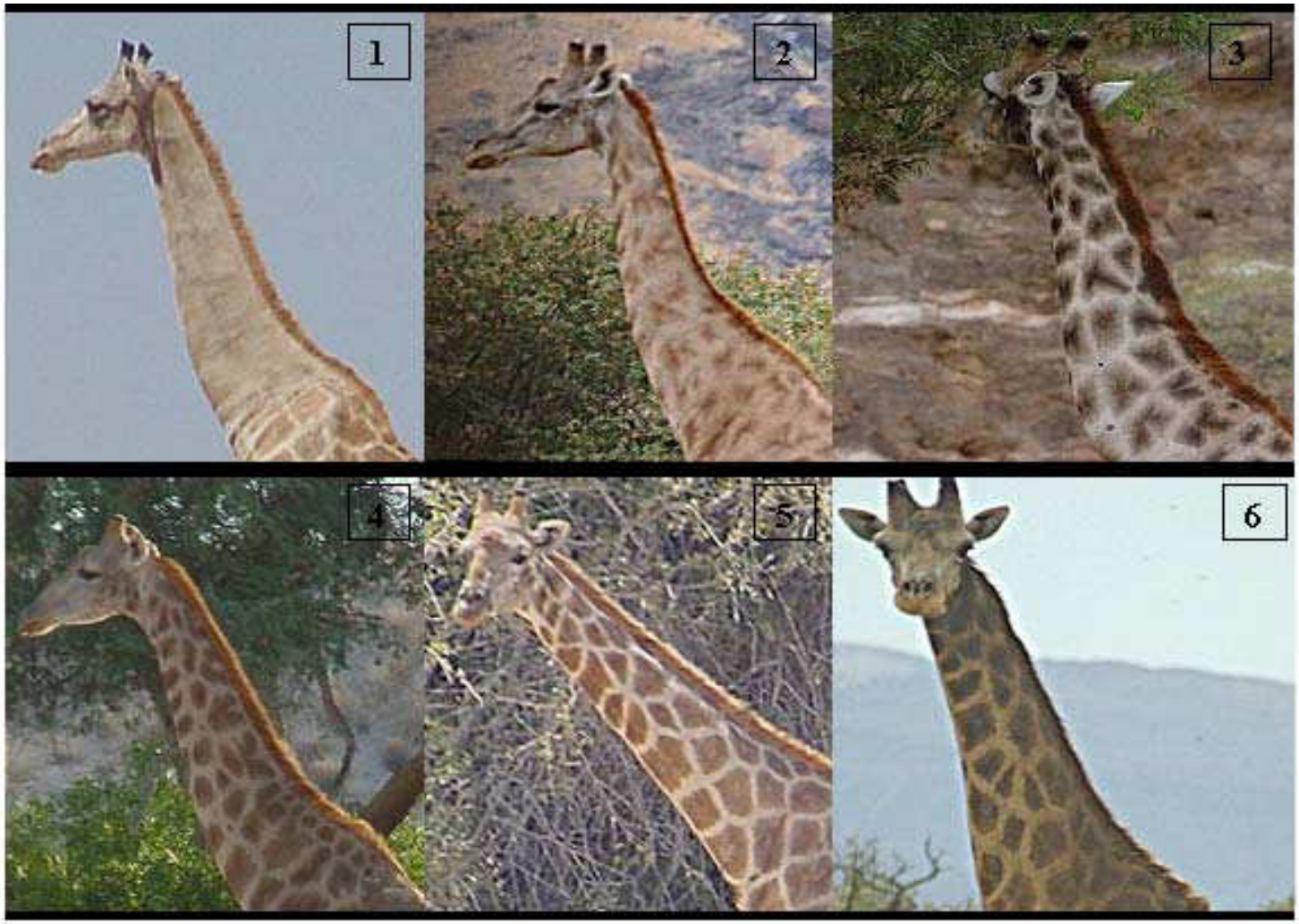
The benefits afforded by long-term research enable one to assess the past, and present processes which impact on giraffe and giraffe habitat, and provide a means to predict the effects of management. Our current knowledge of giraffe ecology represents primarily a 'snap shot' in time; long-term studies should hopefully provide greater insight into many aspects of ecology, including population dynamics, social structure, movements, habitat use, resource competition and the impact of seasonal and periodic climatic conditions. Furthermore, long-term research can be augmented by in-depth analysis of individuals and their associations in the population. By using emerging microsatellite screening methods, it should also be possible to ascertain paternal and maternal associations to explore the importance of apparent matrilineal structures. Such information could provide the basis for sound conservation and management of giraffe.

There is currently an assumption that numbers of giraffe are stable and the taxon is not threatened, and this seems to have allowed some lethargy to creep into the management of giraffe in Africa. Is little conservation really required? No one has yet established the true extent of change in historical and current numbers and range of giraffe, nor the effects of habitat loss, fragmentation and human development. Furthermore, if such beliefs as giraffe

meat being a panacea for HIV/Aids persist, the species may become seriously threatened. As observed for many wild species throughout the continent, giraffe have suffered marked reductions in range and available habitat (e.g. Skinner & Smithers, 1990; East, 1999). Future research should set to develop a model for giraffe conservation and management in Africa using one country, such as Namibia, as an example population. Similar models have been proposed or developed for other wild species (e.g. MacDonald, 1997; Anon, 2004b). By establishing a baseline of past, present and future range, genetic relationships and diversity, population dynamics and structure, a range of conservation and management objectives could be formulated and a model established. This model could be adapted and applied to populations throughout their extant range. Since Namibia has small but potentially stable populations of giraffe that reside both in and out of protected areas, as well as a good legislative and management base in rural areas (CBNRM), using it as a model seems practical.

The desert-dwelling giraffe of the northern Namib Desert have survived a multitude of recent impacts including war, habitat fragmentation and loss, predation, development, disease, drought, tourism and poaching events. The population is unique, not only in its ability to survive, but also to adapt in such a harsh and arid environment. The ecological importance of such a unique 'ecotype' should be enough to support its protected status, even before the added knowledge that the giraffe is one of Africa's most recognised yet little understood and charismatic megafauna.

Appendix 1.



Variation in pelage pattern (colour and spots) of giraffe bulls in the study region.

Appendix 2.

Locations, nomenclature, sex and age class of giraffe DNA biopsy samples obtained from giraffe from the study region and Etosha NP, October 2002.

