

# Demography of lions in the Etosha National Park, Namibia

P.E. STANDER

Etosha Ecological Institute, Ministry of Wildlife, Conservation and Tourism, P. O. Okaukuejo, via Outjo, Namibia

Present address:  
P.O. Box 285, Omaruru, Namibia

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## ABSTRACT

Investigations between 1985 and 1989 into the lion population in woodland habitat in the Etosha National Park, Namibia, facilitated by the individual marking of 83 lions, provide the background for a population estimate of 191 - 266 adult and sub-adult lions in the park in February 1989. Lion densities were highest in western Etosha and correlate with the number of artificial water points and prey densities. Average lion densities elsewhere in Africa are considerably higher, but the age and sex distribution in the Etosha woodland population compare with other studies and suggest a viable population. Home ranges are large relative to those in East Africa, and appear dependant on pride size. Data are presented on pride compositions, group sizes, movements and other population characteristics.

## INTRODUCTION

Previous studies of lion *Panthera leo* demography in the Etosha National Park, Namibia, focused on the plains (Berry 1987; Orford 1986) between 1980 and 1987. These studies concentrated on five prides in an area of 660 km<sup>2</sup> on the plains south and west of the Etosha Pan (Figure 1). Berry, however, extended his studies to prides partly occupying short grassland plains south of the Etosha Pan towards Halali and Namutoni, covering a total study area of approximately 3035 km<sup>2</sup>.

Etosha National Park, referred to as Etosha, occupies a semi-arid area (351 ± 23 mm mean annual rainfall measured at Okaukuejo over 28 years) of 22270 km<sup>2</sup> in northern Namibia (19°S / 16°E). This study covered all of Etosha, excluding the 4590 km<sup>2</sup> Etosha Pan (with no resident lions) and the area studied by Berry (1987), and consisted of mopane and thorn veld savanna, an area of 14645 km<sup>2</sup>. The dominant tree species are *Colophospermum mopane* and *Acacia*, *Combretum* and *Terminalia* species (Le Roux 1980). Artificial water points and natural springs are the only permanently available open water during the dry period (May - December).

The objective of this study (February 1985 - February 1989) was to describe lion demography in the woodland habitat, and to collect data on distribution and movements. Lions were individually marked, as the only reliable method for censusing lions lies in the recognition of groups and individuals. Exemplary studies have been those from the Nairobi National Park (Rudnai 1973), Manyara National Park (Makacha & Schaller 1969) and the Ngorongoro Crater (Schaller 1972; Kruuk 1972). A survey method by marking lions was first described by Smuts *et al.* (1977), and population estimates were performed in Kruger National Park (Smuts 1978) and in the Kalahari Gemsbok National Park (Mills *et al.* 1978) using this method.

## MATERIALS and METHODS

Lions throughout the study area were either wary of, or aggressive towards humans and vehicles. Most observations and immobilizations were performed at night with the aid of a fresh carcass, as lions were more approachable when feeding in the dark. A red-filtered, 50 Watt spot light was used as the primary means of observation, although moonlight along with low light binoculars were also occasionally used.

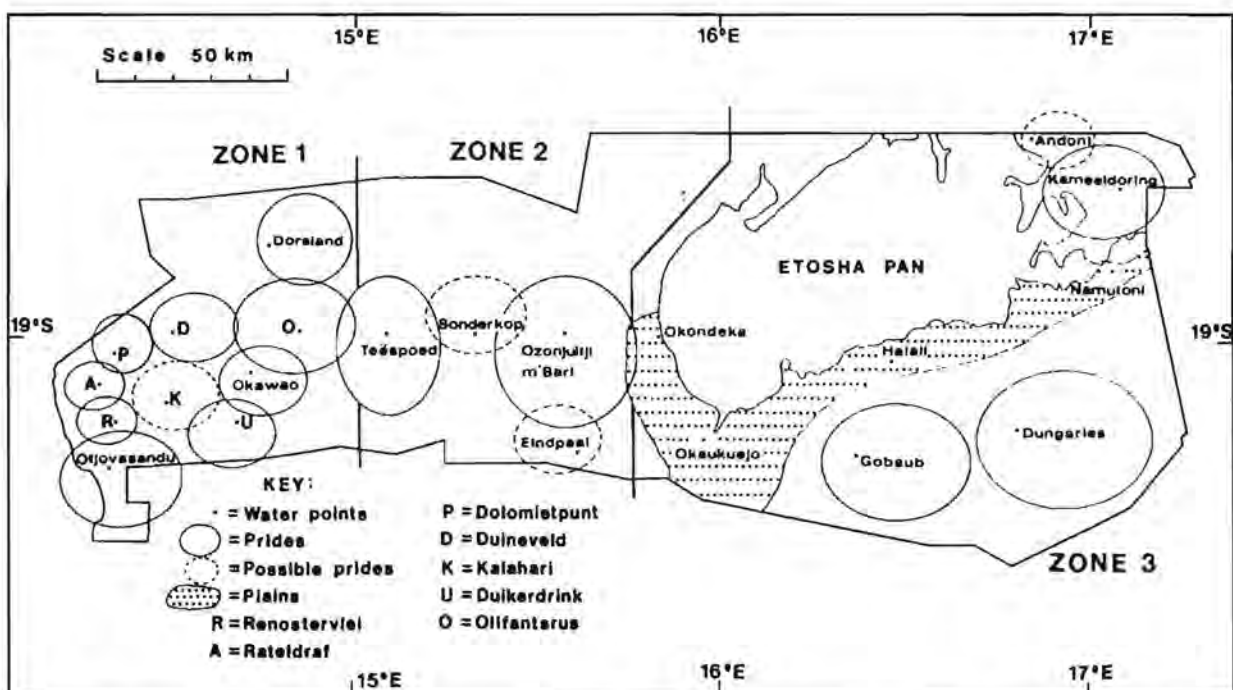


FIGURE 1: Approximate distribution of 18 lion prides in three zones of woodland habitat in the Etosha National Park during February 1989.

