Predator Conservation Trust

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Population ecology & demography of Kunene Lions January 2006

"Towards resolving human-lion conflicts with applied research and proactive management."

Report by: P. Stander
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INTRODUCTION

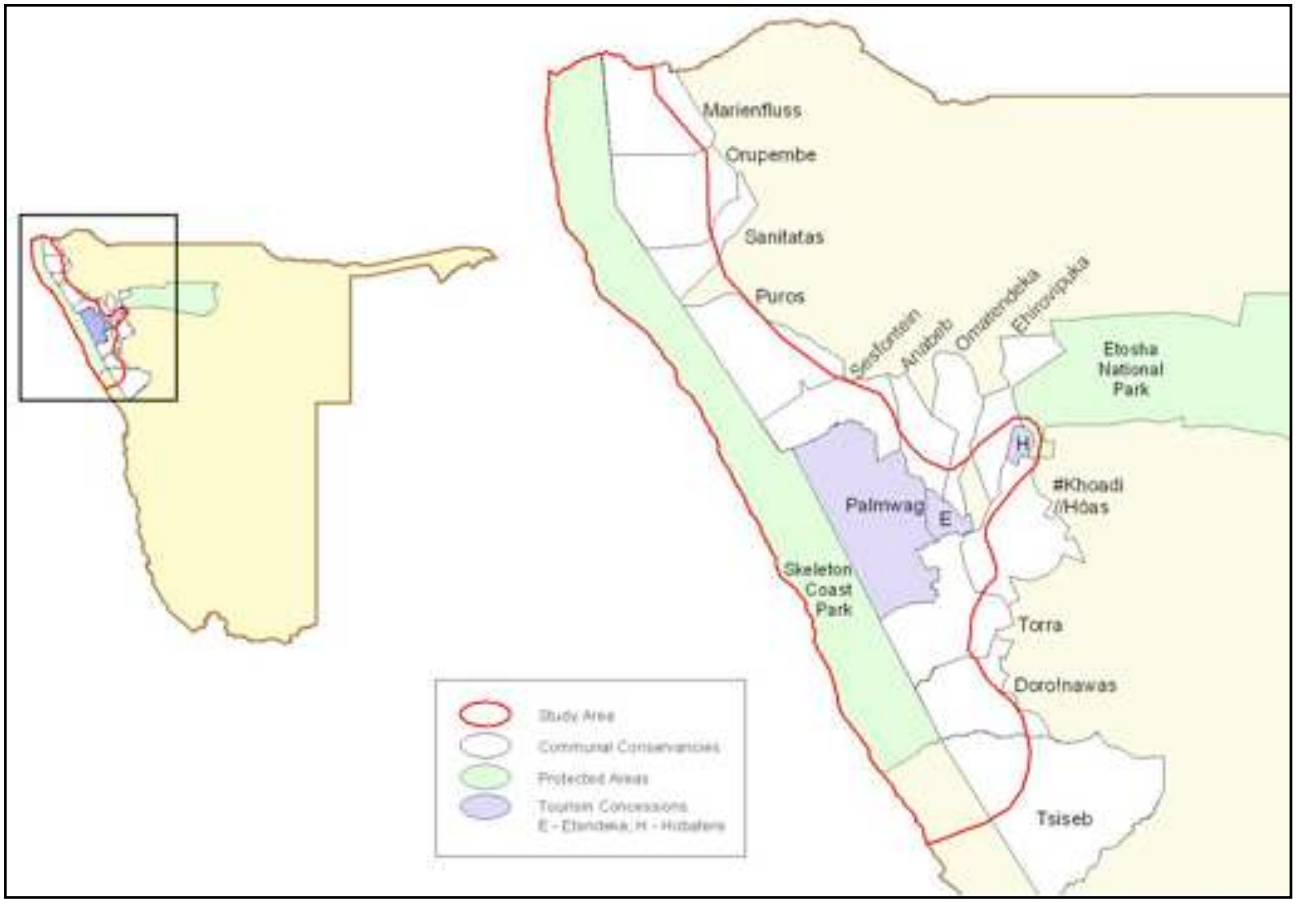
The Namibian lion is the most threatened and endangered of the large carnivore species, and arguably also one of the more vulnerable large mammals in Namibia. Their distribution is confined to large protected areas and extreme arid environments. Throughout their range, and along the borders of the protected areas, conflict between lions and the Namibian people is a regular and significant problem. Lions prey on domestic livestock, and in protection of their livelihood, local people shoot, trap, or poison lions. These incidents of Human Lion Conflict result in significant financial and conservation losses. Furthermore, the lion is a key and flagship species for the influential and growing tourism industry.

The majority of lions that live outside protected areas occur in the arid habitats of the Kunene Region. The local communities share their land with free-ranging lions and, as a result, incidents of Human Lion Conflict are frequent. The Kunene Region, with its' unique landscapes, fauna and flora, is also an important area for tourism. The conservation of lions in the Kunene region is therefore essential to address Human Lion Conflict, and to conserve a flagship species for the tourism industry. The Kunene Lion Project contributes to this process by maintaining a comprehensive database on the density, demography, and population ecology of lions. Through applied research and monitoring, the study collects sound scientific data to guide management strategies and the implementation of a National Lion Conservation Strategy.

STUDY AREA

The Kunene Lion Project covers an area of 51,380 km^2 in the Kunene Region that includes the Palmwag, Etendeka & Hobatere Concessions, the Skeleton Coast Park, and bordering Communal Conservancies (Fig. 1). The area falls in the Etendeka Plateau landscape of the northern Namib Desert, with an annual rainfall of 0 - 100 mm (Mendelsohn et al. 2002), and stretches from the Atlantic Ocean in the west, to the edge of human settlement and livestock farming in the east. The Kunene River runs along the north, and the Omaruru River forms the southern border of the study area.

Fig. 1. Boundaries of the study area of the Kunene Lion Project in the Kunene Region, Namibia.



METHODS

Large carnivores, such as lions, are generally difficult to study, especially in a desert environment such as the Kunene Region. The study area is covered systematically by tracking spoor, setting

out bait and using sound playbacks to locate and capture individual lions. Adult and sub-adult lions are captured and individually marked with a hot brand, and several lions in each group are marked with a radio collar. A light aircraft is used to systematically locate radio-collared animals. Aerial locations are followed-up by ground observations to record group composition in relation to individuals and age/sex structure, and the ratio of marked to unmarked individuals. Life tables are constructed and updated to compute survivorship and mortality rates. The population dynamics of lions are evaluated by monitoring, since 1999, a core group of 13 radio-collared lions. These analyses include several population parameters, such as birth rates, mortality, fecundity, exponential rate of increase, and age-specific survivorship. Home range analyses are based on locating the daytime resting spots of lions by radio telemetry, with at least 24 hours between fixes. Home range size is calculated using the Minimum Convex Polygon (MCP) and Kernel Contour methods (Harris et al. 1990).

RESULTS

Demography & population dynamics

Lion density & population size

Since November 1999 a total of 36 lions have been radio collared and 87 lions marked or individually identifiable (Table 1). Population density is calculated in two intensive study areas where all lions were marked or individually known (Stander 2004). The ecology of the two intensive sites varies, and in the low-density site the habitat is significantly dryer, with low numbers of wildlife. Using the Kunene Sampling Method (Loveridge et al. 2001) lion densities were calculated at 0.05 – 0.1 lion 100 km^{-2} for the low-density area and between 0.38 and 0.62 lion 100 km^{-2} for the high-density area. These two density estimates were then extrapolated, as a range of minimum to maximum, to the calculated low and high density areas for the Kunene Region (Fig. 2). The population estimates of 15 – 30 lions for the low density area, and 83 – 135 lions in the high density area, coincides with the records of known individual lions, and provides confidence to the total estimate of 96 - 165 lions in the Kunene Region.

Fig. 2. The density distribution of lions in the Kunene Region.

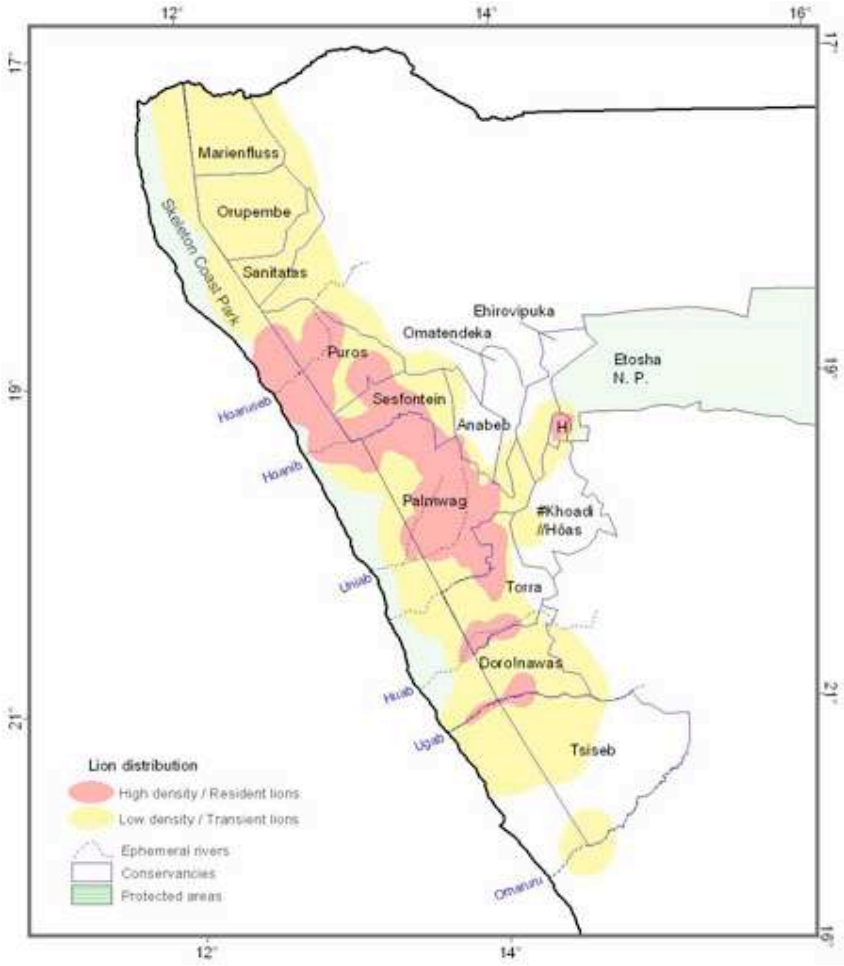


Table 1. Density and population estimates of the Kunene lions.