Namibian Giraffe Genetic Samples					
Location	Nomenclature (Genetic)	Sex	Age	GPS South	GPS East
Etosha NP	ENP M1	M	Adult	-18.5858	16.88842
Etosha NP	ENP M2	M	Adult	-18.6775	16.89789
Etosha NP	ENP M3	M	Adult	-18.8176	16.93242
Etosha NP	ENP M4	M	Adult	-19.1611	15.99076
Etosha NP	ENP M5	M	Adult	-19.312	15.93868
Etosha NP	ENP M6	M	Adult	-19.1785	15.92287
Etosha NP	ENP M7	M	Adult	-19.3097	15.94291
Etosha NP	ENP F1	F	Adult	-18.7106	16.90167
Etosha NP	ENP F2	F	Adult	-18.7372	16.91571
Etosha NP	ENP F3	F	Sub Adult	-18.8208	16.92979
Etosha NP	ENP F4	F	Adult	-18.8216	16.92885
Etosha NP	ENP F5	F	Juvenile	-18.8149	16.9344
Etosha NP	ENP F6	F	Juvenile	-18.9177	16.72452
Etosha NP	ENP F7	F	Adult	-19.3092	15.93385
Etosha NP	ENP F8	M	Adult	-19.3069	15.9417
Hoanib River	HNB M1	M	Sub Adult	-19.2421	13.37168
Hoanib River	HNB M2	M	Adult	-19.3083	13.2676
Hoanib River	HNB M3	M	Adult	-19.3477	13.17382
Hoanib River	HNB M4	M	Adult	-19.2655	13.32759
Hoanib River	HNB M5	M	Adult	-19.3842	31.07459
Hoanib River	HNB M6	M	Adult	-19.3471	13.17762
Hoanib River	HNB M7	M	Adult	-19.2424	13.37185
Hoanib River	HNB F1	F	Sub Adult	-19.2685	13.32778
Hoanib River	HNB F2	F	Adult	-19.2922	13.2886
Hoanib River	HNB F3	F	Juvenile	-19.2922	13.28854
Hoanib River	HNB F4	F	Adult	-19.336	13.32759
Hoanib River	HNB F5	F	Adult	-19.3468	13.17888
Hoanib River	HNB F6	F	Adult	-19.3378	13.19799
Hoanib River	HNB F7	F	Adult	-19.1344	13.39611
Khumib River	KHB F1	F	Sub Adult	-18.6636	13.63874
Khumib River	KHB M1	M	Adult	-18.6543	12.65753
Khumib River	KHB M2	M	Sub Adult	-18.6543	12.65753
Khumib River	KHB M3	M	Sub Adult	-18.6638	12.64076

Appendix 3.

GenePop results (Hardy Weinberg probability test) of the sampled Etosha National Park giraffe populations.

Locus	*P*	±s.e.	FIS. W&C	FIS. R&H	FIS. Matr.
Etosha National Park					
NECK73	0.0314	0.0015	-0.016	+0.081	-
NECK102	1	0.0000	-0.037	-0.038	-
NECK334	0.0005	0.0001	+1	+1	-
NECK443	0.0063	0.0009	+0.451	+0.482	-
NECK447	-	-	-	-	-
NECK480	-	-	-	-	-
NECK484	0.0822	0.0044	-0.012	-0.039	-
NECK550	0.0192	0.0033	+0.205	0.102	-
NECK561	0.9146	0.0032	+0.038	0.022	-
NECK562	0.2127	0.0059	+0.467	+0.341	-
NECK567	-	-	-	-	-
NECK582	0.0029	0.0006	-0.742	-0.413	-
NECK626	0.0647	0.0039	+0.317	+0.438	-
NECK665	0.0178	0.0015	+0.397	+0.361	-
NECK748	0.0003	0.0002	+0.769	+0.638	-
NECK835	0.6386	0.0050	-0.340	-0.186	-
NECK1004	-	-	-	-	-

N.B. All (Fisher's method): χ^2: 90.9225; d.f. 26; $P<0.001$

GenePop results (Hardy Weinberg probability test) of the sampled Hoanib River study area giraffe population.

Locus	P	±s.e.	FIS. W&C	FIS. R&H	FIS. Matr.
Hoanib River study area					
NECK73	0.0007	0.0002	+0.438	+0.531	-
NECK102	1	0.0000	-0.037	-0.038	-
NECK334	0.0099	0.0005	+0.717	+0.761	-
NECK443	0.2886	0.0067	+0.188	+0.166	-
NECK447					-
NECK480	1	0.0000	-0.037	-0.038	-
NECK484	0.2268	0.0020	-0.400	-0.408	-
NECK550	0.0051	0.0007	+0.596	+0.555	-
NECK561	0.5579	0.0065	-0.098	-0.055	-
NECK562	1	0.0000	-0.050	-0.022	-
NECK567	0.1048	0.0014	+0.650	+0.688	-
NECK582	0.0005	0.0003	-0.780	-0.482	-
NECK626	0.0345	0.0021	+0.500	+0.036	-
NECK665	0.1404	0.0037	+0.344	+0.319	-
NECK748	0.0617	0.0036	+0.317	+0.438	-
NECK835	0.8915	0.0041	-0.098	-0.055	-
NECK1004	1	0.0000	-0.037	-0.038	-

N.B. All (Fisher's method): χ^2: 76.9695; d.f. 32; $P<0.001$

GenePop results (Hardy Weinberg probability test) of the sampled Hoarusib River study area giraffe population.

Locus	P	±s.e.	FIS. W&C	FIS. R&H	Matr.
Hoarusib River study area					
NECK73	0.1998	0.0036	+0.600	+0.6677	-
NECK102	-	-	-	-	-
NECK334	-	-	-	-	-
NECK443	0.5969	0.0075	+0.200	+0.111	-
NECK447	-	-	-	-	-
NECK480	-	-	-	-	-
NECK484	-	-	-	-	-
NECK550	0.2012	0.0018	+1	+2	-
NECK561	-	-	-	-	-
NECK562	-	-	-	-	-
NECK567	1	0.0000	-0.333	-0.375	-
NECK582	0.4015	0.0021	-1	-1	-
NECK626	1	0.0000	-0.143	-0.062	-
NECK665	0.2013	0.0016	+1	+2	-
NECK748	-	-	-	-	-
NECK835	1	0.000	-0.500	-0.375	-
NECK1004	-	-	-	-	-

N.B. All (Fisher's method): $\chi 2$:12.4907; d.f. 16; P=0.7096

GenePop results (Hardy Weinberg probability test) of the sampled Khumib River study area giraffe population.

Locus	*P*	±s.e.	FIS. W&C	FIS. R&H	Matr.
Khumib River study area					
NECK73	0.1407	0.0035	+0.625	+0.633	-
NECK102	-	-	-	-	-
NECK334	0.1434	0.0018	+1	+1	-
NECK443	0.03034	0.0068	+0.368	+0.361	-
NECK447	-	-	-	-	-
NECK480	-	-	-	-	-
NECK484	-	-	-	-	-
NECK550	0.1439	0.0018	+1	+1	-
NECK561	0.1424	0.0042	+0.500	+0.167	-
NECK562	-	-	-	-	-
NECK567	-	-	-	-	-
NECK582	0.3213	0.0019	-1	-1	-
NECK626	1	0.0000	-0.091	-0.028	-
NECK665	1	0.0000	-0.091	-0.028	-
NECK748	1	0.0000	-0.500	-0.533	-
NECK835	1	0.0000	-0.200	-0.222	-
NECK1004	-	-	-	-	-

N.B. All (Fisher's method): χ^2: 20.2953;d.f. 20; *P*=0.4396

Appendix 4.