Most lions were not disturbed by the red spotlight. They were observed for age and sex, for previous marks of recognition, and if unmarked, lions from the age of one year were immobilized and individually marked with a hot brand (Berry 1987) on both buttocks or shoulders. Following the procedures described by Smuts *et al.* (1977) fresh carcasses of springbok *Antidorcas marsupialis* or gemsbok *Oryx gazella* were tied to a tree close to a water point, to attract lions. Water points throughout the entire area were covered systematically. Lions were immobilized once they had started feeding on these carcasses. Sound recordings of feeding lions were sometimes used to attract lions in areas with no water points. Whenever possible a radio-collar was attached to one adult member of a pride or to a nomad. Thereafter these lions were relocated between 7 - 57 times and the rest of the pride or associating individuals, immobilized and marked, and / or classified by age and sex. Immobilized lions were aged by the extent of tooth eruption, wear and discolouration (Smuts *et al.* 1978). All lions were placed into one of the following classes: small cubs (0-1 years), large cubs (1-2 years), sub-adults (2-4 years) and adults (4+ years) (Schaller 1972; Smuts *et al.* 1978). Because most lions were retiring and the vegetation hampered visual observations, large cubs were sometimes sexed, but not small cubs.

Radio-collared lions were tracked at irregular intervals from the ground and with the use of an aircraft. Home ranges were calculated using the minimum area method; a line joining the outermost points forms a convex polygon which represents the minimum perimeter of the home range (Mohr 1947; Seidensticker *et al.* 1973). Sample size bias associated with this home range estimation method was tested following procedures described by Anderson (1982).

Lions were immobilized with standard darting equipment. During 1985 and most of 1986 a combination of 6,3 mg/kg ketamine hydrochloride and 3 mg/kg xylazine hydrochloride were used as the immobilizing agents; the xylazine component was antagonized with 4 mg/kg tolazoline hydrochloride (Van Wyk & Berry 1986). Starting in 1986 Zoletil (CI-744: Virbac) was used. Dosage strengths ranged from 0,6 to 15 mg/kg depending on the desired duration of immobilization (Stander & Morkel 1991).

To facilitate analysis, Etosha was divided into three zones (Figure 1) based on broad vegetation (Giess 1971) and physiological differences. Zone 1 lies west of the 15° E latitude and consists largely of *Colophospermum mopane* trees and shrubs interspersed with *Terminalia*, *Acacia* and *Sesamothamnus* species. This area borders on the Kaokoveld, dolomite hills occur in the west, and the zone contains 14 artificial water points. Zone 2 consists of flat sandveld dominated by low *C. mopane* trees. Ten artificial water points were present in this zone, lying roughly between the 15° and 16° E latitude. The third zone had five artificial water points and one artesian spring. It consists of tall *C. mopane* woodland with *Combretum*, *Terminalia* species and *Spirostachys africana*, on sandy loams to black clay with calcareous rocky outcrops. The north eastern corner, however, consists of sandveld with mainly *Acacia* species.

Statistical evaluations were done following procedures described by Ryan *et al.* (1976) for the linear regression test, and Siegel (1956) for nonparametric analyses.

## RESULTS

### Population size

During the four-year period 83 lions were individually branded

and 118 could be individually recognized on natural markings. Eight of the marked animals died during the study and two were unaccounted for. The remainder were resighted at varying intervals. Based on occasional observations on lions in lesser known areas, and groups that were not part of the known prides, I estimate an additional 75 lions. These give a population estimate of between 191 and 266 adult and sub-adult lions in the study area for February 1989. Berry (1987) marked 77 lions in his study area, and the prides were studied intensively. From observations of marked and unmarked lions by Etosha Rangers and members of the Etosha Ecological Institute during 1989, the area contains a minimum of 85 known individuals. This brings the total estimate for Etosha in February 1989 to 276 - 351 adult and sub-adult lions.

TABLE 1: Population estimates, densities and demographic notes of lions in the woodland habitat of Etosha National Park, with notes on lions inhabiting the plains, for February 1989.