Total Study Area (km^2)	*51,380*	
High density study area (km^2)	875	
Low density study area (km^2)	*770*	
Number of marked / known lions	87	
Number of radio-collared lions	36	
Lion population estimate	Low density	High density
Calculated number of lions	*0.4 – 0.7*	*2.9 – 5.4*
Lion density (lions 100 km^{-2})	0.05 – 0.1	0.38 – 0.62
Area inhabited by lions - calculated (km^2)	29,566	21,814
Extrapolated density estimates	15 - 30	83 - 135
Total lion population estimate	96 - 165	

Population growth

In 1999/2000, when the Kunene lions were restricted in their distribution to the central Palmwag Concession area, a core group of 13 lions were marked with radio collars. The life history of these individual lions has subsequently been documented, and forms the bases of assessing population growth and expansion. During the first two years (1999 & 2000) the population increased at a phenomenal rate 22% and 23% per year respectively. Between 2001 and 2003 the rate of increase remained high (>15% p.a.), but dropped to below 15% p.a. in 2004, and leveled off to 1.6 % by the end of 2005. This phenomenal initial increase and stabilising of the population growth is best expressed by a logarithmic rate of increase (Fig. 3), and the annual growth rates, by the Log exponential rate of annual growth (Fig. 4).

Fig. 3. Exponential annual rate of increase of the Kunene lion population between 1999 and 2005.

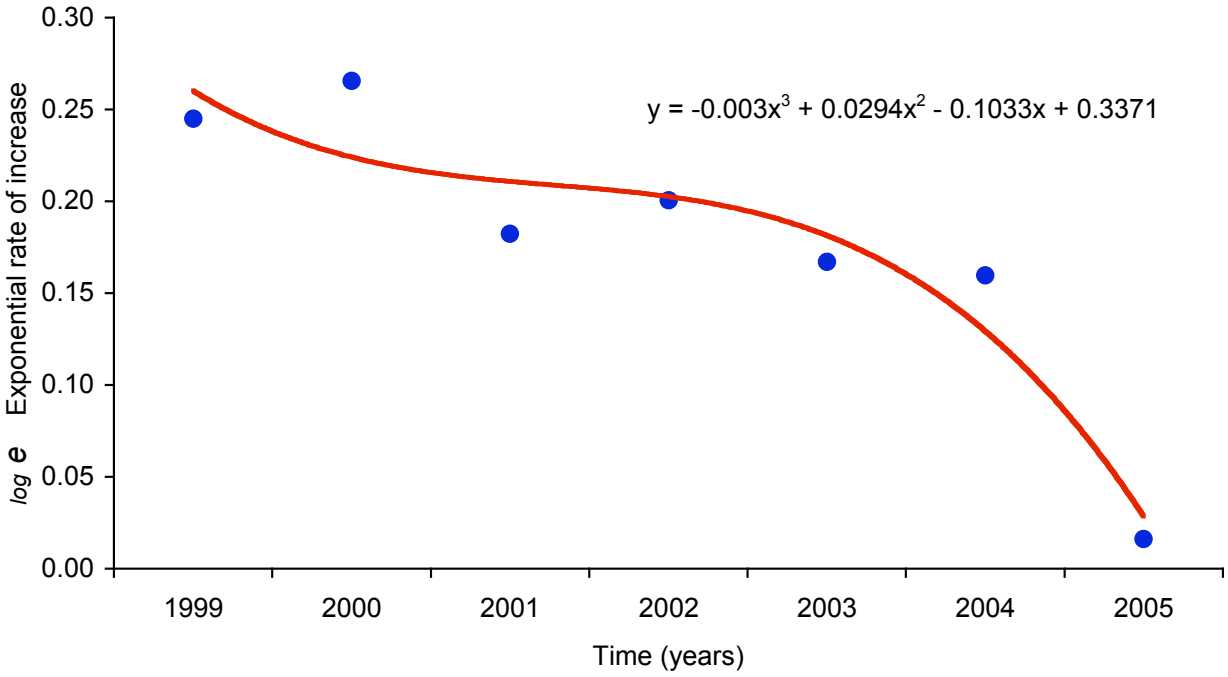
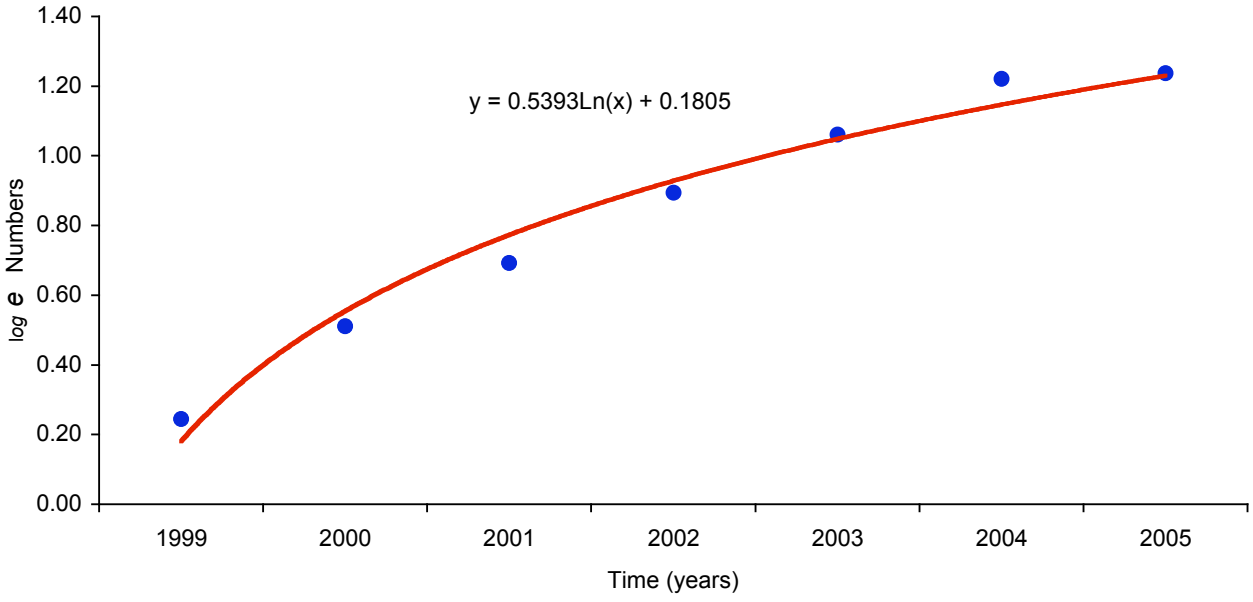


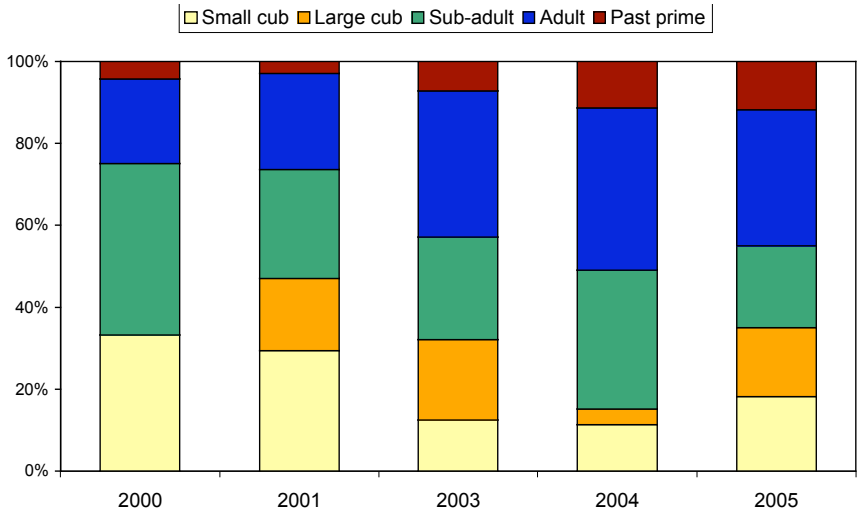
Fig. 4. Growth rate of the Kunene lion population between 1999 and 2005.



Age and sex structure

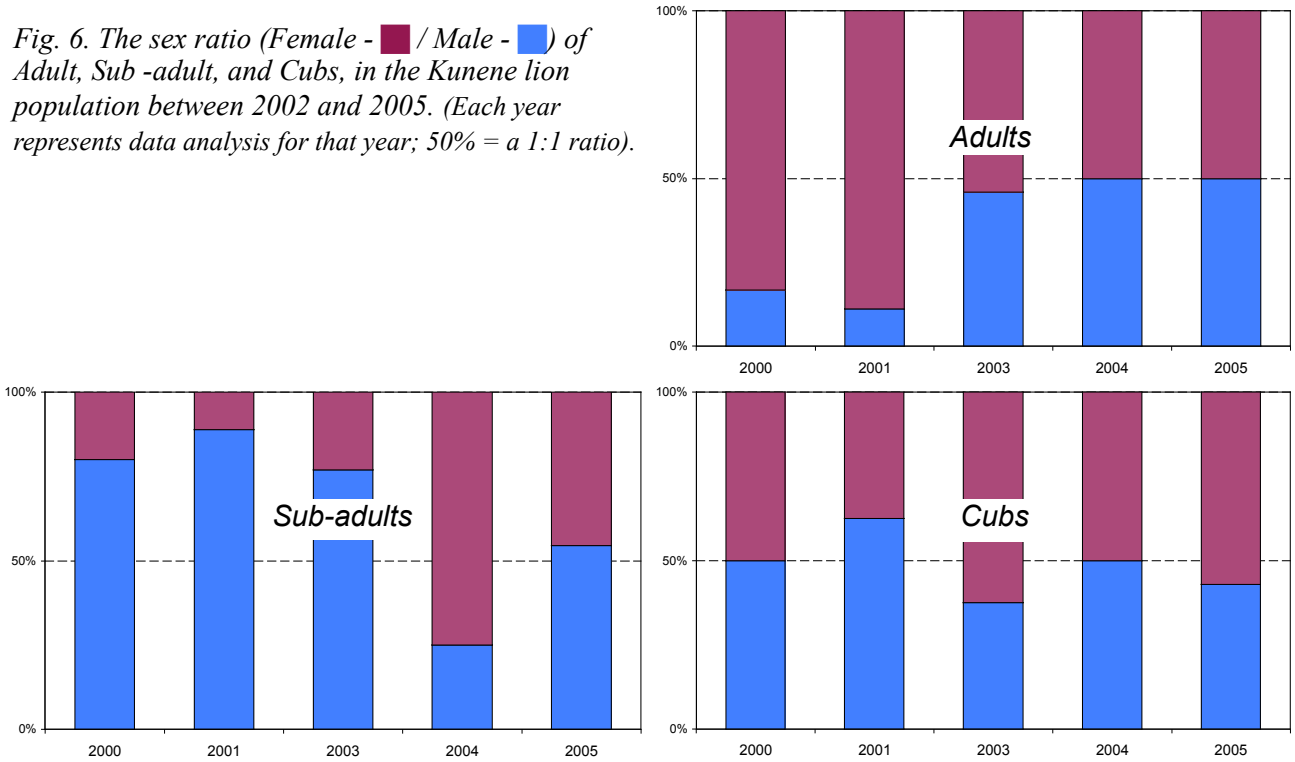
Despite high fecundity and growth there were discrepancies in the age structure of the population during some years (e.g. 2004 - a preponderance of sub-adult and adult lions). However, the composition of age classes is expected to vary, and the annual data, between 2000 and 2005, clearly show this fluctuation (Fig. 5). These results may demonstrate the population's ability to self-regulate, but notwithstanding, depicts the characteristics of a healthy and stable population.

