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
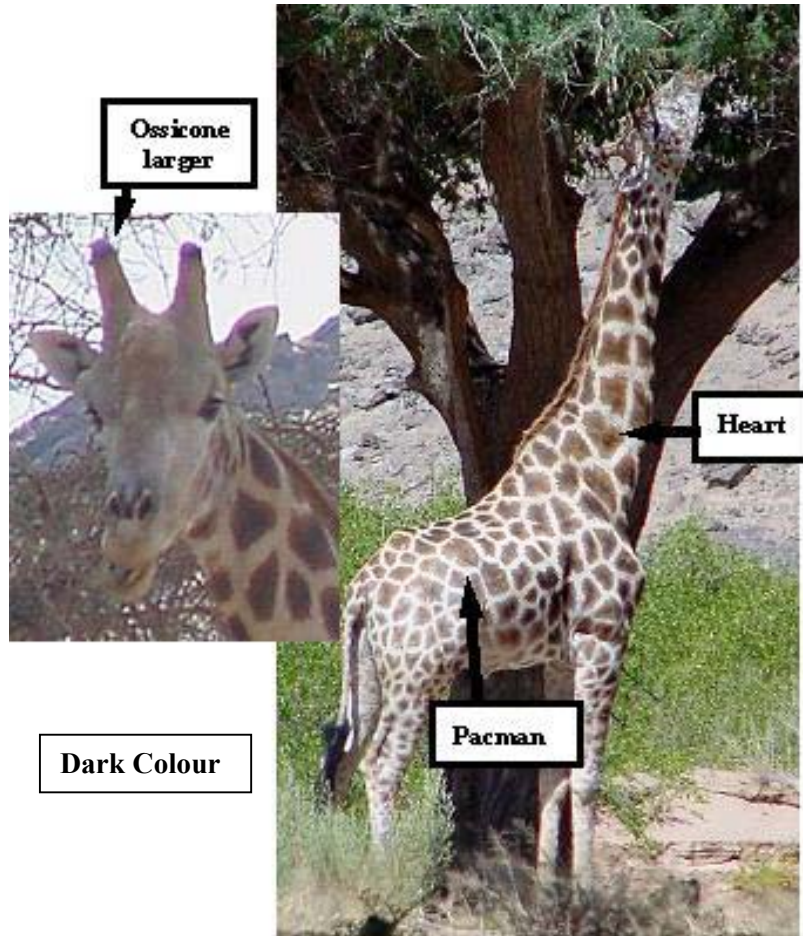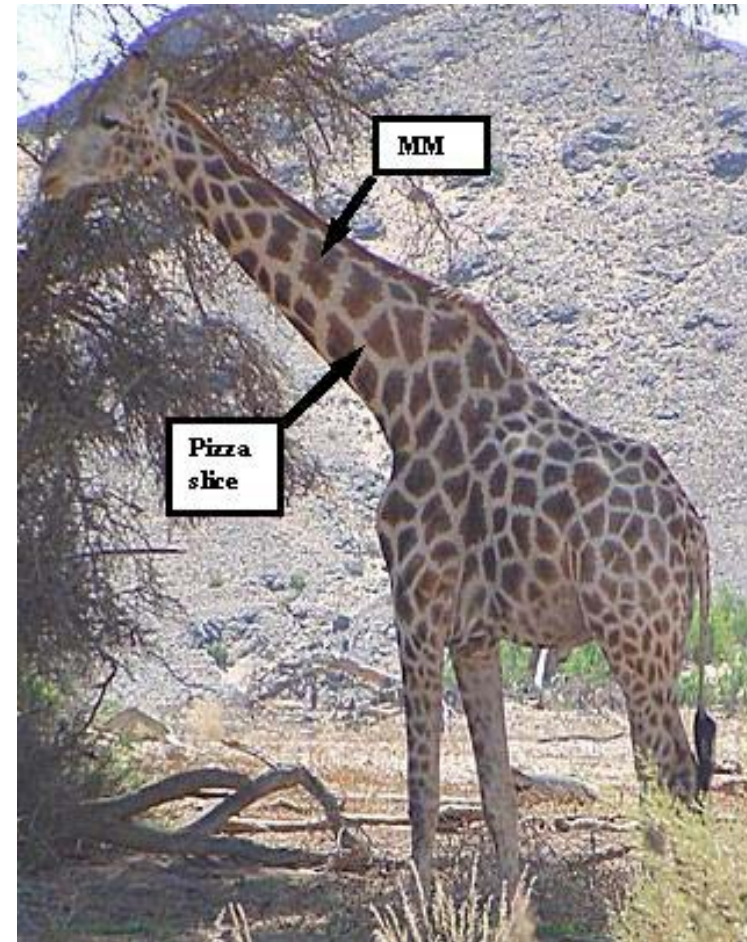
Figure 4.1. Example of giraffe identification field manual developed during this study.