Area	Population estimate	Size of area/km <sup>2</sup>	Lion density per 100 km <sup>2</sup>	Number of prides	Number of waterpoints
Zone 1	92 - 107	3700	2.5 - 2.9	8 - 9	14
Zone 2	62 - 97	6400	1.0 - 1.5	3 - 5	10
Zone 3	37 - 62	4545	0.8 - 1.4	3 - 4	6
Study area	191 - 266	14645	1.3 - 1.8	14 - 18	30
Plains	85	3035	2.8	9*	32
Total Etosha	276 - 351	17680	1.6 - 2.0	23 - 27	62

\* From Berry (1987)

Density estimates for the number of lions in Etosha ranged between 1,6 and 2,0 adults and sub-adults per 100 km<sup>2</sup> (Table 1). Densities varied considerably between zone 1 and zones 2 and 3. The reason for this difference is probably because of the greater number of artificial water points in zone 1, and thus presumably a higher prey density. No quantitative data on prey biomass in these areas were available, but aerial censuses (Berry 1982, 1984; Nott 1983; Scheepers 1986) show higher herbivore concentrations on the plains and in zone 1. These lion densities are low compared to those in other conservation areas in Africa (Table 2), but similar to the Kalahari Gemsbok National Park (Mills *et al.* 1978).

TABLE 2: Lion densities in ten conservation areas in Africa

Conservation area	Source	Lion density per 100km <sup>2</sup>
Manyara	Makacha & Schaller 1969	40
Ngorongoro	Schaller 1972	27
Nairobi	Rudnai 1973	26
Kafue	Mitchell <i>et al.</i> 1965	12
Kruger	Smuts 1976	9
Serengeti	Schaller 1972	7.9 - 9.4
Selous	Rodgers 1974	8
Kalahari Gemsbok	Mills <i>et al.</i> 1978	1.5
Etosha	This study	1.6 - 2.0
Masai Steppe	Lamprey 1964	0.3

### Population characteristics

In February 1989 there were 1,4 females to each male in the population (n=146) (Table 3). The sex ratio for subadults varied from year to year and was measured as 1 ♂ : 1,6 ♀ (n=39) at the

end of 1986, the adult class ratio however remained similar.

TABLE 3: Sex ratio ( $\sigma$  :  $\varphi$ ) of adult and sub-adult lions in the woodland habitat of Etosha National Park for February 1989 (n = 146).

Adults	Sub-adults	Adults and Sub-adults
1 $\sigma$ : 1,6 $\varphi$ 49:73	1 $\sigma$ : 1 $\varphi$ 12:12	1 $\sigma$ : 1,4 $\varphi$ 61:85

Age composition of the population varied slightly between January 1987 and February 1989 (Table 4). The ratio of sub-adults to adults dropped significantly from 0,63:1 in January 1987 to 0,23:1 in February 1989 ( $P < 0,001$ ;  $X^2$  test), but the ratio of cubs remained the same ( $P > 0,95$ ;  $X^2$ ). Immature lions (0-4 years) represented 49% of the population in 1987 and 36% in 1989.

TABLE 4: Age composition of lions for 1987 and 1989 in the woodland habitat of Etosha National Park.

Date	Adult (4+ years)	Sub-adult (2-4 years)	Cubs (0-2 years)	Immature (0-4 years)	Total
January 1987	51,0% Ratio 1 : 0,63 n = 79	32,3% : 0,33 n = 50	16,8% : 0,33 n = 26	49,0% : 0,96 n = 76	n = 155
February 1989	64,3% Ratio 1 : 0,23 n = 133	14,5% : 0,33 n = 30	21,3% : 0,33 n = 44	35,7% : 0,56 n = 74	n = 207

Ages of known adult pride males in February 1989 ranged from five to 12 years ( $x = 9$ ;  $n = 14$ ). Adult pride females were on average 6-7 years old (range 4 - 10;  $n = 29$ ). One lioness of the Okawao pride lived to the estimated age of 16+ years before she disappeared at the end of 1988.

Eleven lions were radio-collared which helped in the identification of 9 distinct prides (Figure 1). A further 5 prides were identified by the resightings of 26 branded and naturally marked individuals. In addition to the 14 known prides (Figure 1), 13 marked individuals and a larger number associating with them were not observed within these prides. This gives reason to expect four additional prides in the area.

TABLE 5: Mortality records of 23 lions for the woodland habitat of Etosha National Park, recorded between 1986 and 1989.

Cause of death	*A $\sigma$	A $\varphi$	*SA $\sigma$	SA $\varphi$	SA?	Total
Destroyed on farm land	0	1	10	4	5	20
Natural	1	2	-	-	-	3

\*A = Adult  
SA = Sub-adult

During the study 23 of the known lions died (Table 5). This figure does not include cub mortalities, and is biased towards lions killed by farmers on bordering commercial farmland. However, the annual mortality rate of the sample recorded ranged between 3% and 8% for the four year period. Twenty (87%) of these animals were destroyed on bordering farmland after raiding domestic stock, and consisted mainly of sub-adult males. One lioness died of old age and two other lions from unknown causes.

## Pride Composition

On average prides had 1,8 adult males and 4,8 adult females ( $n = 12$  prides) (Table 6). Since the observations on large and small cubs were not consistent, and due to the high mortality rate of cubs (Schaller 1972), pride sizes are best measured by the number of adults and sub-adults (Smuts 1976), which ranged from 5 to 16 lions with a mean at 8,8.

TABLE 6: Pride structures of 12 prides in the woodland habitat of Etosha National Park during February 1989.