Fig. 5. Distribution of age classes if the Kunene lion population between 2000 and 2005. (Small cub <1 yr; Large cub 1-2 yrs; Sub-adults 2-4 yrs; Adult 4-10 yrs; Past prime >10 yrs).



The skewed sex ratios favouring sub-adult males, and adult females between 2000 and 2002 raised concern in 2003. However, corresponding fluctuations between 2003 and 2004, resulted in stable structures by 2005 (Fig. 6). It was feared in 2003/4, that In the event that this population come under pressure due to drought and/or conflict with humans, the disproportionately low number of breeding females may result in low fecundity. A long-term analysis, such as this presented In Fig. 6, may serve to negate these concerns, and instead demonstrate normal fluctuations and a possible ability of the population to self-regulate.

Fig. 6. The sex ratio (Female - ■ / Male - ■) of Adult, Sub -adult, and Cubs, in the Kunene lion population between 2002 and 2005. (Each year represents data analysis for that year; 50% = a 1:1 ratio).

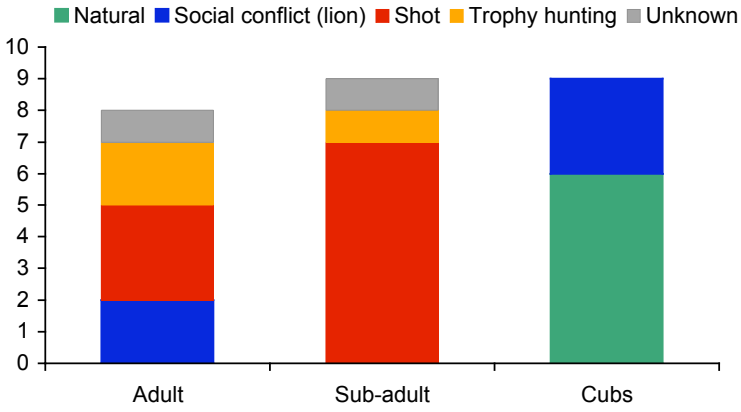


Fecundity and mortality

Between 1999 and 2005, eight lionesses gave birth to 59 cubs in 21 litters. The mean litter size was 2.8 cubs (SD = 0.75, range 2 – 5 cubs). Cub survival was high (83%), and all mortalities occurred within the first six months. The mean birth interval between surviving litters was 2.05 years (SD = 0.41; range 1.3 – 2.7 years; *N* =16).

Mortality in the lion population was recorded in al three main age classes (N = 26; Fig. 7). Human Lion Conflict was the main cause of mortality (50 %) when adult and sub-adult lions (mainly sub-adult males; n = 7) were shot or trophy hunted. Cubs died of starvation, and during 2005 other lions killed several cubs and adults during social conflicts.

Fig. 7. Causes of mortality in each age class of the Kunene lion population, between 2000 and 2005.



Life tables of individual lions allowed for the calculation of mortality rates (Fig. 8) and survivorship (Fig. 9) at different ages. The probability of survivorship (Fig. 9) is highest at birth (P = 1), and then drops progressively over time, so that the older a lion becomes the lower its' probability of survivorship. Mortality rate (Fig. 8) is a measure of the probability of a lion dying at any specific age. Low cub mortality in the Kunene resulted in a slight reduction of survivorship in the fist year. Interestingly, survival of Kunene lions between 1 and 4 years is high. Elsewhere in Africa, lions at that age are at risk and mortalities are high. For a Kunene lion the risk of dying is highest at three to four years (Fig. 8), and as a result, the probability of survivorship is reduced sharply to approximately 50%. These mortalities are all related to Human Lion Conflict. Once lions overcame the critical period, between 3 and 6 years, when they may have acquired the skills to avoid conflict with humans, mortality rates drop to P < 0.1, and their probability of survivorship remain stable, up to the age of sixteen years.

Fig. 8. Age-specific probability of mortality rates in the Kunene population.

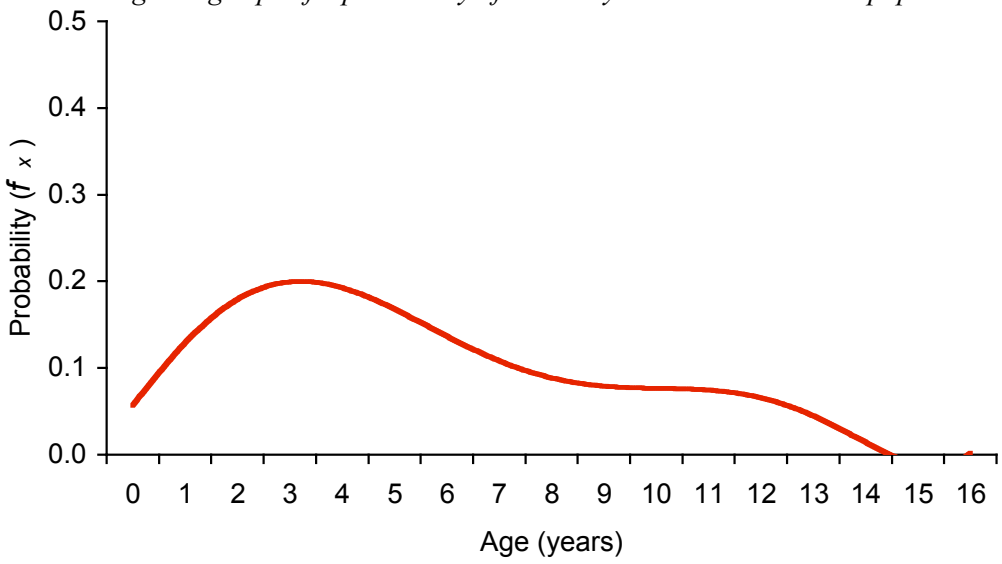
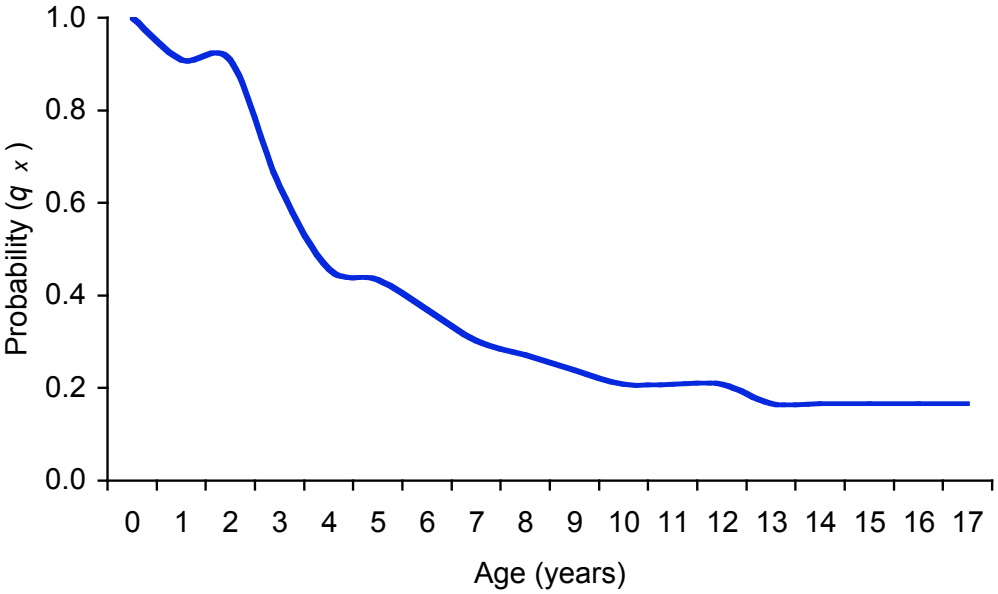


Fig. 9. Age-specific probability of survivorship in the Kunene population.



Socio-ecology

Genealogy

There are currently eight distinct groups/units of lions, consisting of prides, sub-groups, and nomadic individuals, in the Kunene population. Long-term individual records reveal that, irrespective of the areas that the eight groups currently occupy, they all originate from one genetic lineage (Fig. 10). The Aub Pride (blue) is the largest and most significant group (Fig. 11), and all the lions that have re-populated new habitats, including the Agab group, originate from this pride. Individual records and almost five generations of life table and genealogy data of the Kunene lions provide valuable baseline data and an in-depth understanding of the socio-ecological parameters of dispersal and population growth. Some lions in this genealogy tree have subsequently died (Fig. 12). Of the 98 individually known lions, presented in the genealogy tree (Fig. 10), 26.5 % have died, but their role in, and contribution to, the genealogy of the Kunene lions remain important.

Fig. 10. Genetic origins and relatedness of all known Kunene lions.