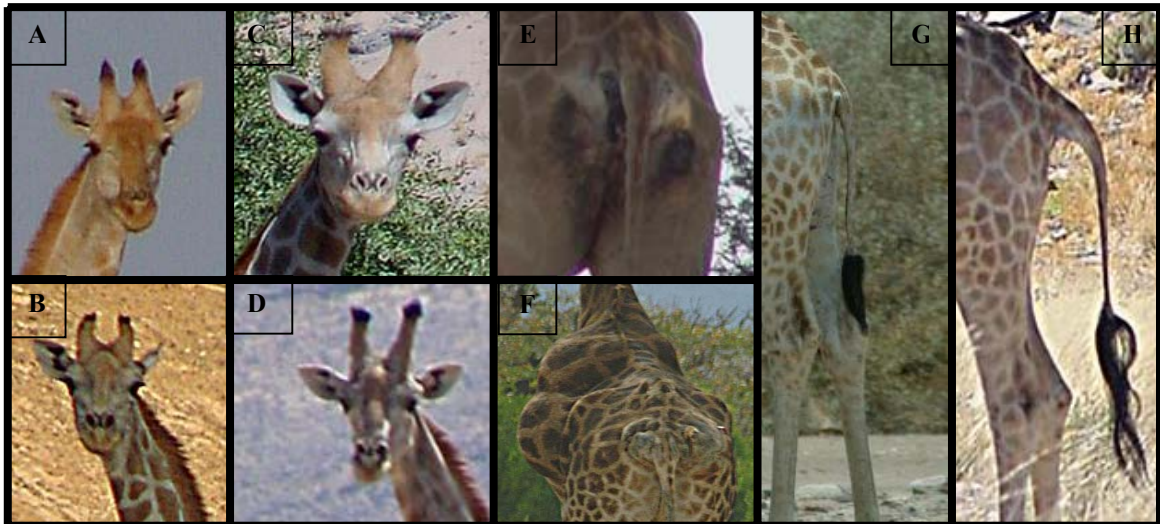
Figure 4.2. Prominent identification features used to assist in recognising individual giraffe in the study region [(A-D) ossicones; (E) markings; (F) tumours; (G-H) tail length].

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).

	n	Wet season			Cold-dry season			Hot-dry season					
		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																Total herd no.	Mean herd size (± s.d.)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	21		
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 $\geq$ 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.