Pride	Adult		Sub-adult		Larve cubs	Small cubs	Total	Adults & Sub-adults
	M	F	M	F				
Ojovasandu	1	5	1	0	3	3	13	7
Renostervlei	1	6	0	2	-	-	9	9
Dolomietpunt *	1	3	3	2	-	-	9	9
Duikerdrink	2	2	1	1	4	-	10	6
Okawao	2	5	1	1	3	8	20	9
Dorsland	2	4	0	0	4	-	10	6
Olifantsrus	1	4	1	1	3	4	14	7
Teespoed	3	5	1	2	4	6	21	11
Ozonj. m'Bari	3	9	3	1	-	-	16	16
Gobaub	2	5	1	1	-	-	9	9
Dungaries	1	4	0	0	4	-	9	5
Kameeldoring	2	6	1	2	-	-	11	11
Total	21	58	13	13	25	21	150	105
Mean	1,8	4,8	1,1	1,1	2,8	2,6	12,5	8,8
Range	1-3	2-9	0-3	0-2	0-4	0-8	9-20	5-16

\* Pride composition determined in August 1987.

Group sizes during 161 sightings including single animals, indicate that group sizes of 1, 2, 3, and 4 lions represent 85% of all observations (Figure 2), with the mode at 2,2 and a mean of 5,4 (S.D. 3,8). For each year during the study period group sizes were equivalent.

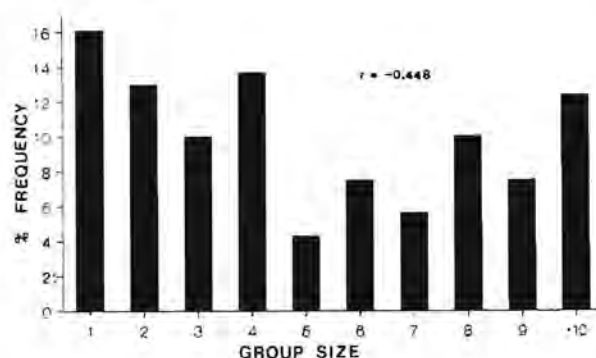


FIGURE 2: Frequency of observed group sizes of lions in the woodland habitat of Etosha National Park between 1985 and 1989, n = 161.

In five prides it was possible to monitor the activities of pride males for the duration of the study. A coalition of two males held tenure over the Ozonjuitji m'Bari pride since first observed in February 1985 until my last observations in February 1989, a minimum period of four years. At the end of this period the age of these two males were about 10 and 12 years. For the Dolomietpunt pride a single male held that tenure for at least 30 months. Throughout these years of observations on the Okawao pride, a coalition of two males remained with this pride. In two other prides, male takeovers occurred during the study but no details are available.

TABLE 7: Home range sizes of seven lion prides and two nomadic males in the woodland habitat of Etosha National Park.

Pride	Period	No. of locations	Area (km <sup>2</sup> )
Otjovasandu	1986-1989	57	263
Renostervlei	1986	14	150
Dolomietpunt	1986-1988	13	325
Okawao	1986-1989	36	550
Ozonjuitji m'Bari	1986-1989	52	2075
Gobaub	1982-1988	15	550
Kameeldoring	1986-1987	16	590
Kalahari male	1987-1989	14	250
Tsam male	1987	7	650

### Home Range and Movements

The home ranges of seven of the 14 discrete prides, were estimated, as well as those of two adult males (Table 7). The Gobaub pride's range was based on occasional resightings between 1982 and 1988.

The Otjovasandu pride occupied a home range of 263 km<sup>2</sup> between April 1986 and February 1989 (Figure 3). This home range fell partly in Kaross (a quarantine camp in Etosha for rare species) and the "Five farms", a conservation area in Damaraland). The Kalahari male covered an area of 250 km<sup>2</sup> (Figure 3), well within the ranges of three prides. During 1988 this male joined with the Otjovasandu pride and was observed with them although he still moved back to the centre of his former range occasionally.

The Renostervlei pride's home range was monitored by the movements of the pride male (Figure 3) who moved in an area