Nomenclature and names of giraffe cows in the study region.*

Hoanib River				Hoarusib River		Khumib River	
HNBF1	Butterfly	HNBF27	Prego	HSBF1	Betty	KMBF2	Super Girl
HNBF2	Exclamation	HNBF28	Pseudovalentine	HSBF2	Etosha	KMBF3	Evelyn
HNBF3	Beany	HNBF29	Tornado	HSBF3	Bettunia	KMBF4	Cheli
HNBF4	Hannah	HNBF30	Windy	HSBF4	Fetosha	KMBF5	Bonnie
HNBF5	3-D	HNBF31	Pinwheel	HSBF5	G Spot	KMBF6	Minnie M
HNBF6	Beadie	HNBF32	Wednesday	HSBF6	Les	KMBF7	Bad Girl
HNBF7	Colloseum	HNBF33	Morticia	HSBF7	Bowling	KMBF7	Ghost
HNBF8	Daisy	HNBF34	Stephster	HSBF8	Porkchop		
HNBF9	Sandy	HNBF35	Swara	HSBF9	Kunene		
HNBF10	FOSA	HNBF36	Tuna	HSBF10	Salvadora		
HNBF11	Clover	HNBF37	Ice-Cream	HSBF11	Auntie Em		
HNBF12	FTD	HNBF38	Pebbles	HSBF12	Namibia		
HNBF13	Ragedy Ann	HNBF40	Deva	HSBF13	Dorothy		
HNBF14	Sailor	HNBF41	Ana				
HNBF15	S. A	HNBF42	July				
HNBF16	Angel	HNBF43	Cause				
HNBFF17	BAM	HNBF44	London				
HNBF18	Suzie Q	HNBF45	Tag-Y				
HNBF19	Ace	HNBF46	Pisa				
HNBF20	Bookie	HNBF47	Spiderwomen				
HNBF21	Fungus	HNBF48	May				
HNBF22	Thing	HNBF49	ABS				
HNBF23	Peach	HNBF50	Vert				
HNBF24	Madam X	HNBF51	Bellybutton				
HNBF25	Mutti	HNBF52	IT 1				
HNBF26	Parcel	HNBF53	IT 2				

*Grey box denotes adult, white subadult.

Nomenclature and names of giraffe bulls in the study region.*

Hoanib River		Hoarusib River		Khumib River	
HNBM1	Ambiguous	HSBM1	Blackjack	KMBM1	Wilber
HNBM2	Angelo	HSBM2	Bucket	KMBM2	Ryma
HNBM3	Big D	HSBM3	Andy	KMBM3	V
HNBM4	Birdman	HSBM4	Double V	KMBM4	Orion
HNBM5	George	HSBM5	Franky	KMBM5	KB
HNBM6	Sandman	HSBM6	Goofy	KMBM6	Longhorn
HNBM7	Geronimo	HSBM7	Jester	KMBM7	Shrubbery
HNBM8	Grey	HSBM8	Mr Big	KMBM8	Stubby
HNBM9	Leffelhund	HSBM9	Mr Brown	KMBM9	OJ
HNBM10	Obi 1	HSBM10	NFL		
HNBM11	One Spot	HSBM11	Oz		
HNBM12	Scarface	HSBM12	Picasso		
HNBM13	….Sharky	HSBM13	Pretzel		
HNBM14	Spotty	HSBM14	Rocketman		
HNBM15	U-Bolt	HSBM15	Scratchy		
HNBM16	Vader	HSBM16	Shoulders		
HNBM17	Chopper	HSBM17	Six Pack		
HNBM18	Fuzzhead	HSBM18	SSS		
HNBM19	Capone	HSBM19	Sting		
HNBM20	Criss-Cross	HSBM20	New Guy		
HNBM21	Red	HSBM21	Big Spot		
HNBM22	Elvis	HSBM22	Tower		
HNBM23	T2	HSBM23	Tumor		
HNBM24	Goober	HSBM24	Lone Ranger		
HNBM25	Retic	HSBM25	Dr Doom		
HNBM26	A2	HSBM26	Batman		
HNBM27	Harry	HSBM27	Bluey		
HNBM28	Maple	HSBM28	Pinto		
HNBM29	Rugby	HSBM29	Toto		
HNBM30	V-Neck	HSBM30	Nawa		
HNBM31	Tags	HSBM31	Fenno		
HNBM32	Bender				
HNBM33	Drummer				

*Grey box denotes adult, white subadult.

Nomenclature and names of juvenile giraffe in the study region.

Hoanib River	Hoarusib River	Khumib River
HNBJ1 Small Fly	HSBJ2 Kaoka	KMBJ3 Gilly
HNBJ6 Lil' Beadie	HSBJ4 Savannah	
HNBJ8 Pettle	HSBJ? Hair	
HNBJ11 Lucky		
HNBJ34 JJ		
HNBF39 Robin		
HNBJ? Squirt		
HNBJ? Sears		

Appendix 5.

Sex ratios of giraffe in the study region and Africa-wide.

Area	Sex Ratio			Source
	Bull		Cow	
Henderson Ranch, Zimbabwe	1	:	1.94	Dasmann, 1960*
Luangwa Valley, Zambia	1	:	1.67	Berry, 1973
Hoanib River, Namibia	1	:	1.6	Scheepers, 1992
Nairobi NP, Kenya	1	:	1.56	Bourliere, 1961
Wankie (Hwange) NP, Zimbabwe	1	:	1.27	Dasmann, 1960*
Arusha NP, Tanzania	1	:	1.1	Pratt & Anderson, 1982
Nairobi NP, Kenya	1	:	1	Foster, 1966
Nairobi NP, Kenya	1	:	1	Foster & Dagg, 1972
Niger	1	:	1	Le Pendu & Ciofolo, 1999
Lake Manyara NP, Tanzania	1	:	1	van der Jeugd & Prins, 2000
Northern Namib Desert, Namibia	1	:	0.99	This study
Tsavo East NP, Kenya	1	:	0.833	Leuthold & Leuthold, 1978
Amboseli GR, Kenya	1	:	0.69	Bourliere, 1961
Skeleton Coast Park, Namibia	1	:	0.6	Cooper, 1980
Luangwa Valley, Zambia	1	:	0.5	Berry, 1978
Fleur de Lys, South Africa	1	:	0.45	Innis, 1958

N.B: Adult/subadult combined, juveniles excluded. Source: *Foster & Dagg, 1972

Appendix 6.

Estimated giraffe densities Africa-wide.