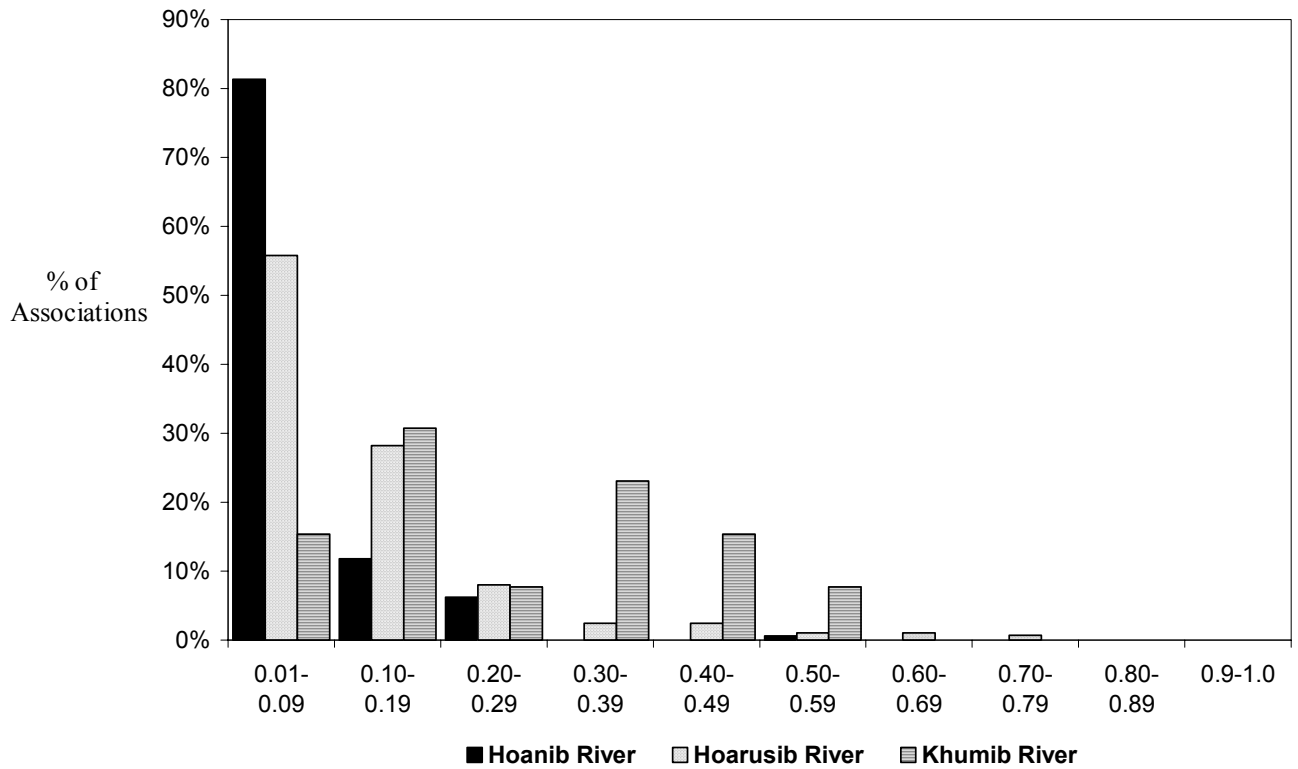
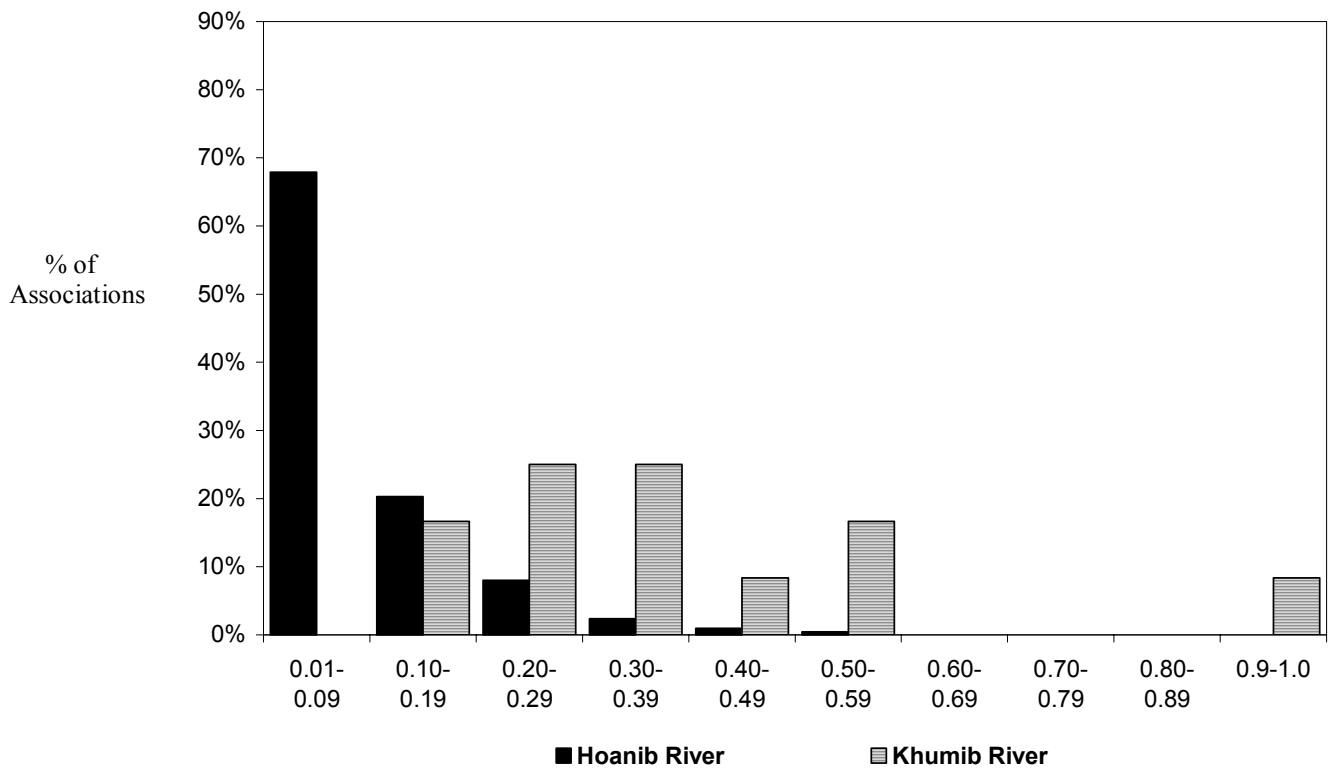Figure 4.3. SR Index for inter-individual dyad associations of giraffe bulls in the study region.

Figure 4.4. SR Index for