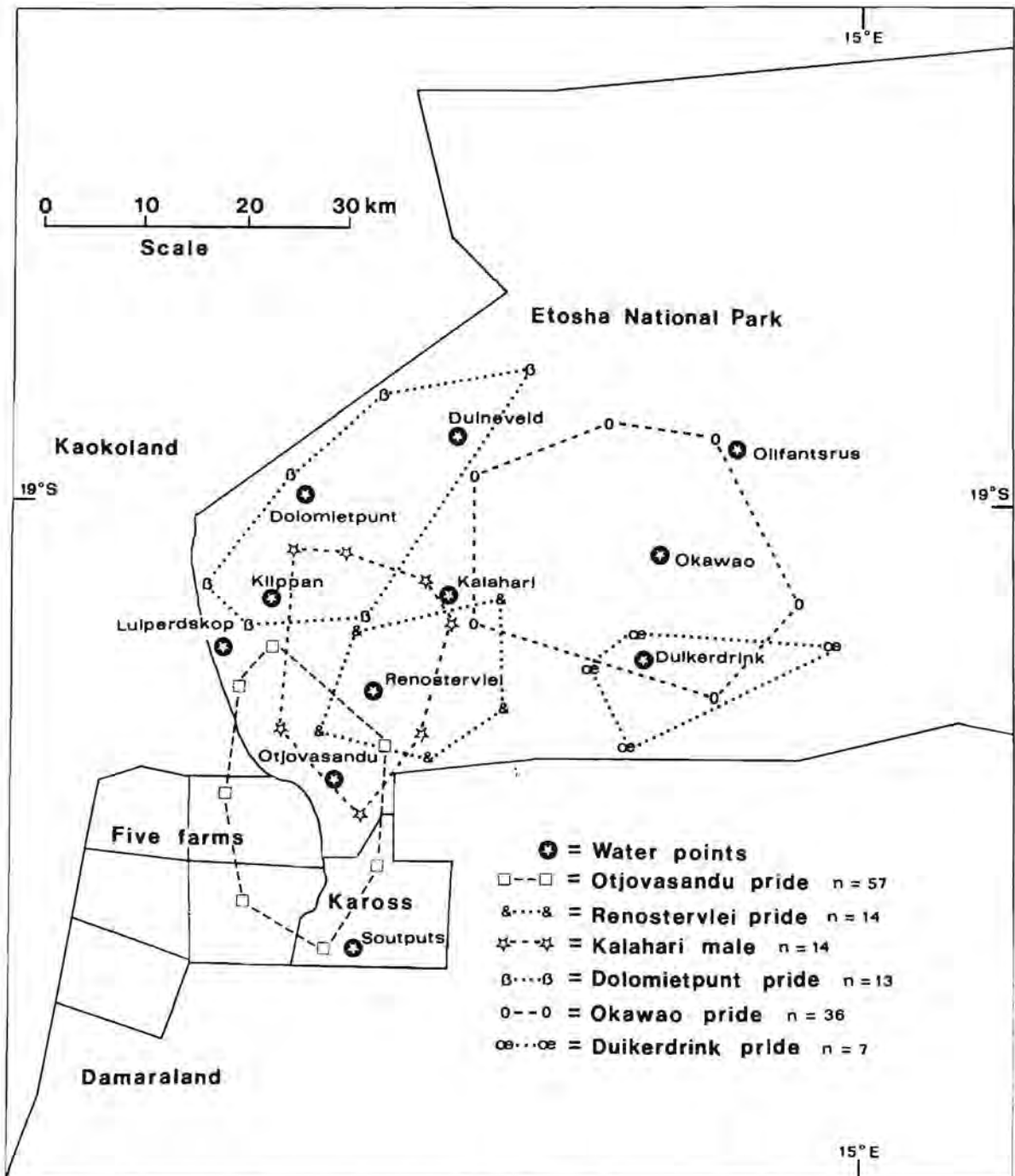


FIGURE 3: Home ranges of five lion prides and one adult male in Zone 1 of Etosha National Park. Points plotted are outermost radio-tracking locations, n = the total number of locations.