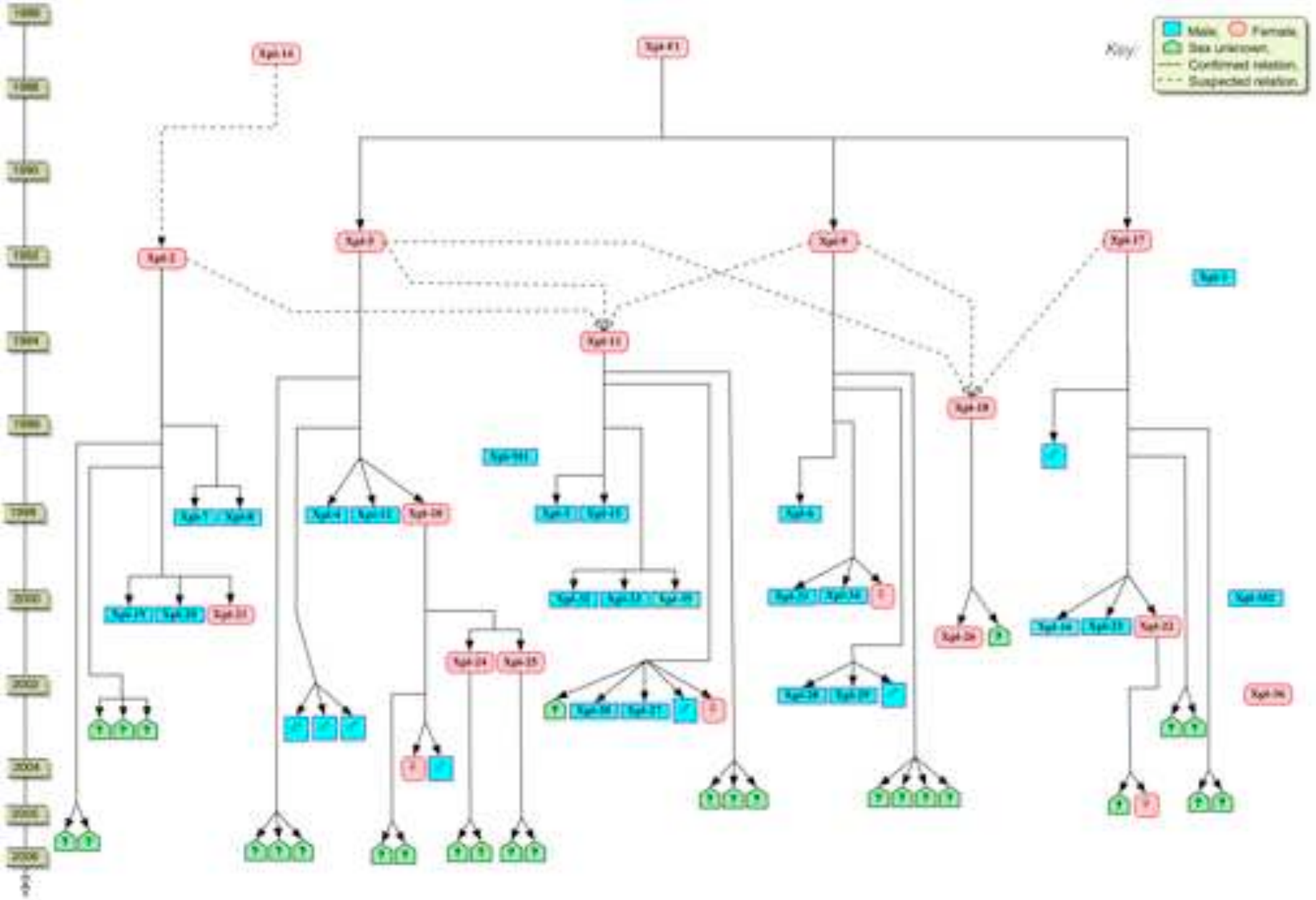


Fig. 11. Schematic layout of eight groups of lions the Kunene Region in relation to genetic origins and relatedness..

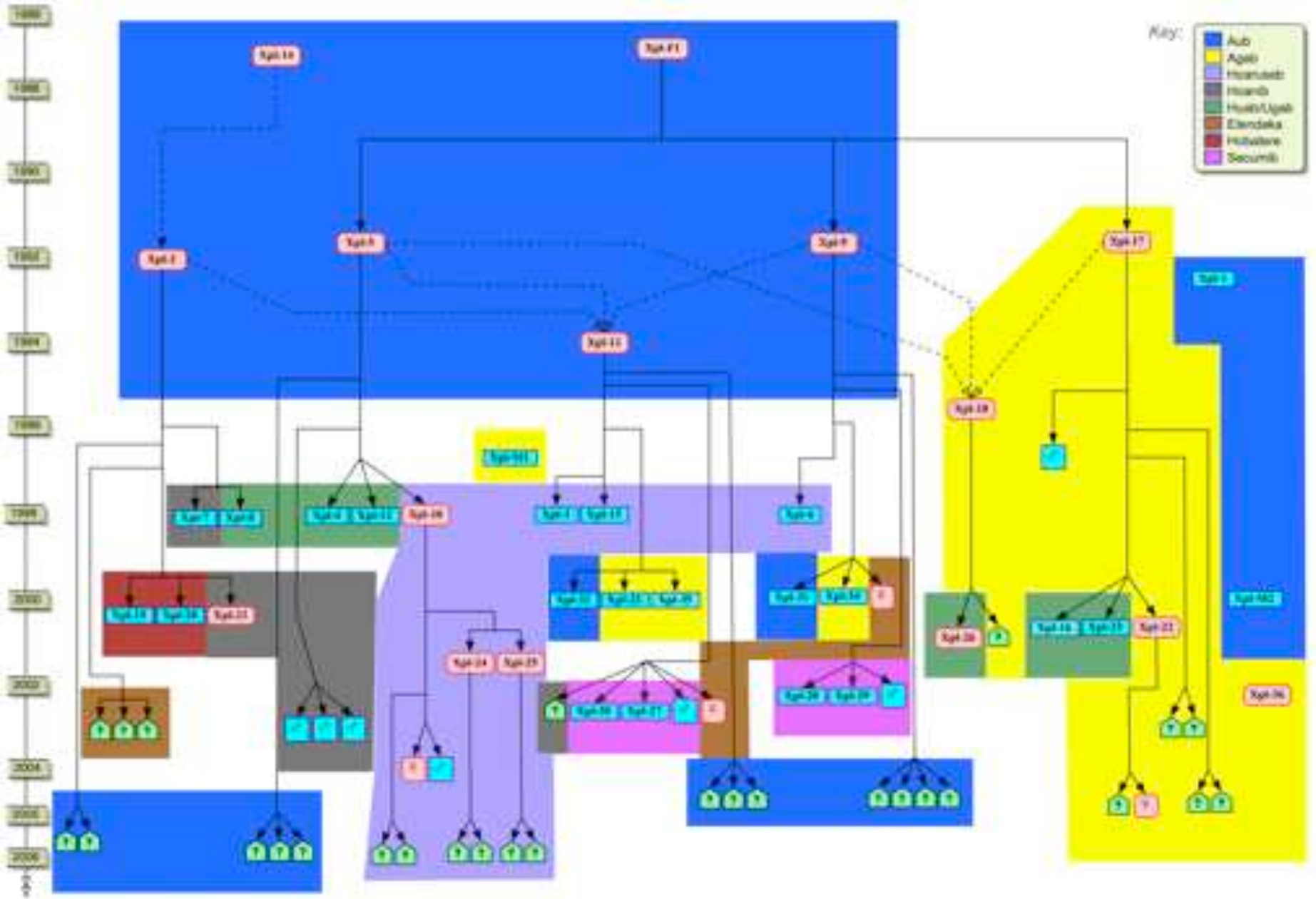
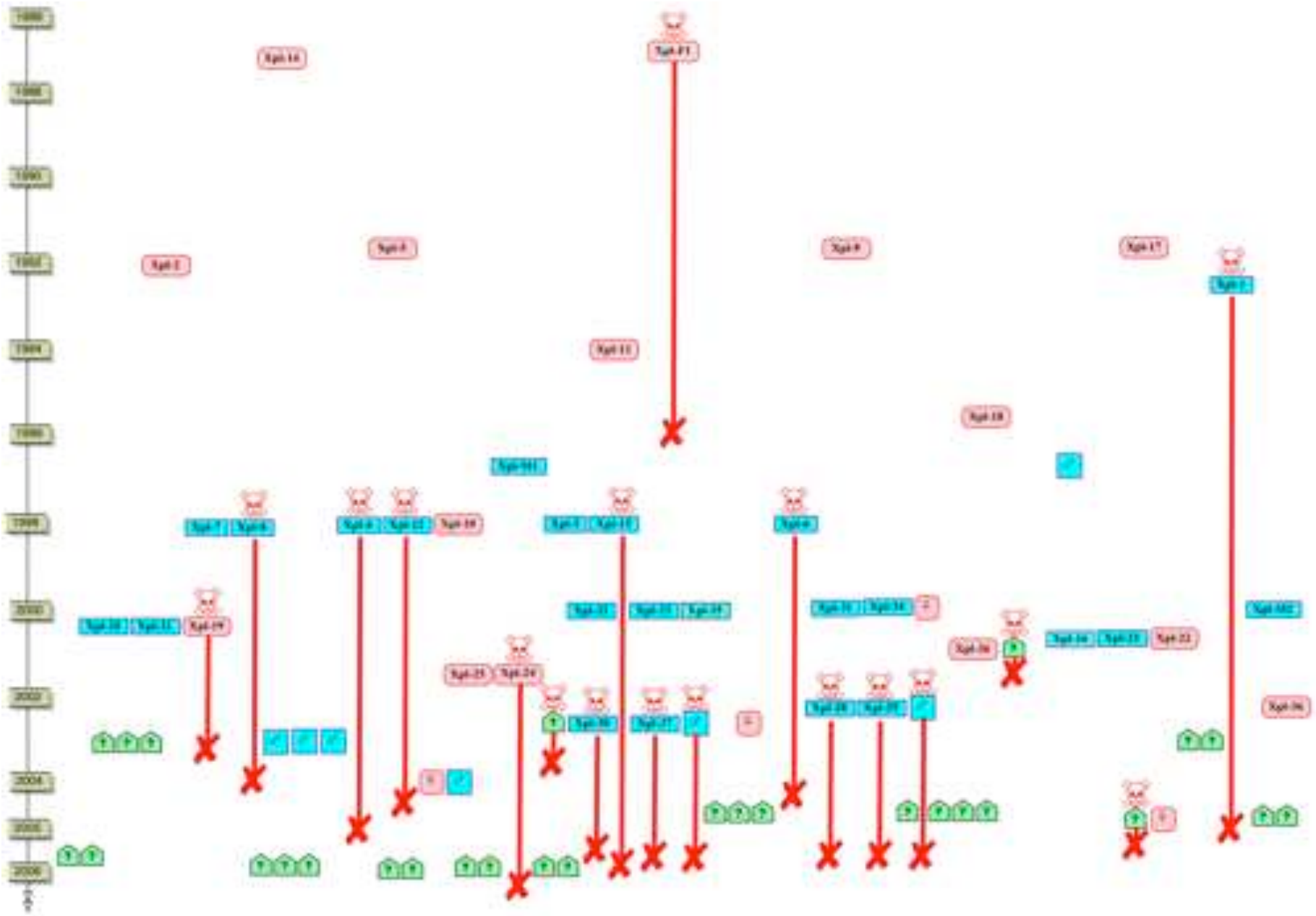


Fig. 12. Schematic layout depicting the lifespan of lions that have died, following the structure of genetic origins and relatedness presented in Fig. 9.



Grouping patterns

Adult lionesses in the Kunene, that belong to the same group or pride, frequently spend long periods apart. Such long separations are unusual in lion social behaviour. Adult females form the core of the social structure of lions, known as prides (Schaller 1972). Lionesses in a pride are normally related, and they form sub-groups that regularly rejoin. This typical fission-fusion strategy has a frequency pattern that is measured in days (Packer 1986). In the Kunene population, long-term data on the grouping patterns of the Aub Pride are analysed to demonstrate the unusual fission-fusion characteristics. During 396 observations of the five lionesses of the Aub Pride, the preference of individuals spending time together is presented in a matrix of association (Table 2). Lionesses spend most of the time alone, or with cubs, or adult males (50%), followed by groups of two lionesses (38%) and groups of 3 to 5 lionesses (12%). Average group size for the whole Kunene lion population is small (Table 3), with an average of 1.17 adult females per group.

Table 2. Matrix of association between lionesses of the Aub pride in the Kunene Region (N = 396). Rows depict an index of association between the lioness listed in the row heading with those in the column headings, where and index value of 1.0 will result when lionesses are always together. Yellow squares present the proportion of observations where lionesses were alone, or with males and/or cubs, but not with another lioness.

	Xpl-2	Xpl-5	Xpl-9	Xpl-11	Xpl-14
Xpl-2	***64%***	0.30	0.70	0.67	0.03
Xpl-5	0.24	***58%***	0.05	0.07	0.71
Xpl-9	0.35	0.03	***13%***	0.95	0.02
Xpl-11	0.32	0.03	0.86	***6%***	0.11
Xpl-14	0.03	0.79	0.03	0.18	***30%***

Table 3. Average group sizes of lions in the Kunene Region (N = 451).