Study Area	Size (km^2)	Density (n/km^2)	Source
Main camp area, Wankie (Hwange) NP, Zimbabwe		14.1	Dasmann, 1960*
El Karama Ranch, Kenya	37	6-12	Moore, 1974†
Arusha NP, Tanzania	119	3.96	Pratt & Anderson, 1982
Timbavati PNR, South Africa	183	3.4	Langman, 1973
Seronera, Serengeti NP, Tanzania	175-240	1.42-2.64	Pellew, 1983
Kruger NP, South Africa	19 500	2.5	Mills & Hes, 1997
Sweetwaters, Kenya	*ca*100	1.9	Birkett, 2002
Eldoret, Kenya	72	1.45	MacTaggart*
Fleur de Lys, Sth. Africa	80	1.2	Innis, 1958
Tarangire, Tanzania	*ca*100	1.13	Lamprey, 1964*
Isiolo, Kenya	1140	0.87	Stewart & Zaphiro, 1963
Lake Manyara NP, Tanzania	100	0.85	van der Jeugd & Prins, 2000
Serengeti NP, Tanzania	9 576	0.76	Sinclair, 1969*
Nairobi NP, Kenya	114	0.75	Foster & Dagg, 1972
Nairobi NP, Kenya	122	0.72	Foster, 1966
Lake Manyara NP, Tanzania	100	0.60	Prins & Douglas-Hamilton, 1990
Serengeti NP, Tanzania	12 800	0.56	Schaller, 1969*
Ruaha NP, Tanzania	9 640	0.34	Barnes & Douglas-Hamilton, 1982
Mara Plains, Kenya	2 560	0.27	Darling, 1960
Wambo, Congo	1 680	0.22	Stewart & Zaphiro, 1963
Tarangire + GCAs, Tanzania	8 359	0.17	Campbell & Huish, 1991∞
Kruger NP, South Africa	19 500	0.16	Hall-Martin, 1975
Sth of Garamba NP, Congo		0.16	Backhaus, 1961
Tsavo East NP, Kenya	*ca*75	0.3	Leuthold, 1979
Masai Ecosystem	35 000	0.07	van der Jeugd & Prins, 2000
Baragoi, Kenya	2 040	0.01	Stewart & Zaphiro, 1963
Niger		0.01	Le Pendu *et al*., 2000
Northern Namib Desert, Namibia	72 000	0.01	This study

Sources: *Foster & Dagg, 1972; †Leuthold & Leuthold, 1978; ∞van der Jeugd & Prins, 2000

Appendix 7.

Observed herd sizes of giraffe, expressed as percentages, from selected populations Africa-wide.

	Fleur de Lys South Africa†	Nairobi NP Kenya∞	Serengeti NP Tanzania+	Other areas Africa wide+
Herd Size	151	439	147	75
1	44.4%	23.0%	16.3%	24.0%
2	13.2	17.1	10.9	13.3
3	8.6	13.7	8.9	9.3
4	1.0	10.7	10.2	16.0
5	8.6	9.8	8.9	6.7
6	6.6	7.1	8.9	2.7
7	2.6	4.5	0.7	6.7
8	2.0	4.5	2.0	2.7
9	1.3	1.9	6.1	6.7
10	0.7	1.9	3.4	1.3
11	0.7	1.6		
12		0.7	2.7	1.3
13		1.0	2.7	1.3
14		0.4	0.7	
15	1.3	1.4	3.4	
16		0.4	0.7	2.7
17		0.2		
18		0.2	0.7	
19			2.0	
20			1.4	
21			1.4	
22			1.4	1.3
23				
24				
25			0.7	1.3
26			0.7	
27			0.7	
28			1.4	
29				
30			2.0	
31				
32				
33				1.3
34				
35			0.7	
≈				
45				1.3
46				
47			0.7	

†Innis, 1958; ∞Foster, 1966; +Foster & Dagg, 1972

Appendix 8.

GPS satellite collar configurations and specifics for study of giraffe.

Internal configuration data	
• Data generated from the unit's ports, inputs and outputs • Pre-scheduled reporting of GPS data (i.e. latitude, longitude, speed, heading), digital • Input status, analogue input level, input voltage and temperature • Event-triggered reporting of GPS data, RS 232 short message input, or digital or analogue input conditions	
Physical characteristics	
• Dimensions (W x H x D)	15,7 x 10.6 x 3.5 (cm)
• Weight	< 900mg
• Receive frequency band	1525 to 1559 MHz
• Transmit frequency band	1626.5 to 1660.5 MHz
• Power consumption	Sleep, Transmit, Receive
• Processing	0.4 mA, 2200 mA, 125 mA, 40 mA
Receive antenna	
• Element type	Microstrip PCB patch
• Polarisation	RHC
• Number of elements	1
• Azimuth antenna coverage	0° to 360°
• Elevation coverage for	20° to 60°
• Elevation coverage for GPS communications link	0° to 90°
Transmit antenna	
• Element type	Microstrip PCB patch
• Polarisation	RHC
• Number of elements	1
• Azimuth antenna coverage	0° to 360°
• Elevation coverage	25° to 60°
GPS subsystem	
• GPS receive band	1575.42 plus / minus 1 MHz
Parameter	
• Location accuracy	100m 2° RMS
• Speed accuracy	1 m/s; (2.2 mph)
• Heading accuracy	5°
Mean time to position fix	
• Cold initialise	< 2 minutes @ 20° C
• Hot initialise	< 30 seconds @ 20° C
Main input power port	
• Input voltage	4 to 9 VS. DC
• Peak input current	2 A
• Reverse power survival	15 VS. DC for external resistance greater than 3ohms
Collar	
• 3 ply machine belting	

Appendix 9.

Specifications of GPS satellite collared giraffe, including nomenclature, age, sex, date collared, collaring time, collaring frequency and drugs used, September, 2002.

Nomenclature (Name)	Sex	Age Class	Collared Date	Location	GPS °S	GPS °E	Collar No.	Collar Frequency	Dosage* (A3080)	Blood & Genetics	Down Time**
HNBM17 (Chopper)	Bull	Subadult	30/09/02	Hoanib River	-19.34653	13.16715	1	148.150	16 mg	Yes	4.30 min
HNBF18 (Suzie Q)	Cow	Adult	30/09/02	Hoanib/Mudorib	-19.33013	13.23291	2	148.200	13 mg	Yes	4.20 min
HSBM12 (Picasso)	Bull	Adult	28/09/02	Gomatum River	-18.78531	12.97938	3	148.300	14 mg	Yes	<6 min
HSBM3 (Andy)	Bull	Adult	28/09/02	Gomatum River	-18.78531	12.97938	4	148.360	14 mg	Yes	<6 min