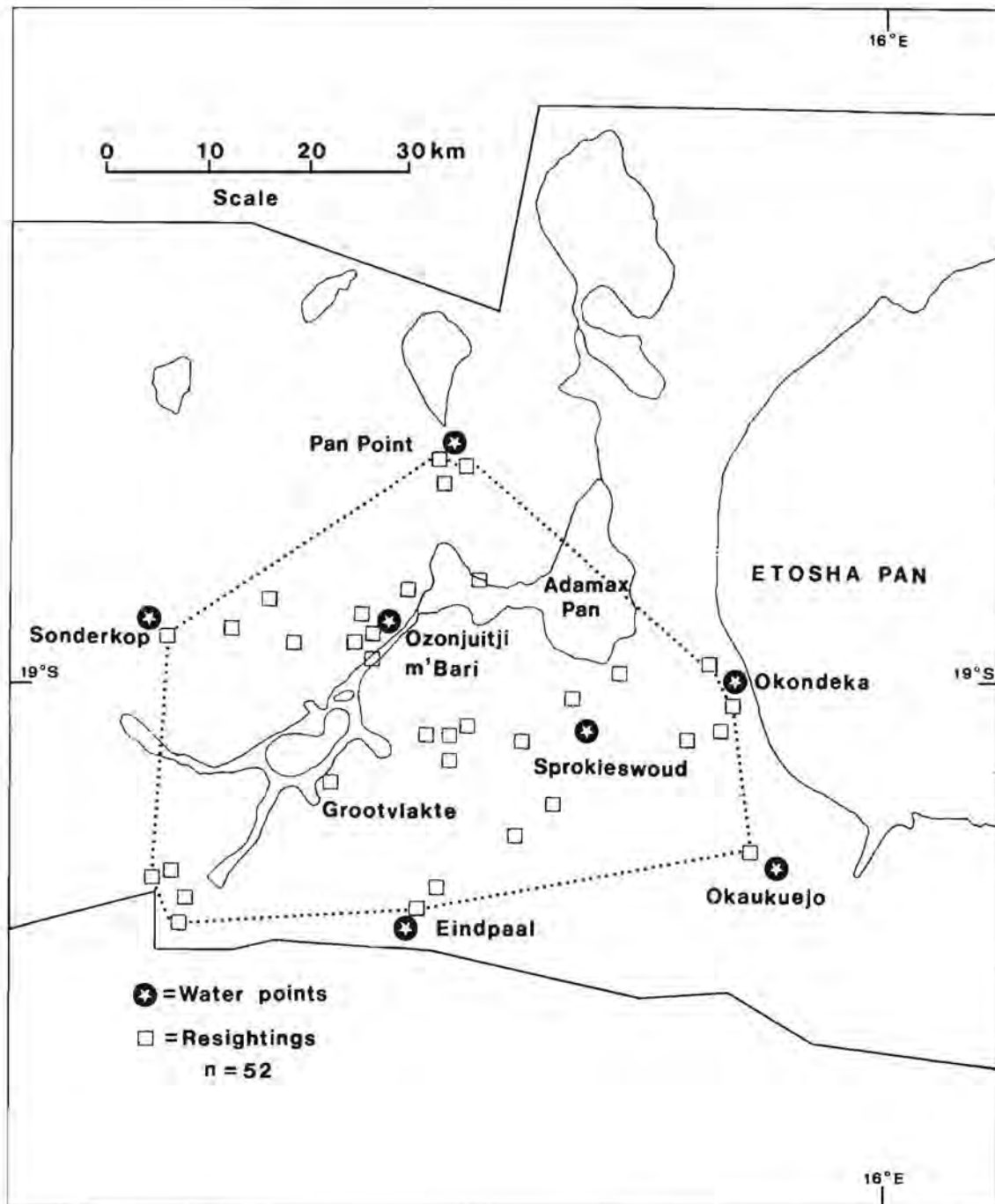


FIGURE 4: Home range of the Ozonjuitji m' Bari lion pride in Zone 2 of Etosha National Park. Points plotted are radio-tracking locations,  $n$  = the total number of locations.

of 150 km<sup>2</sup>. This home range is likely to be an under estimation as the male was only tracked for 3 months (14 locations). The Dolomietpunt pride's range of 325 km<sup>2</sup> as measured over a period of 2 years. Movements of the Okawao pride were followed between June 1986 and February 1989 and they occupied a home range of 550 km<sup>2</sup>. The few locations obtained for the Duikerdrink pride (Figure 3) do not make a home range estimate possible, but show an overlap with the range of the Okawao pride.

The Ozonjuitji m' Bari pride covered a large home range of 2075 km<sup>2</sup> (Figure 4), although 550 km<sup>2</sup> of that was occupied during the wet season (January to May) when following large concentrations of Zebra *Equus burchellii* and wildebeest *Connochaetes taurinus* found on the plains of Grootvlakte, near Sprokieswoud, and as far west as Okondeka.

From occasional sightings the Gobaub pride had a minimum home range of 550 km<sup>2</sup> (Figure 5). The Tsam male covered an approximate area of 650 km<sup>2</sup> over a period of four months based on seven resightings. The Kameldoring pride was located on sixteen occasions during two years to give an approximation of their 590 km<sup>2</sup> home range.

Tests for sample size bias in the minimum convex polygon method for each pride showed that the variance of the home range estimate did not decrease with the increase of sample size, a fact described by Jennrich & Turner (1969) and Anderson (1982). For the seven prides when home ranges were estimated with a similar sample size, there was a significant positive linear relationship between the number of adult females, a measure of pride size (Bertram 1973), and the size of their home range ( $F$  value = 25.57;  $P < 0.01$ , Ryan *et al.* 1976)