inter-individual dyad associations of giraffe cows in the study region.
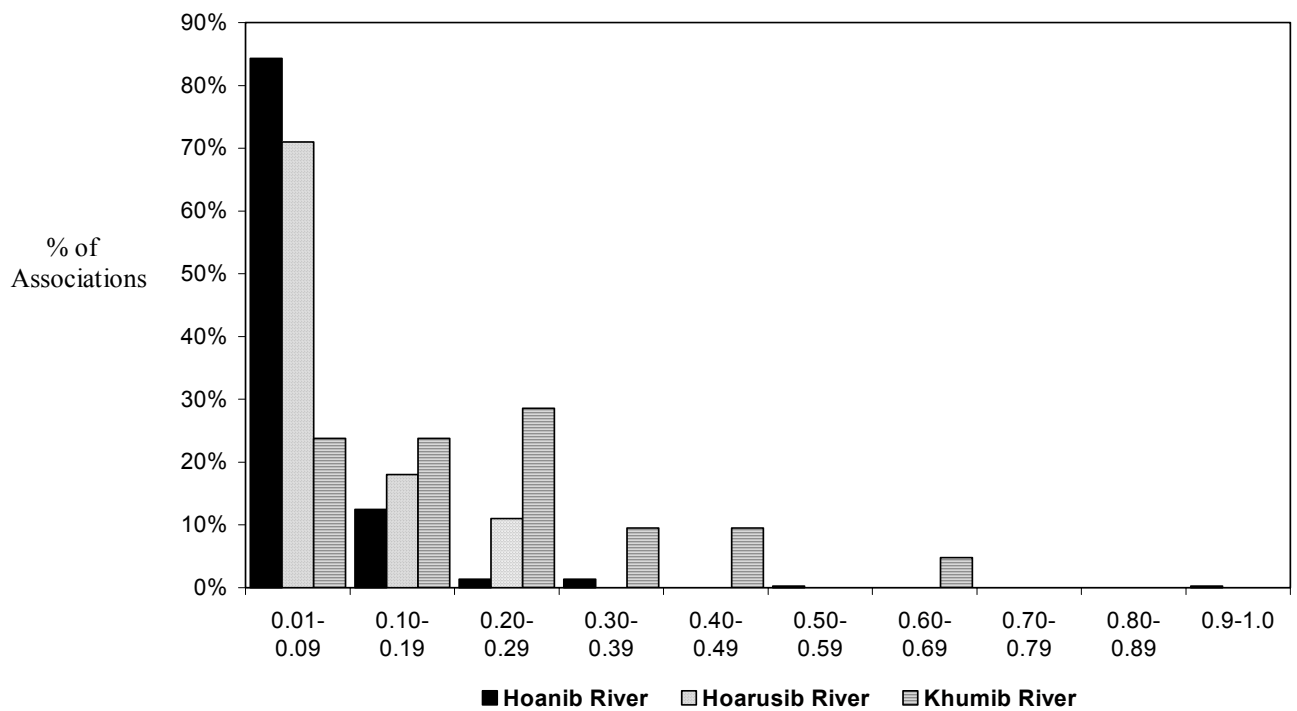
Figure 4.5. SR Index for inter-individual dyad associations of giraffe bulls and cows in the study region.