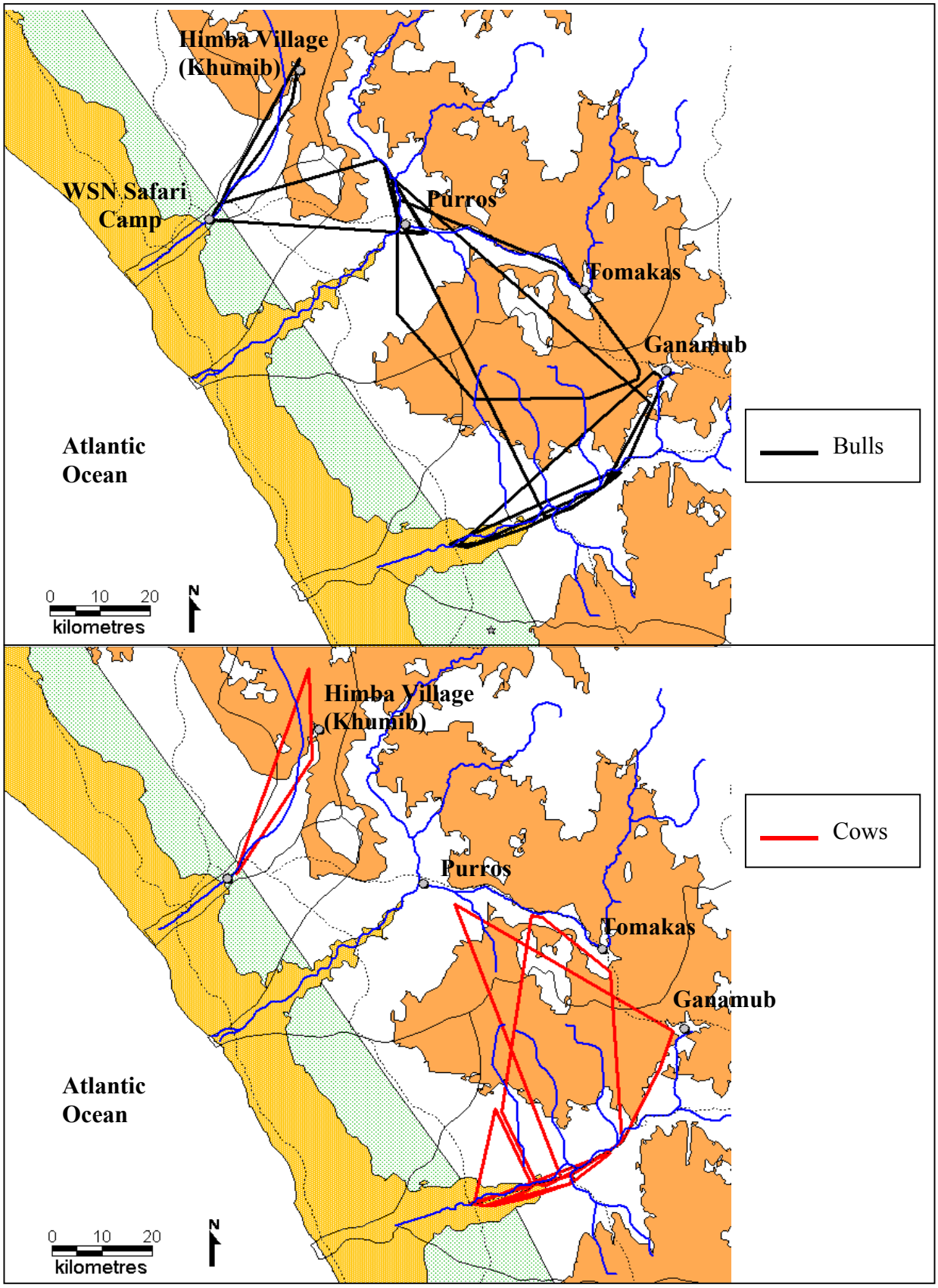
*Dosage – drug used to sedate the giraffe was A3080; **Down Time – period for which the giraffe were sedated.

Appendix 10.

Giraffe bull home range estimates (km^2) of bull giraffe in the study region.

	Hoarusib River			Hoanib River			Khumib River	
	MCP			MCP			MCP	
	100%	95%		100%	95%		100%	95%
HSBM1	111.5	25.07	HNBM1	1173	26.9	KMBM2	68.09	23.68
HSBM2	800	32.4	HNBM2	320.2	43.97	KMBM3	66.06	21.78
HSBM3	1260	1092	HNBM3	920.8	862.1			
HSBM4	805.8	20.59	HNBM4	72.83	46.79			
HSBM5	397.2	50.83	HNBM5	402.7	348.6			
HSBM6	611.9	490.9	HNBM6	445.3	28.89			
HSBM7	822.7	378.2	HNBM7	235.9	32.2			
HSBM8	3377	226.4	HNBM8	1538	1290			
HSBM9	878.7	701.5	HNBM9	94.23	79.81			
HSBM10	805.8	19.64	HNBM10	1950	1773			
HSBM11	219.3	71.77	HNBM11	539.6	97.22			
HSBM12	2962	784.3	HNBM12	356.6	305.7			
HSBM13	1532	1492	HNBM13	508.4	264.7			
HSBM14	1627	63	HNBM14	128.3	11.46			
HSBM15	1102	1059	HNBM17	222.2	214.9			
HSBM17	800.6	18.3	HNBM18	282.4	136			
HSBM18	915.2	669.4	HNBM19	1278	999.8			
HSBM19	437.6	274	HNBM22	26.67	14.87			
HSBM20	231.2	49	HNBM23	953.2	273.4			
HSBM21	589.7	18.78	HNBM26	1169	242.8			
HSBM24	1303	1295						
HSBM26	33.97	14.93						
Mean	982.92	402.14		652.38	362.01		67.08	22.73

Appendix 11.



Selected home ranges of giraffe bulls and cows in the study region.

Appendix 12.

Home range size estimates of giraffe populations Africa-wide.

Study Area	Density (n/km^2)	Home Range (km^2) Mean	Home Range (km^2) Range	n	Source (Year)
Bulls					
Niger (non-resident)	0.01	992	202-1564	8	Le Pendu & Ciofolo, 1999
(resident)	0.01	641	127-1559	6	
Tsavo NP [K]	0.1-0.3	164	5-654	60	Leuthold & Leuthold, 1978
Luangwa Valley [Z]		82	-145	14	Berry, 1978
Nairobi NP [K]	0.72	62		10	Foster & Dagg, 1972*
Timbavati PNR [S]	3.28	23		2	Langman, 1973
El Karama Ranch [K]	6-12	16.5			Leuthold & Leuthold, 1978
Lake Manyara [T]	0.85	5.2	0.1-21.5		van der Jeugd & Prins, 2000
Cows					
Niger (non-resident)	0.01	487	200-1307	5	Le Pendu & Ciofolo, 1999
(resident)	0.01	324	151-1378	14	
Kruger NP [S]		282		1	du Toit, 1990
Tsavo NP [K]	0.1-0.3	162	9-484	50	Leuthold & Leuthold, 1978
Serengeti NP, [T]	1.47	120			Pellew, 1984b
Nairobi NP [K]	0.72	85		10	Foster & Dagg, 1972*
Luangwa Valley [Z]	?	68	-82	4	Berry, 1978
Timbavati PNR [S]	3.28	25		3	Langman, 1973
	3.28	41		1	Langman, 1977
El Karama Ranch [K]	6-12	13			Leuthold & Leuthold, 1978
Lake Manyara [T]	0.85	8.6	0.5-27		van der Jeugd & Prins, 2000
Juveniles					
Timbavati PNR [S]	3.28	13			Langman, 1973

NB: [K] - Kenya; [S] – South Africa; [T] - Tanzania; [Z] – Zambia; All home ranges calculated by convex polygon, except *Foster & Dagg used dot grid method.

Appendix 13.

Seasonal diurnal activities of giraffe cows in the study region expressed as a percentage, standard deviation and range.