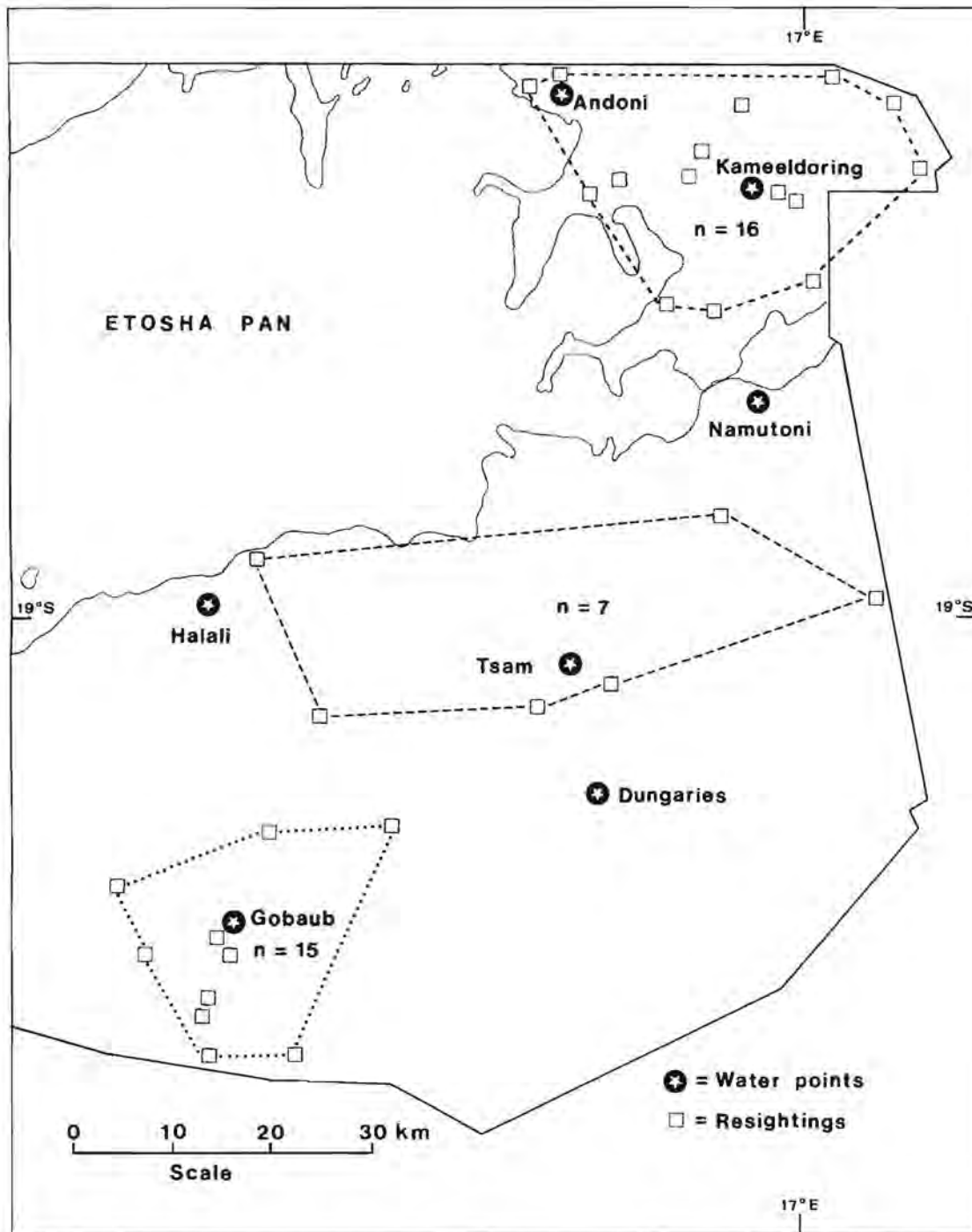


FIGURE 5: Home ranges of two lion prides and one adult male in Zone 3 of Etosha National Park. Points plotted are radio-tracking or resighting locations,  $n$  = the total number of locations.

Resightings of marked adult males reflect long distance movements by both nomadic and pride males. A nomadic male was marked near Sprokieswoud in February 1985 and observed at Eindpaal (30 km) six months later (T.J. Archibald, October 1985, pers. comm.). Two years later the same male was seen 70 km to the east of Eindpaal (R. Jones, August 1987, pers. comm.), and during June to December 1988 it was seen with a pride at Okondeka (50 km to the north west). In September 1984 an adult male was marked by H.H. Berry at Okaukuejo; this lion was observed 100 km to the east at Dungaries in June 1986 (K. Payne, August 1986, pers. comm.). I then immobilized this male in October 1987 at Namutoni, 45 km to the north east, and 140 km from the first observation three years earlier. A coalition of three adult males was observed and marked on the plains at Okondeka in the rainy season of 1985 (March 1985). During this period large numbers of zebra, wildebeest and springbok were congregating on the plains and deaths due to anthrax (Ebedes 1976;

Berry 1981) provided an abundant supply of carrion. During the following dry season (June to November 1985) the three males were observed in an area 80 - 100 km to the west, holding tenure over the Teëspoed pride (Figure 1). During the following rainy season (1985/1986) two of these males were seen on the Okondeka plains again during the prey concentrations, only to return to the Teëspoed area for the dry season. The following year only one male was seen on the plains during the wet season.

## DISCUSSION

### Population Size

The lion population estimate of 191 - 266 adults and sub-adults for the study area are minimum figures since lions are difficult to census (Schaller 1972; Smuts 1976). It is not possible to determine accuracy levels for these estimates, but reasonable

accuracy is likely for two reasons; (a) continuous attempts to capture lions during the last year of the study failed to reveal large groups with unmarked lions, and (b) resightings of lions throughout the study area mostly contained marked individuals, and the numbers, age and sex composition of accompanied unmarked lions, coincided with my records. The likelihood of overlooking a large number of lions or prides during this four-year study is therefore slight. The population estimate is applicable only for the period up to February 1989, as the population day fluctuate from year to year due to environmental and other changes.

Density estimates (1.6 - 2.0 lions per 100 km<sup>2</sup>) for the Etosha population are low compared to other areas in Africa. Berry (1981) measured a high lion density for the plains of Etosha at 15.9 - 22.2 per 100 km<sup>2</sup> for the period 1976-78. There are two possible reasons for this discrepancy: either a large number of lions inhabited the plains area during that period due to unusually high rainfall (Berry 1980) and a resulting abundance of ungulates on the plains throughout the year; or the population (285 - 400 lions, Berry 1981) was over estimated as few lions were marked. Kalahari Gemsbok National Park, also a semi-arid environment, supports a lion density comparable with this study (Mills *et al.* 1978).

Zone 1 appears to have a higher lion carrying capacity than zones 2 and 3, based on greater lion and pride densities and smaller home ranges. Substantially more artificial water points are present in zone 1, which leads to higher resident prey populations. Before these artificial waterholes were erected and before large numbers of ungulates utilized these water points, few lions were observed in this area (J. Meyer, C. Eyre & A. Cilliers, August 1987, pers. comm.). These observations suggest that artificial water points attracted resident prey species and possibly increased overall numbers of certain species like springbok, hartebeest *Alcelaphus buselaphus* and gemsbok, resulting in an increase in the density of lions and the number of prides. For the Kruger National Park, Smuts (1976) provides substantial evidence of a correlation between the increase in lion numbers and the development of artificial waterholes which allowed a population of animals to become resident. Mills *et al.* (1978) made a similar suggestion for the Kalahari Gemsbok National Park where artificial water points have led to a sedentary blue wildebeest population. Berry (1980, 1981) mentions the establishment of sedentary herbivore populations after the provision of artificial water points on the plains in the vicinity of Okaukuejo, Etosha, with the subsequent establishment of lion prides.