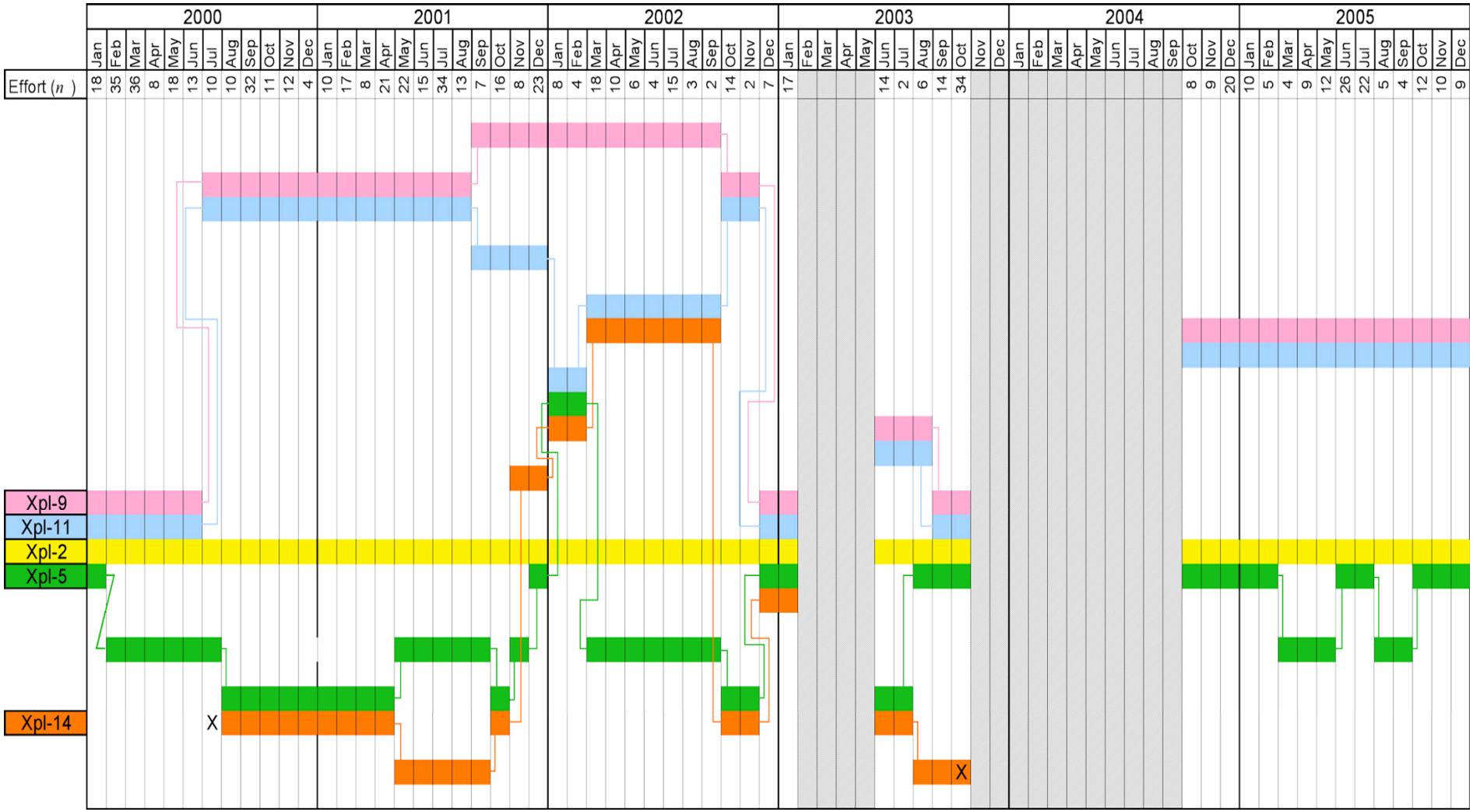
Category	Adult Female	Adult Male	Sub-adult	Young	Total
Group size[1]	1.17	0.49	0.77	1.47	3.9
Range	0-5	0-3	0-10	0-12	1-18

[1] *Mean group size*

Lionesses of the Aub pride regularly spent more than one month apart. In a rough monthly schematic presentation (Fig. 13) the patterns and frequency of association between individual lionesses is displayed on a monthly scale. The lioness, Xpl-2, lived in the centre of the Aub Pride's home range, and the grouping patterns of the other lionesses are presented in relation to Xpl-2. For example, the lioness Xpl-11 was observed with Xpl-2 and Xpl-9 from January to June 2002. In July 2000 Xpl-11 and Xpl-9 separated from the rest and lived together for 14 months, until August 2001, when Xpl-11 moved away and lived alone for four months. In January 2002 she joined Xpl-5 and Xpl-14 for two months, and then stayed with Xpl-14 for the next seven months. In October 2002 she joined her old partner, Xpl-11, after a separation of 13 months. They remained together for two months before joining Xpl-2 (and Xpl-5 & Xpl-14), after 2 years and 4 months apart. For the remaining observations, Xpl-9 and Xpl-11 remaining together, spending some months with Xpl-2 and/or Xpl-5, but mostly in a separate sub-group.

Between January 2000 and January 2003, the longest period of continuous observation, there are 14 records of individual lionesses spending more than one month apart (Fig. 13). In this fission-fusion dataset, individual lionesses of the Aub Pride rejoined after being apart for an average of 17.9 months (range: 2 months – 2 years & 10 months). Such extended fission-fusion time periods have not previously been documented for lions. It is suggested that the unique fission-fusion grouping patterns of Kunene lionesses is a display of behavioural adaptation to the demanding condition imposed by the desert habitat.

Fig. 13. Schematic presentation of the months, between 2000 and 2005, that lionesses of the Aub Pride where observed together or apart. The number of observation (N = 746) are listed for each month and the grey areas reflect the months where no data where collected. For Xpl-14, the X at the start and end of her records indicate the time when she was first radio-collared, and when she disappeared in October 2003.

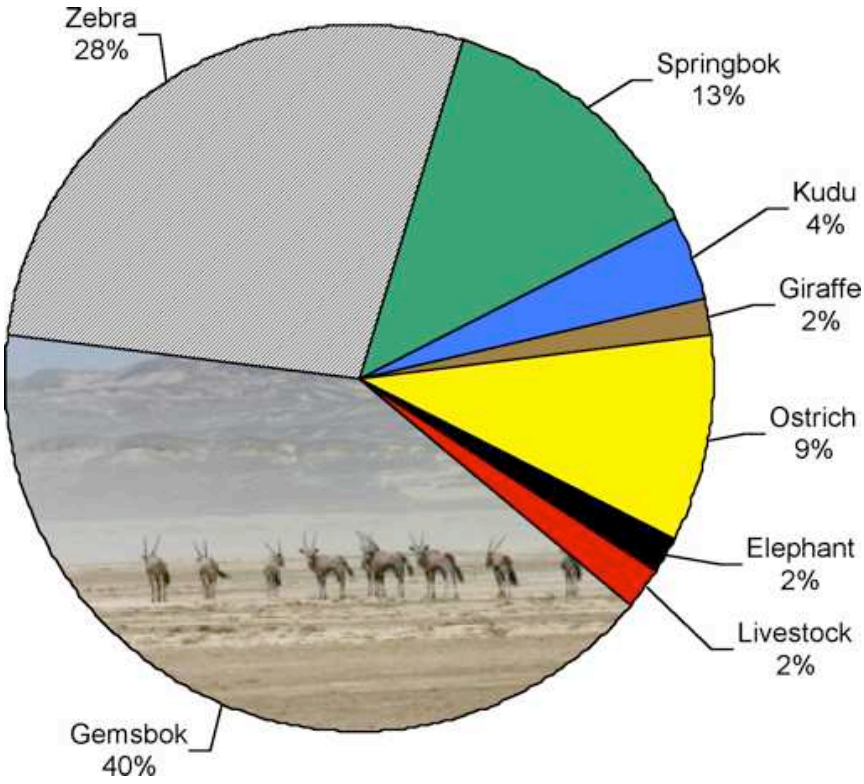


Behaviour and habitat utilisation

Predation

Records on predation and prey selection by Kunene lions are limited to daytime radio tracking observations (*N* = 565) and may therefore be biased towards larger prey species. Lions may capture and totally consume smaller prey, like springbok, at night. Acknowledging this potential bias, lions were observed with prey species that they had killed on 10% (*N* = 54) of observations. Gemsbok and Hartmann's zebra were the two most important prey species (Fig. 14), followed by springbok and ostriches. Livestock was killed by lions on one occasion, and form an insignificant part of their diet.

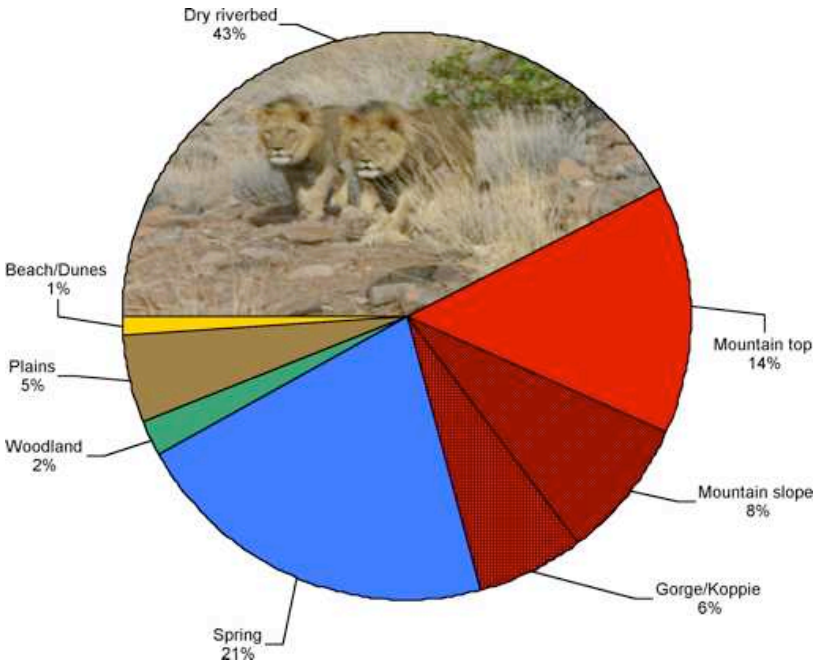
Fig. 14. Summary of prey species killed by Kunene lions (N = 54).



Habitat preferences

During daytime radio tracking sessions (N = 597) lions were observed in eight habitat categories (Fig. 15). Ephemeral rivers, mountains (28%) and springs are the three most important habitat types (total = 92%) that lions utilise for daytime resting. During nocturnal movements and foraging, lions are expected to utilise the habitat more uniformly.

Fig. 15. Summary of habitats favoured by Kunene lions (N = 597).