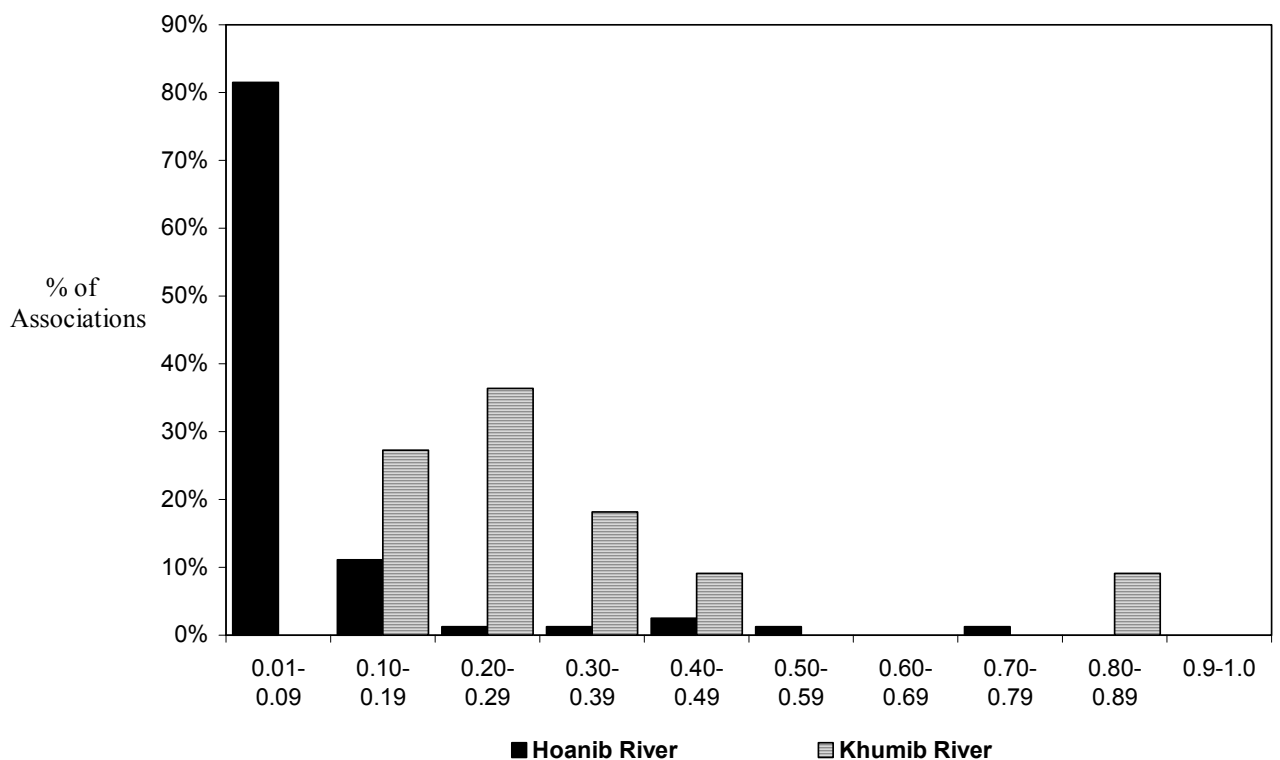

Figure 4.6. SR Index for inter-individual dyad associations of juvenile giraffe in the study region. N.B. No SR indices were calculated for Hoarusib River as number of associations <10.