	Season								
	Wet			Cold-dry			Hot-dry		
Activity	Mean (%)	±S.D	Range (%)	Mean (%)	±S.D	Range (%)	Mean (%)	±S.D	Range (%)
Cows									
Feeding	60.94	±11.70	39-73	65.71	±10.30	53-81	55.95	±14.20	31-69
Ruminating	7.00	±6.70	0-21	8.34	±6.10	1-24	9.46	±5.80	2-19
Resting	13.19	±11.20	1-33	7.92	±6.60	2-22	16.20	±13.60	3-40
Walking	15.88	±5.90	8-26	14.97	±4.20	11-24	15.71	±6.10	9-29
Grooming	0.73	±0.80	0-3	0.66	±2.20	0-4	0.53	±0.30	0-1
Vigilance	1.98	±2.90	0-10	1.92	±2.20	0-7	1.26	±0.60	0-2
Interaction	0.18	±0.39	0-0.14	0.10	±0.10	0-0.4	0.14	±0.13	0-0.3
Sex. behaviour	0.01	±0.04	0-0.14	0.04	±0.04	0-0.2	0.02	±0.04	0-0.1
Excretion	0.09	±0.12	0-0.4	0.24	±0.24	0-0.13	0.13	±0.13	0-0.4
Drinking	0	0	0	0.10	±1.10	0-1	0.58	±2.00	0-7

Seasonal diurnal activities of giraffe bulls in the study region expressed as a percentage, standard deviation and range.

Activity	Season								
	Wet			Cold-dry			Hot-dry		
	Mean (%)	±S.D	Range (%)	Mean (%)	±S.D	Range (%)	Mean (%)	±S.D	Range (%)
Bulls									
Feeding	48.74	±15.20	25-79	50.44	±8.30	37-60	53.12	±12.90	33-68
Ruminating	14.13	±5.60	1-21	14.52	±6.50	7-23	10.67	±7.10	1-23
Resting	14.87	±12.80	1-46	11.30	±8.00	3-25	13.68	±14.00	1-40
Walking	18.11	±7.60	8-39	17.01	±5.70	9-26	18.15	±6.70	9-32
Grooming	0.89	±0.60	0-2	0.55	±0.20	0-1	0.86	±0.50	0-2
Vigilance	1.96	±1.30	0-5	2.57	±3.30	0-12	1.35	±0.80	0-2
Interaction	0.79	±1.00	0-3	3.41	±2.60	0-10	1.33	±2.00	0-7
Sexual Behaviour	0.21	±0.20	0-1	0.07	±0.10	0-0.2	0.51	±0.60	0-2
Excretion	0.20	±0.20	0-0.6	0.13	±0.10	0-0.3	0.04	±0.10	0-0.3
Drinking	0.12	±0.40	0-1	0	0	0	0.29	±1.00	0-3

Seasonal diurnal activities of juvenile giraffe in the study region expressed as a percentage, standard deviation and range.

	Season								
	Wet			Cold-dry			Hot-dry		
Activity	Mean (%)	±S.D	Range (%)	Mean (%)	±S.D	Range (%)	Mean (%)	±S.D	Range (%)
Juveniles									
Feeding	60.15	±14.70	31-79	±47.38	±15.40	19-68	45.26	±23.00	12-78
Ruminating	6.42	±7.30	0-21	3.14	±4.10	0-14	8.90	±10.30	0-31
Resting	14.36	±14.30	1-42	±30.99	±22.60	6-68	25.40	±25.40	0-66
Walking	15.44	±6.90	7-27	±14.54	±10.40	1-38	15.09	±9.80	4-31
Grooming	0.77	±0.90	0-3	1.98	±2.90	0-10	1.06	±1.10	0-4
Vigilance	2.55	±2.80	0-10	0.77	±1.10	0-3	3.40	±2.90	0-10
Interaction	0.22	±0.40	0-1	1.20	±1.50	0-5	0.70	±1.30	0-4
Sex. behaviour	0	0	0	0	0	0	0	0	0
Excretion	0.09	±0.14	0-0.4	0	0	0	0.19	±0.31	0.09
Drinking	0	0	0	0	0	0	0	0	0

Appendix 14.

Publication:

- Fennessy, J. 2003. Palewinged Starling gleaning on desert dwelling Giraffe, northwestern Namibia. *Bird Numbers*. **12(1)**: 20-21.

The Yellowbilled Oxpecker *Buphagus africanus*, Redbilled Oxpecker *B. erythrorhynchus,* Cattle Egret *Ardeola ibis* and Forktailed Drongo *Dicrurus adsimilis* have all been observed in direct feeding association with Giraffe *Giraffa camelopardalis* (Innis 1958; Berry 1973; Tilson 1977; Dean & MacDonald 1981; Maclean 1993). While the first two are highly adapted obligate ectoparasite gleaners, the latter two species are facultative ectoparasite gleaners that otherwise actively prey upon insects incidentally flushed by mammals (Dean & MacDonald 1981).

The allopatric Palewinged Starling *Onychognathus nabourup* has been observed to have an affinity with Klipspringer *Oreotragus oreotragus,* similar to that of the Redwinged Starling *O. morio* in the southern part of its distribution range (Tilson 1977). Starling/Klipspringer feeding relationships are a commonly observed bird/mammal feeding association (Tilson 1977; Dean & MacDonald 1981; Maclean 1993). The feeding strategy of such ectoparasite gleaners is almost entirely restricted to open habitats and areas of increased biomass of large mammals. Therefore areas such as Namibia offer increased potential for the development of bird/mammal feeding associations (Dean & MacDonald 1981).

A number of recent observations of Palewinged Starlings gleaning from giraffe *Giraffe camelopardalis angolensis* in northwestern Namibia, are the first known annotated records, although observations of their gleaning on Klipspringers and other mammals have been recorded (Tilson 1977; Dean & MacDonald 1981; Maclean 1993). Both Redbilled and Yellowbilled Oxpeckers regularly glean giraffe, as well as a host of other wildlife and livestock species throughout Africa. These birds, however, do not occur in the study area. In Namibia, Palewinged Starlings have been observed occasionally gleaning on other mammals, including klipspringer, Hartmann's mountain zebra *Equus zebra hartmannae* (Joubert 1972) and gemsbok *Oryx gazella* (Dean & MacDonald 1981), while Cape Glossy *Lamprotornis nitens* and Wattled Starlings *Creatophora cinerea* have been seen gleaning from gemsbok in the Skeleton Coast Park (Bridgeford, 1985b).

It has been suggested that starlings occupy the feeding niche filled elsewhere by Oxpeckers (Bean *in* Tilson 1977). Gargett (*in* Tilson 1977) postulated that in areas where Redwinged Starling and klipspringer cohabitat, starlings will exploit the gleaning niche, but only in environs where Oxpeckers are excluded. The Palewinged Starling's distribution, unlike that of the Redwinged Starling, does not overlap that of the oxpeckers (Tilson 1977; Harrison *et al*. 1997).