Home ranges

The areas occupied by the Kunene lions are the largest home ranges ever recorded for the species (Table 4). With the increase in sample sizes the two methods (MCP and Kernel) are calculating similar estimates of home ranges size for most individuals. The home ranges of the Aub and Agab prides, that utilise similar habitats, are similar in size, for both the MCP and Kernel methods. There is extensive overlap between the different groups, and especially so for the male groups, where the size of the habitats they utilise increase continuously. Detailed maps showing the home range size and areas utilised are presented for each group of lions (Fig. 16 - 23). Land tenure systems appear to be driven by ecological factors, such as prey availability, and density dependent factors, but more research is needed to address this.

Table 4. Home ranges of Kunene lions.

Pride / group	ID	Group description	N	Home range (km ^{2})		Accuracy of fixes[1]
				MCP	Kernel (95%)	
Aub	Xpl-2, 5, 9	Female & cubs	173	2,632	2,721	41%
Agab	Xpl-17,18	Female & cubs	110	2,826	2,909	44%
Hoaruseb	Xpl-10	Female & cubs	120	8,034	6,939	51%
Huab/Ugab (1)	Xpl-4	Male group	127	5,912	5,393	Negative
Huab/Ugab (2)	Xpl-16	Male group	71	16,377	13,365	Negative
Hoanib	Xpl-3	Male & females	112	9,084	6,543	Negative
Hobatere	Xpl-20	Male group	36	4,907	3,608	83%
Secumib	Xpl-29	Male group	33	27,650	17,221	Negative

[1] *The percentage of fixes where the MCP home range estimate reached an asymptote of at least 95% of the total MCP-estimate, based on bootstrap analyses.*

Fig. 16. Locations and home range (MCP & Kernel Contour) of the Aub Pride. N = 173; MCP = 2,632 km^2; 95% Kernel 2,721 km^2

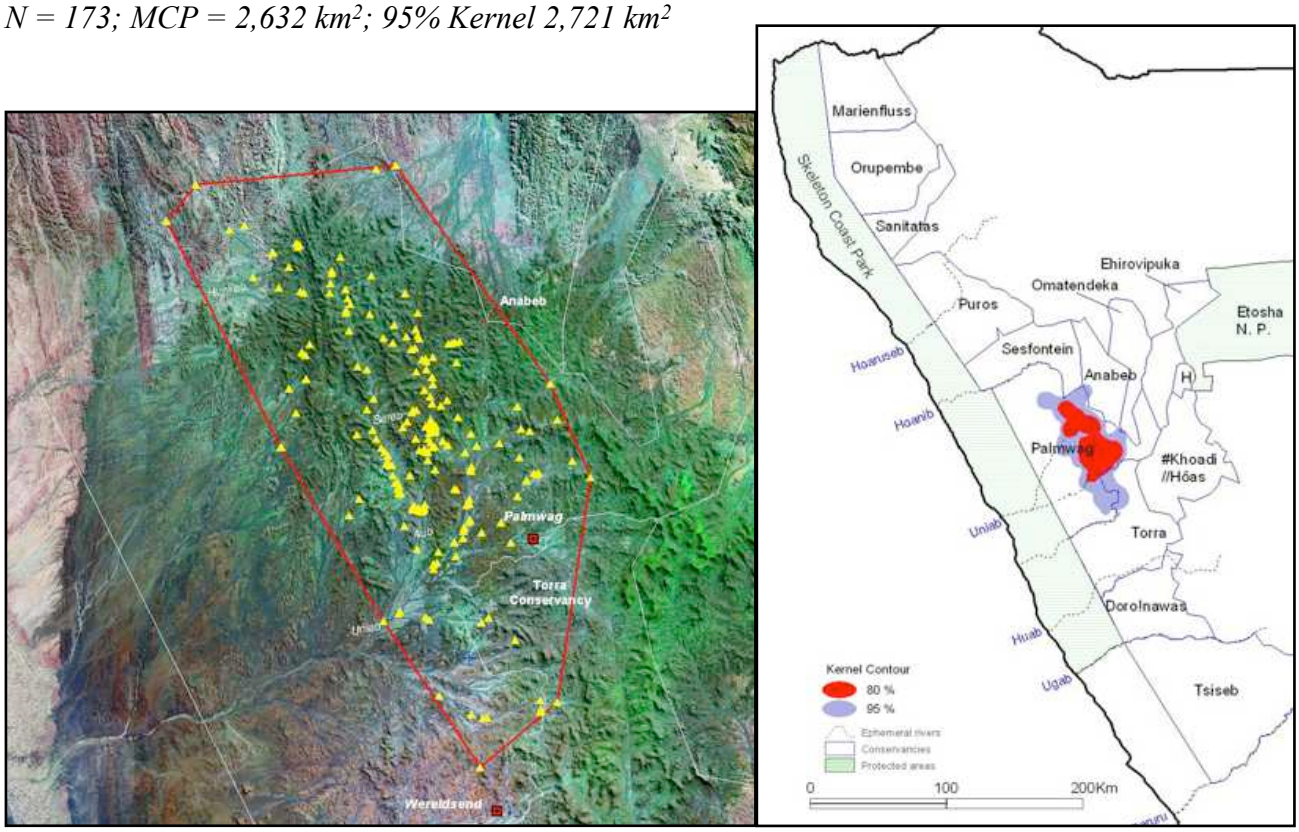


Fig. 17. Locations and home range (MCP & Kernel Contour) of the Agab Pride.
N = 110; MCP = 2,826 km²; 95% Kernel 2,909 km²

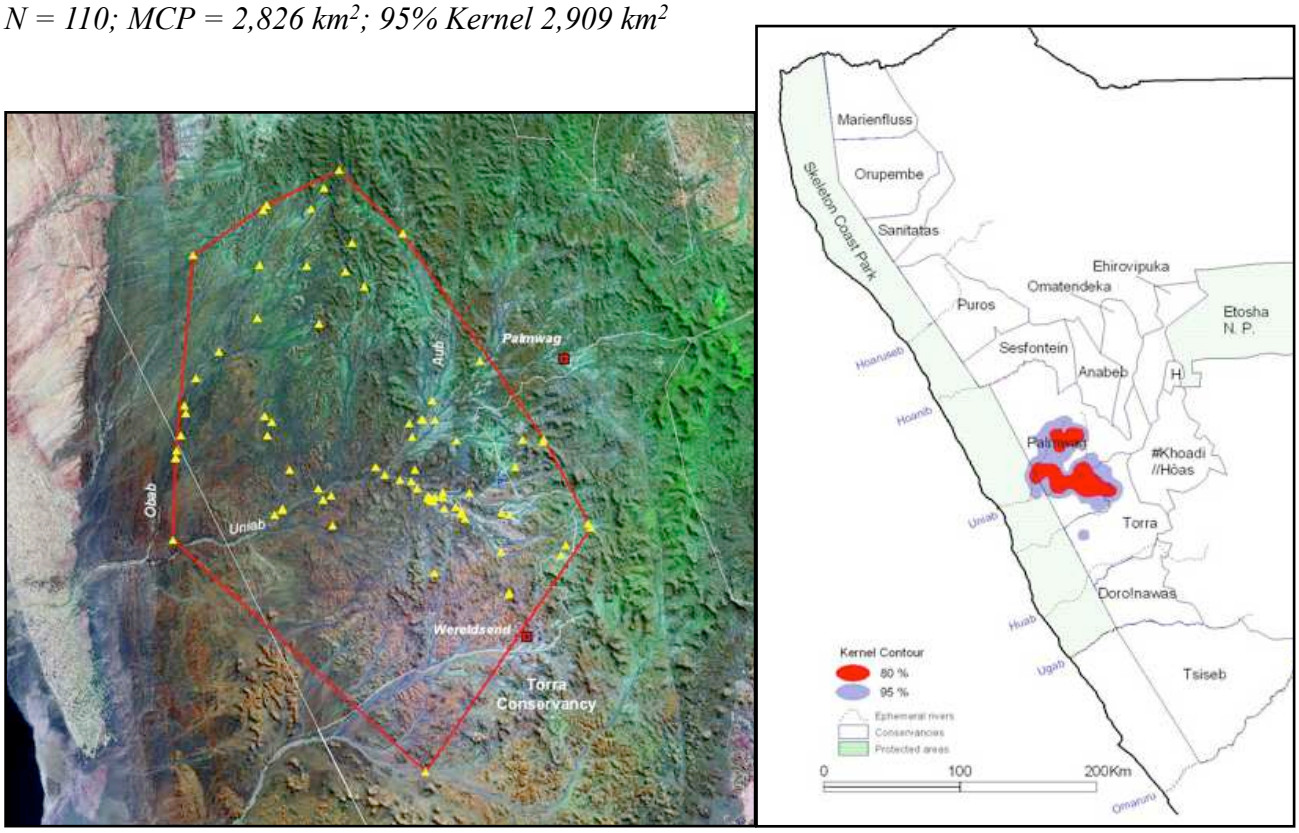


Fig. 18. Locations and home range (MCP & Kernel Contour) of the Hoaruseb Pride (Xpl-10).
N = 120; MCP = 8,034 km²; 95% Kernel 6,939 km²