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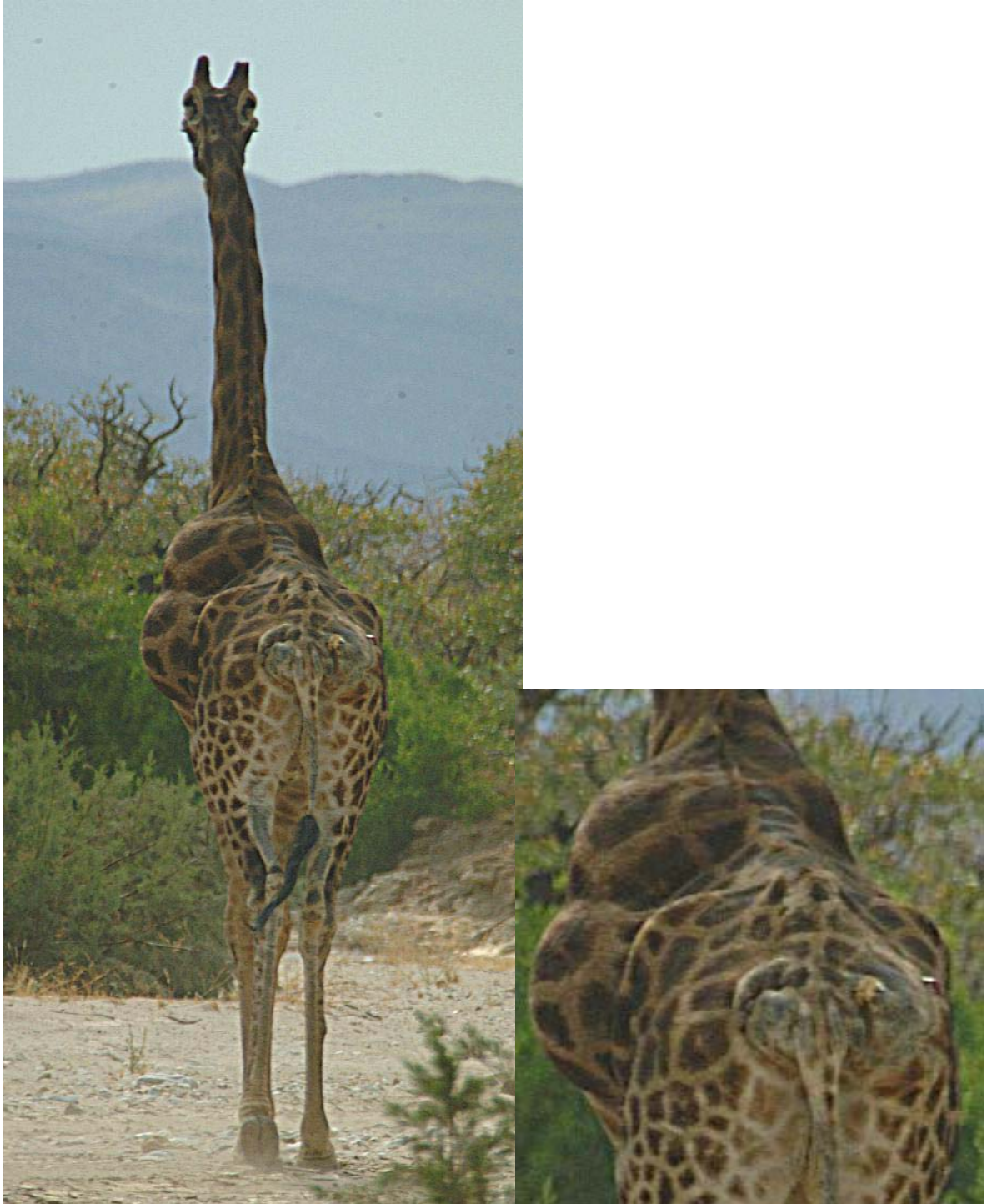
Figure 4.7. HSBM23 sighted one month prior to its death in the Hoarusib River study area. Note large tumour-like protrusions on both sides of the body and around the rump.

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.