### Population Characteristics

Sex ratio figures for the woodland habitat of Etosha (1♂:1.4♀) are marginally more in favour of females than data presented by Schaller (1972) for the Serengeti, which were 1♂:1.1 - 1.3♀. The Etosha figures, however, are slightly less distorted than found in the Kruger National Park (1♂:1.4-1.8♀, Smuts 1978) and the Kalahari Gemsbok National Park (1♂:1.8♀, Mills *et al.* 1978).

On the Serengeti plains 43% of all lions were young (Schaller 1972), as were 47% in the Kruger National Park (Smuts 1976). Berry (1981) recorded 37% young on the plains of Etosha. In the present study, during January 1987, 49% of 155 lions were less than four years old. The adult: subadult ratio of 1:0.63 dropping to 1:0.23 in 1989 as subadults moved into the adult age class, but were not replaced at the same rate. This was probably due to high cub mortalities in 1985-1987. By February 1989 young lions (0-4 years) represented 36% of the population.

Pride males and females were on average 9 and 6-7 years old. Schaller (1972) found in the Serengeti National Park that most lionesses in four prides were between 4 and 6 year old. One Etosha lioness disappeared at about 16+ years, whereas a lioness died at the estimated age of 22 years in Nairobi National Park (Foster & Coe 1968). In Kruger National Park, Whyte and Smuts (1988) recorded a 16 year old known-age male.

Mortalities of known lions were mostly those of sub-adult males shot on bordering domestic stock farms. Stock-raiding lion mortalities for the whole of Etosha between 1985-1988, however, consisted mostly of adult and sub-adult males (Stander 1990). In the Serengeti 41% of twenty deaths recorded by Schaller (1972) were snared or shot. Van Orsdol *et al.* (1985) states that mortality of emigrating sub-adult males is high, and that these males are often driven into unsuitable habitat where prey is scarce, or into areas of human settlements. Sub-adult females tended to remain in their natal prides (Schaller 1972; Bertram 1975; pers. obs.). Although most known lion deaths for Etosha are from those killed on bordering farms, this mortality does not appear to limit the population. A management strategy to limit the conflict of interest between farmers and conservation authorities by reducing and solving stock-raiding lion problems along the Etosha borders, is suggested by Stander (1990).

### Pride Composition

Total pride sizes, including cubs ( $\bar{x}$  = 12.5; range 9 - 20), are slightly smaller than the average of 15 lions (4 - 37) found in the Serengeti (Schaller 1972), but similar to the Kruger National Park where Smuts (1976) recorded an average pride size of 11.8 lions (range 4 - 21). Bertram (1973) found that the most stable measure of pride size was the number of adult females. In this study the number of adult females in prides ( $\bar{x}$  = 4.8; range 2 - 9, Table 6) were not different from the Kruger National Park ( $\bar{x}$  = 4.2; range 2 - 9 [Smuts 1976]) but slightly lower than the Serengeti,  $\bar{x}$  = 5.9; range 2 - 11 (Schaller 1972).

The average group size (five lions) measured during this study, falls in the order of observations elsewhere. Serengeti National Park supported an average group size of four (Schaller 1972), in Kruger National Park 3-4 (Pienaar 1969) and in Kafue National Park, Zambia, between four and five lions (Mitchell *et al.* 1965). Wright (1960) estimated the average in East Africa as six, excluding solitary males. For the plains along the Etosha Pan, Berry (1981) counted the average "pride/group" size at 7.2 lions.

The minimum period of tenure of dominant males measured in three prides was longer ( $\bar{x}$  = 3.2 years, range 2.5 - 4 years) than that measured in East Africa. In the Serengeti the average tenure of male coalitions was 26 months (Packer *et al.* 1988).

### Movements

Home ranges of seven prides and two adult males range from 150 km<sup>2</sup> to 2075 km<sup>2</sup> (Table 8), and were on average larger than those of lions in East Africa. Serengeti lion pride ranges were between 30 and 400 km<sup>2</sup> (Schaller 1972), and 20 to 100 km<sup>2</sup> (Bertram 1975). Two prides in Manyara National Park each occupied areas of about 20 km<sup>2</sup> (Schaller 1972), and two adult males moved in an area of about 39 km<sup>2</sup> (Makacha & Schaller 1969). This difference is presumably the result of substantially higher prey densities in East Africa.

### CONCLUSIONS

Although no measurable level of accuracy is available, the

estimate of 191 - 266 adult and sub-adult lions for the woodland habitat of Etosha, based on recognition of individuals and groups, appears to be a realistic representation of the population for February 1989. Lion densities in western Etosha appear to have increased substantially since the establishment of artificial water points. Pride and group sizes are similar to most other African conservation areas although the densities are considerably lower. Home ranges are larger and increase with pride size. Age and sex distributions of lions throughout Etosha are similar to other populations in Africa and present the characteristics of a viable population that, at its present status, requires little management.

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