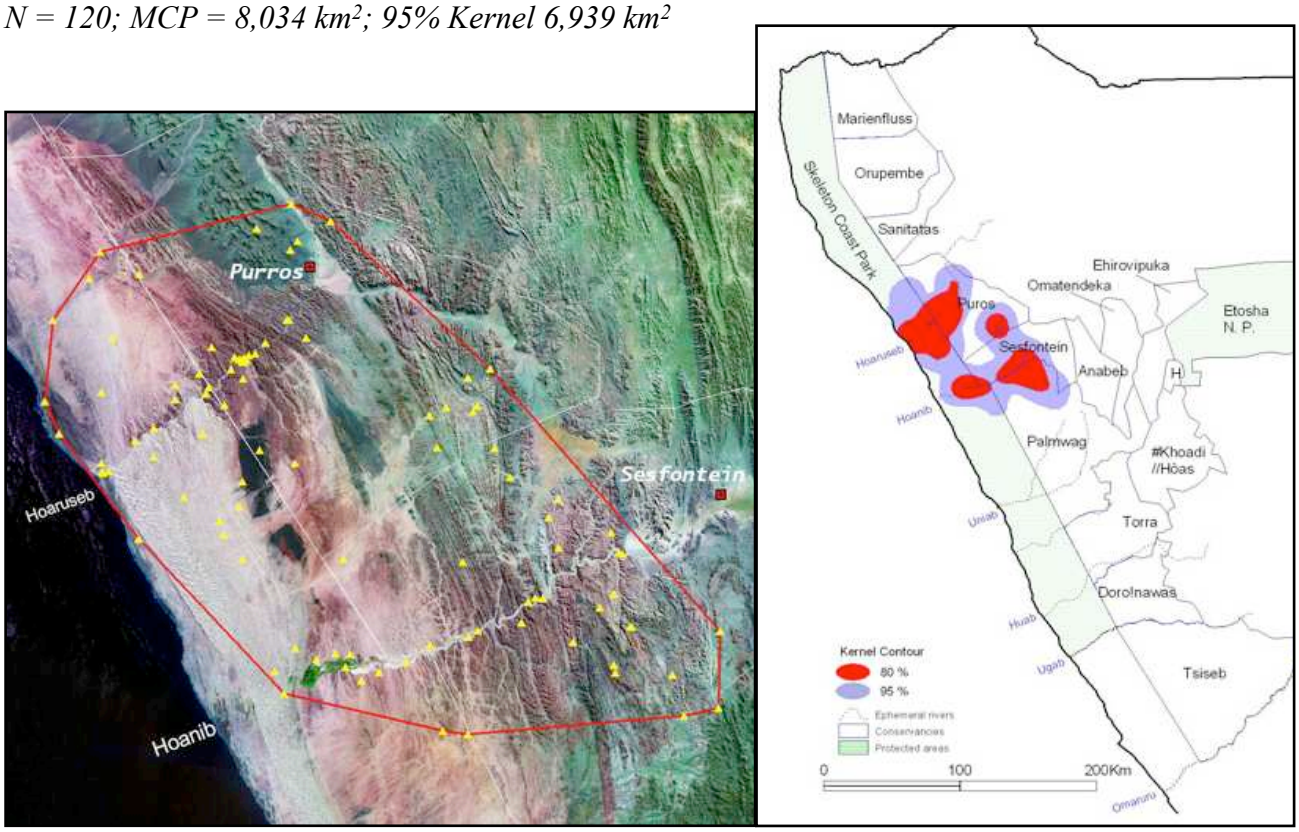


Fig. 19. Locations and home range (MCP & Kernel Contour) of Xpl-4, Huab/Ugab Group. N = 127; MCP = 5,912 km²; 95% Kernel 5,393 km²

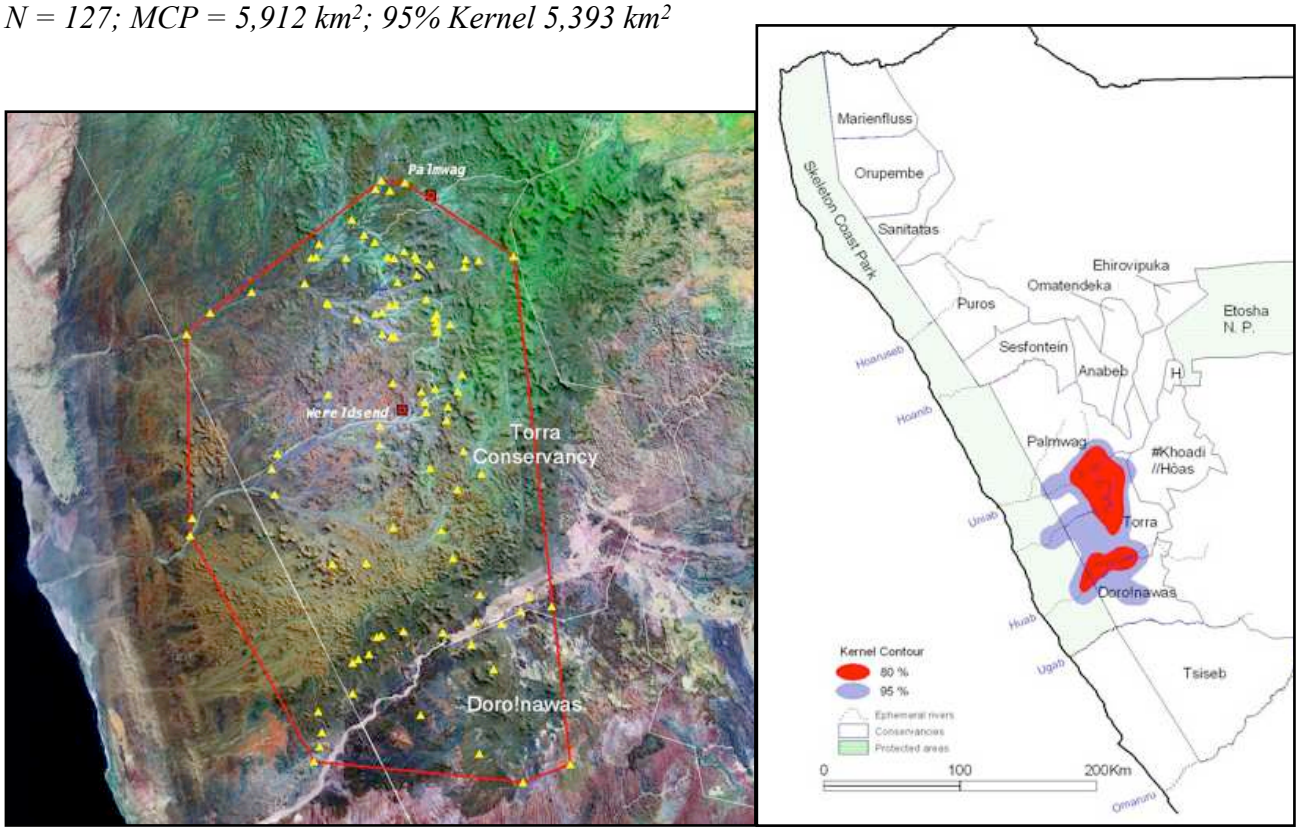


Fig. 20. Locations and home range (MCP & Kernel Contour) of Xpl-16, Huab/Ugab Group. N = 71; MCP = 16,377 km²; 95% Kernel 13,365 km²

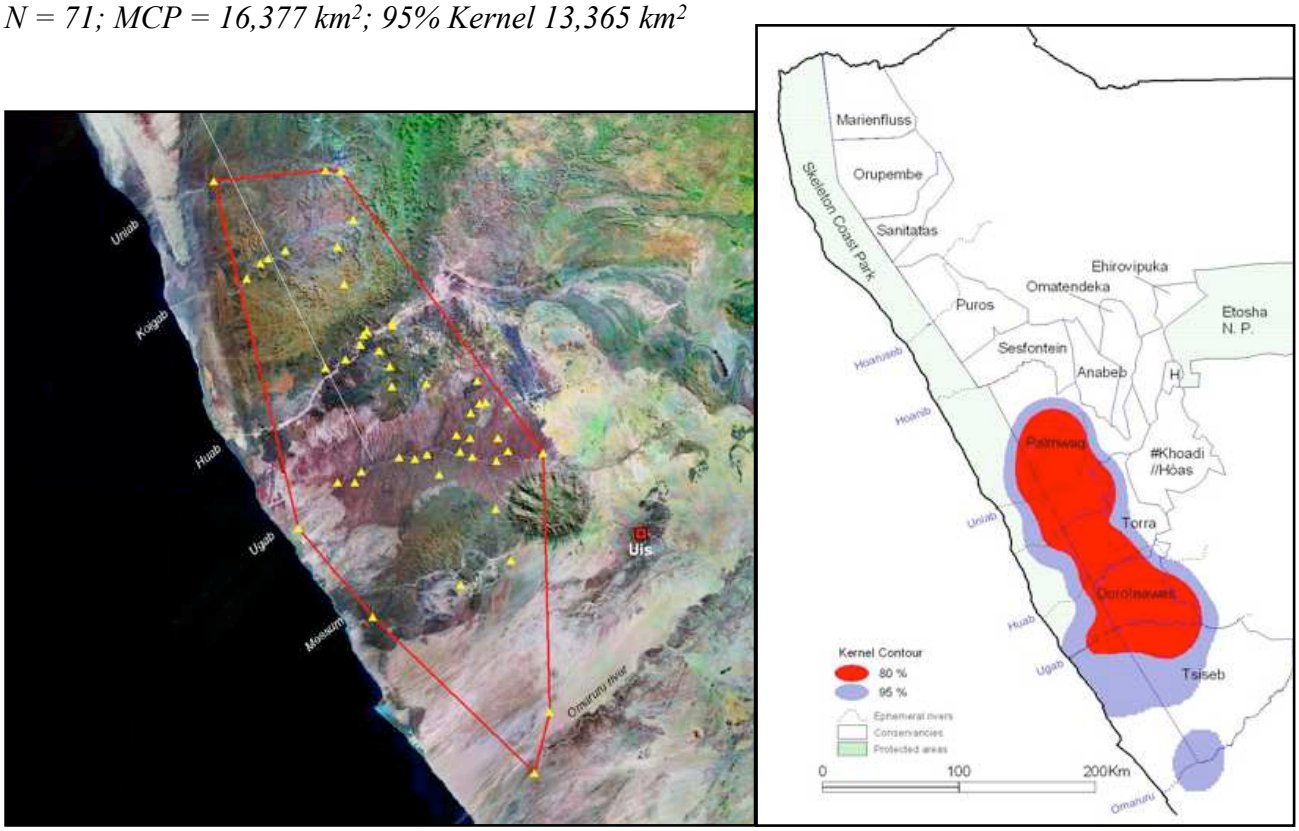


Fig. 21. Locations and home range (MCP & Kernel Contour) of Xpl-3, Hoanib Group.
N = 112; MCP = 9,084 km²; 95% Kernel 6,543 km²