Of the four separate observations, the following is an account of the first occasion. Two Palewinged Starlings were observed, for c.15 min, gleaning arthropod ectoparasites from two giraffe cows (one adult and one sub-adult), in the Hoanib River study area (19.30523°S, 13.27019°E) in the cold-dry season 2002.

The giraffe were content while the Palewinged Starlings were gleaning, except when the ears and head were the target areas. The starlings concentrated their gleaning activities on the mane and back of the giraffe, as well as the underbelly and tail hair.

While gleaning on both the mane and back, the starlings perched for up to 30 seconds at a time. On four separate occasions, the giraffe shrugged its body to displace the birds. However, they returned to the host and continued gleaning immediately. On another six occasions, while hovering and gleaning from the tail hair of the giraffe, the starlings flew off into nearby branches of the *Faidherbia albida* between bouts. Gleaning from tail hair has been observed in other bird/ mammal feeding associations (Dean & MacDonald 1981; Maclean 1993). In this observation, however, concentration on the whole tail rather than the base and nearby orifices, was significant.

The desert dwelling giraffe populations in the study area do not appear to rely heavily upon the gleaning of ectoparasites by birds for grooming, although observations suggest that it is not uncommon. However, they have been regularly observed using small shrubs and bushes, for example *Colophospermum mopane, Salvadora persica* and *Pechuel-Loeschea leubnitziae*, and tree branches of, for example, *F. albida, Acacia erioloba* and *A. tortilis,* to scratch themselves (pers. obs.). This behaviour is assumed to assist in the removal of ectoparasites as large ticks are obvious and parasite load, although not measured, is estimated high.

A number of other ectoparasite gleaning observations in northwestern Namibia have been recorded. Both Pied Crow *Corvus albus* and Black Cows *C. capensis* were observed gleaning ectoparasites from gemsbok in the study area (Bridgeford, 1985b; J. Bartlett & B. Paterson pers. comm.). Both crow species have been observed in feeding associations with other mammals throughout their range (Dean & MacDonald 1981; Maclean 1993), included records of perching on giraffe in the study area (R. Braby pers.comm.), although no gleaning behaviour was reported.

It is assumed that the feeding association of African Sturdinae (Starlings and Oxpeckers) with mammals evolved when prey were flushed out by mammals. This subsequently led to the birds perching on the host mammals, and finally evolved to gleaning of ectoparasites on the host mammals (Dean & MacDonald 1981). The evolution of bird/ mammal feeding associations in areas where facultative ectoparasite gleaning is commonly observed, positively correlates with the absence of specialist ectoparasite gleaners from the same habitat (Dean & MacDonald 1981). Such a scenario is observed in Namibia's arid northwest where it is assumed that the evolutionary process is dynamic. The feeding niche of the Palewinged Starling and other facultative ectoparasite gleaners may become more obvious with increased research.

Appendix 15.

Preferred forage use of giraffe in the Hoanib River study area.

Season	←Hot-dry→		←Wet→			←Cold-dry→			←Hot-dry→					
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Combined Mean (%)	Seasonal use comparisons (P)*
Faidherbia albida	34	10	23	26	18	45	25	23	12	17	9	46	24	0.145
F. albida (pods)	17	4	4	5	8	4	4	2	2		3	21	(6.2)	(0.041)
Acacia erioloba & tortillis	31	23	42	28	18	20	36	33	31	17	35	21	27.9	0.487
Salvadora persica	17	17	7	14	24	22	18	28	23	22	32	20	20.3	0.026
Combretum wattii	3	8		4	13	1	6	3		13		4	4.6	0.330
Cordia sinensis		3	4		1	1	5	4	2		3	1	2	0.121
Colophospermum mopane	11	15	4	3	9	3		2	2	17	16	9	7.6	<0.001
Maerua schinzii		9				1	2	2	8		3		2.1	0.180[a]
Euclea pseudebenus	3	13	21				1	3		4			3.8	<0.001
Termanalia prunioides		1											<0.1	*i*
Combretum imberbe				1	1	1	2	1					0.5	*i*
Tamarix usneoides				3	1	2			3	4			1.1	0.735
Parkisonia africana							1		7				0.7	*i*
Mundulea sericea								2	7	4			1.1	0.206
Catophractes alexandrii				1									<0.1	*i*
Pechuel-Loeschea leubnitziae						1							<0.1	*i*
Calicorema capitata									2				0.2	*i*
Adenolobus gariepina													<0.1	*i*
Commiphora spp.													<0.1	*i*
Grass spp.				5					2				0.6	0.034[∞]
Tribulus zeyheri				13	16	1	2						2.7	<0.001
Zygophylum maxima									2				0.2	*i*
Zygophylum simplex						3							0.2	*i*
Forb (annnual)		1					2	1					0.3	*i*
Forb (annual)				1									<0.1	*i*

*χ^2 test; P<0.05; all seasonal; [†]cold-dry vs. hot-dry season only; *i*, insufficient data; [∞]wet vs. hot-dry season; *i*, insufficient data

Appendix 16.

Preferred forage use of giraffe in the Hoarusib River study area.

Season	← Hot-dry →		← Wet →			← Cold-dry →			← Hot-dry →					
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Combined Mean (%)	Seasonal use comparisons (P)*
Faidherbia albida	9		23		13	14	13	2	16	2		6	8.9	0.338
F. albida (pods)	3				3								(0.5)	*(i)*
Acacia erioloba & tortillis	62		23	55	40	50	45	47	44	22	30	51	42.6	0.591
Salvadora persica	15		15	36	11	9	8	20	28	16	20	14	17.4	0.568
Combretum wattii			8			5		1	3	31		17	5.9	<0.001
Colophospermum mopane	6				7	9		4	3	16	5		4.6	0.417
Maerua schinzii					2		3	5		4	10		2.2	0.497
Euclea pseudebenus							3	11					1.2	0.004†
Balanites welwitschtii	6		15	9	19	14	21	10	6	4	30	6	12.7	0.057
Combretum. imberbe			15				5			6		6	2.9	0.607
Tamarix usneoides					2		3						0.4	*i*
Mundulea sericea											5		0.4	*i*
Calicorema capitata													<0.1	*i*
Adenolobus gariepina													<0.1	*i*
Commiphora spp.													<0.1	*i*
Grass spp.					2								0.2	*i*
Tribulus zeyheri					3								0.3	*i*
Forb (annual)					3								0.3	*i*

*χ^2 test; $P<0.05$; all seasonal; †cold-dry vs. hot-dry season only; *i*, insufficient data

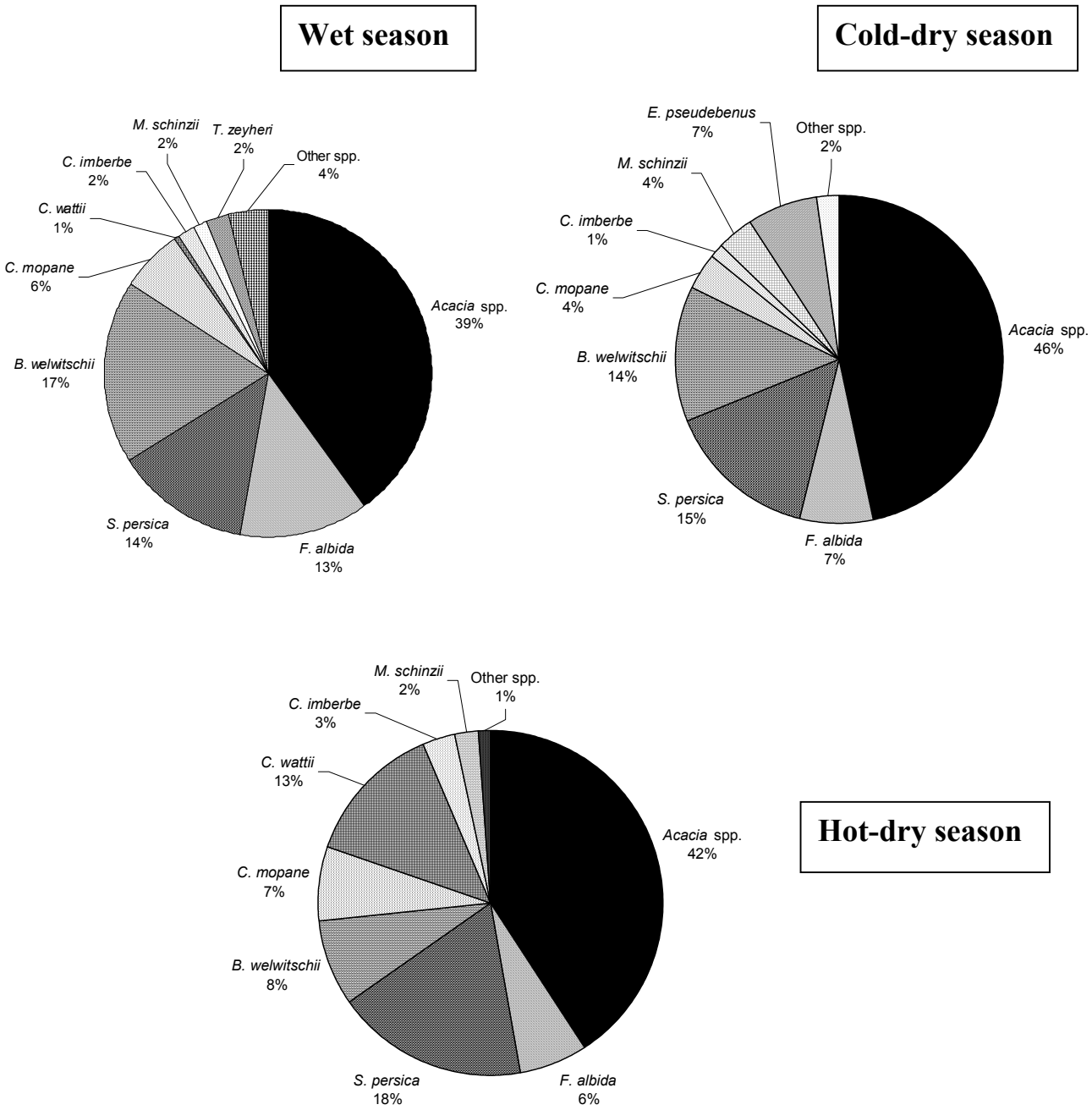
Appendix 17.

Preferred forage use of giraffe in the Khumib River study area.

Season	← Hot-dry →		← Wet →			← Cold-dry →			← Hot-dry →				
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Combined Mean
Faidherbia albida								12					2
Acacia erioloba	11		50		43			4				10	19.7
Salvadora persica	17					8						15	6.6
Combretum wattii												8	1.3
Colophospermum mopane			50		57	28		32				25	32
Maerua schinzii								4				3	1.1
Balanites welwitschtii						51		20				10	13.5
Combretum imberbe	28					8		24				10	11.6
Tamarix usneoides												8	1.3
Salsola spp.						5							0.8
Acanthosicyos horrida	22							4				3	4.8
Rhigozium spp.	22											5	4.5
Forb *(Cleome)* spp.												5	0.8

N.B. Insufficient observation for seasonal forage use comparisons

Appendix 18.



Seasonal selection of different plant species by giraffe in the Hoarusib River study area, expressed as percentages of total numbers of foraging observations.

Appendix 19.

Woody plant densities, mean heights and percentage plant availability across two preferred giraffe habitat types in the study region (adapted from Viljoen , 1988).

Woody plant species	Density plant per hectare	Plant height (m) Mean ± s.d.	Percentage plant availability
Riparian woodland			
Acacia spp. (tortilis & erioloba)	3.07	5.83 ± 3.94	9.05
Balanites welwitschii	1.80	3.02 ± 1.25	5.41
Boscia foetida	1.31	1.84 ± 1.43	3.94
Colophospermum mopane	6.85	4.02 ± 2.17	20.73
Combretum imberbe	1.52	4.24 ± 4.25	4.56
Combretum wattii	0.10	1.03 ± 0.78	0.31
Cordia sinensis	0.26	2.02 ± 0.61	0.77
Euclea pseudebenus	0.46	2.63 ± 1.04	1.39
Faidherbia albida	3.68	5.62 ± 5.32	11.83
Maerua schinzii	0.28	3.61 ± 2.15	1.08
Mundulea sericea	0.33	0.82 ± 0.06	1.01
Pechuel-Loeschea leubnitzea…	2.22	1.08 ± 0.18	6.65
Salsola spp.	5.31	0.62 ± 0.21	15.93
Salvadora persica	3.09	2.52 ± 1.33	9.59
Sueda plumosa	1.03	0.58 ± 0.19	3.09
Tamarix usneoides	1.55	3.29 ± 0.99	4.64
Mountain habitat			
Colophospermum mopane	0.36	1.00 ± 0	0.18
Pachypodium lealii	1.09	1.57 ± 0.81	0.55
Sesamothamnus spp.	0.36	1.00 ± 0.00	0.18
Termenalia prunioides	4.73	1.70 ± 0.28	2.38
Boscia foetida	8.00	1.18 ± 0.81	4.03
Parkisonia africana	1.82	2.50 ± 1.41	0.92
Adenolobus spp.	2.91	0.13 ± 0.06	1.47
Commiphora kraeuseliana	19.27	0.92 ± 0.24	9.71
Commiphora multijuga	1.09	1.5 ± 0.50	0.55
Maerua schinzii	2.91	2.63 ± 1.06	1.47
Commiphora virgata	22.55	0.82 ± 0.26	11.36
Commiphora wildii	9.82	0.52 ± 0.21	5.49
Commiphora saxicola	27.27	0.61 ± 0.63	13.74
Euphorbia damarana	10.55	1.64 ± 0.51	5.31
Calicorema capitata	3.27	0.40 ± 0.18	1.65
Petalidium spp.	81.82	0.38 ± 0.19	41.21
Salvadora persica	0.36	0.50 ± 0	0.18
Catophractes alexandri	0.36	0.50 ± 0	0.18

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