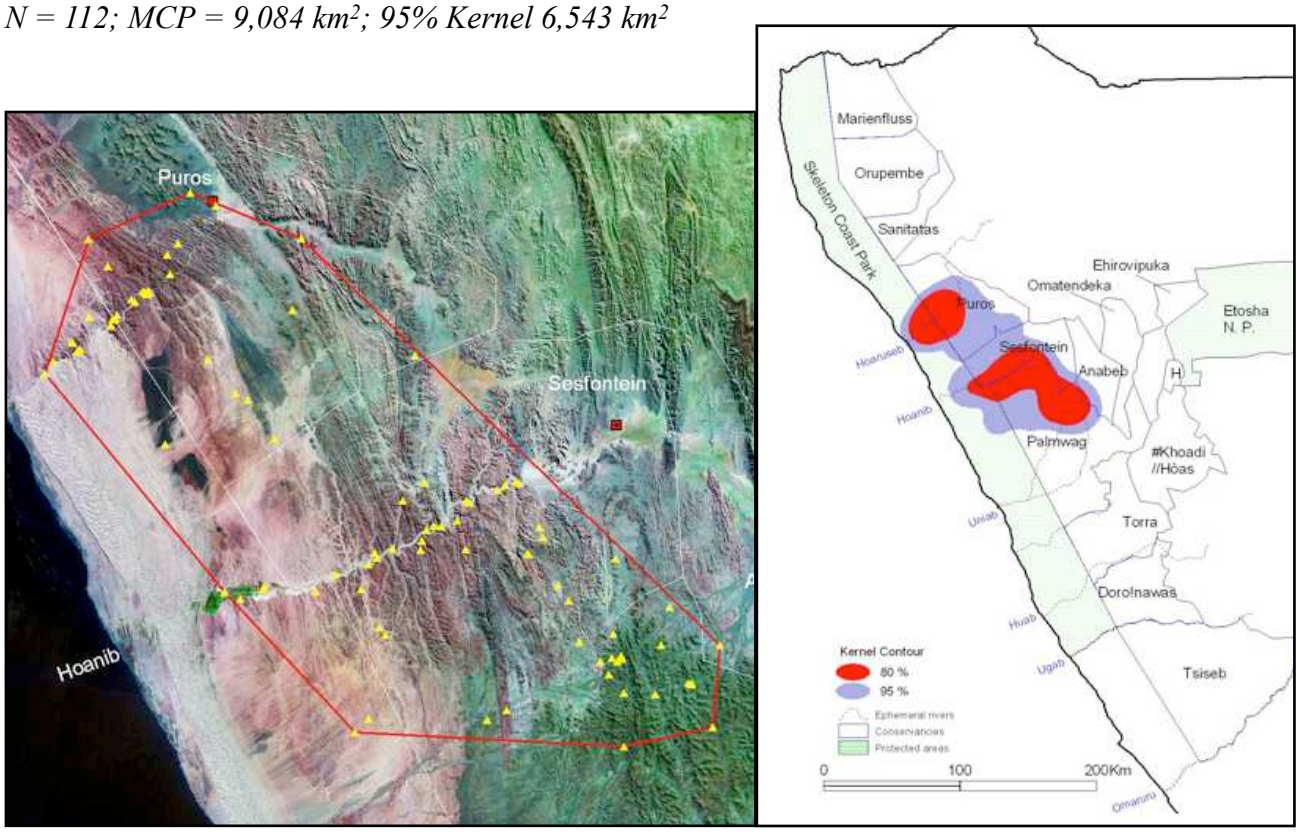


Fig. 22. Locations and home range (MCP & Kernel Contour) of the Hobatere Group (Xpl-20).
N = 36; MCP = 4,907 km²; 95% Kernel 3,608 km²

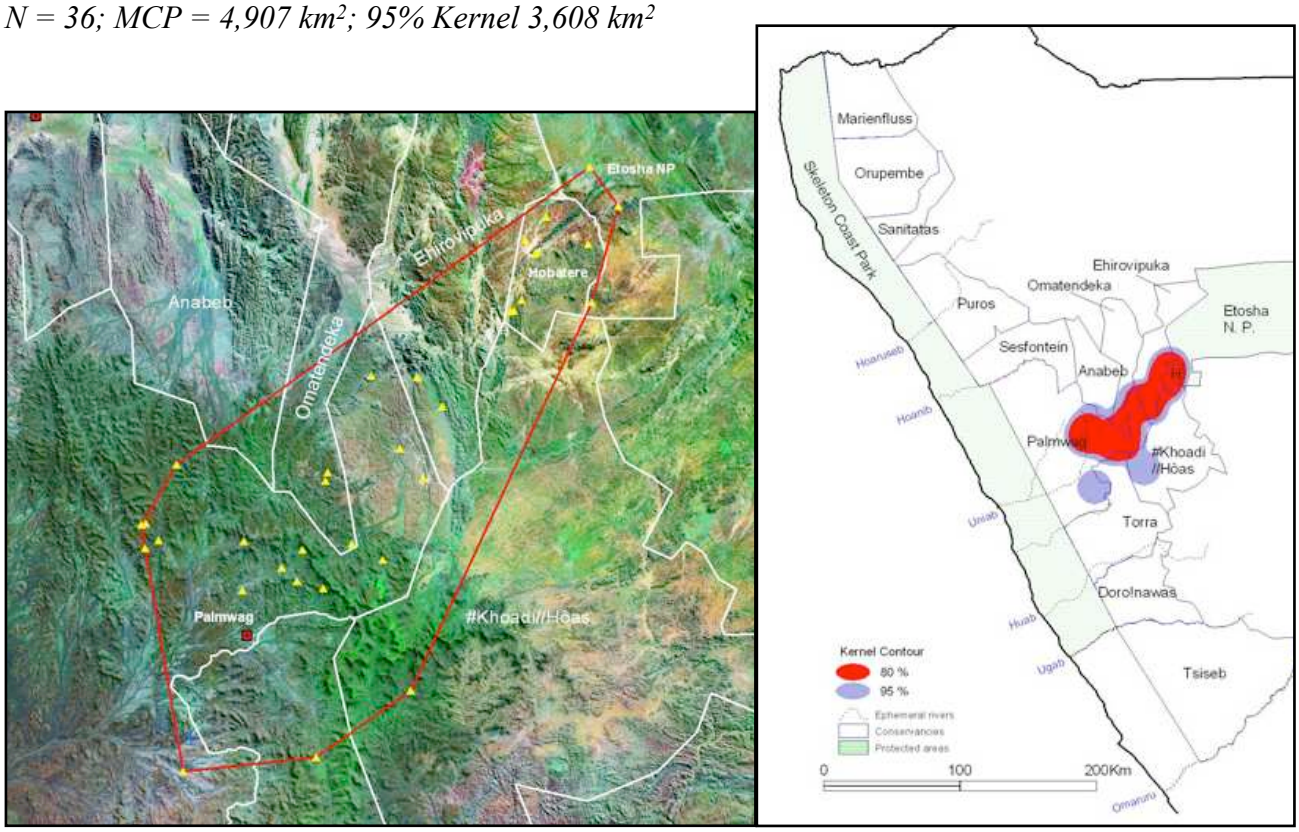
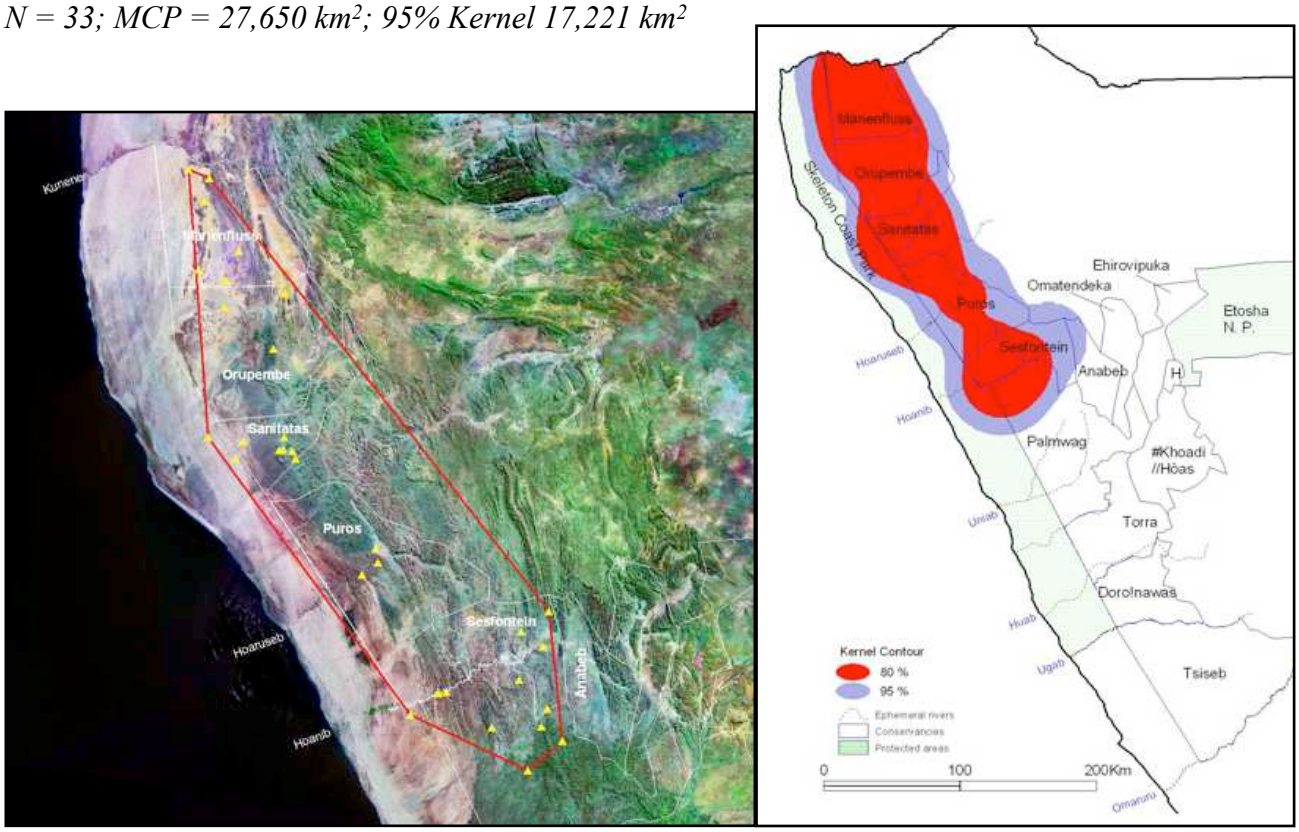


Fig. 23. Locations and home range (MCP & Kernel Contour) of the Secumib Group (Xpl-29). N = 33; MCP = 27,650 km²; 95% Kernel 17,221 km²



Nocturnal movements

Due to constraints imposed by the terrain, observations on marked lions are restricted to daytime radio tracking. Anecdotal observations suggest that lions move extensively at night and that they may utilise habitats not reflected by the conventional radio tracking data. To address this concern a GPS radio collar (courtesy of Ingrid Wiesel) was fitted to a lioness (Xpl-18) of the Agab Pride, for a three-month period in July 2005. The GPS radio collar was programmed to record daily position coordinates (fixes) every two hours, between 17h00 and 10h00 (UTC). Over the three months the GPS radio collar recorded 893 fixes during 104 nights (Table 5). The lioness moved an average calculated distance of 8.3 km per night, but utilised only 22% of the pride's known home range (Table 5). Over the same period Xpl-18 was also located 17 times, using conventional VHF techniques (see Methods). These aerial radio-tracking locations reflected only 8% of the known home range, and 34% of the area recorded by the GPS collar (Fig. 24).

Table 5. Summary of data collected by a GPS radio collar and aerial tracking on the movements of Xpl-18 (Agab Pride), between 11 July and 22 October 2005.

Category	GPS collar	Aerial tracking (VHF)
Total number of fixes recorded	893	17
Number of nights (data units)	104	17 (days)
Number of fixes per night (ϒ ± SD)	8.6 ± 1.3	-
Mean distance moved per night (ϒ ± SD)	8.3 ± 5.8 km	-
Range of distances moved per night	0.08 – 24.1 km	-
Total distance moved	858 km	-
Size of area used (MCP)	592 km^{-2}	201 km^{-2}
Percentage of the known home range[1]	22%	8%

[1] Home range of the Agab Pride over 5 years 2656 km² (MCP), see Table 4 & Fig. 17.

Extended nocturnal movements to the north and northeast, and outside the ephemeral river systems (GPS collar data), was not captured by the conventional daytime methods. The GPS data on nocturnal movements of Xpl-18 revealed interesting patterns, not previously known, and in support of the anecdotal information on extended movements at night.

Fig. 24. Locations of Xpl-18, of the Agab Pride from a GPS radio collar and aerial radio tracking, 11 July - 22 October 2005.

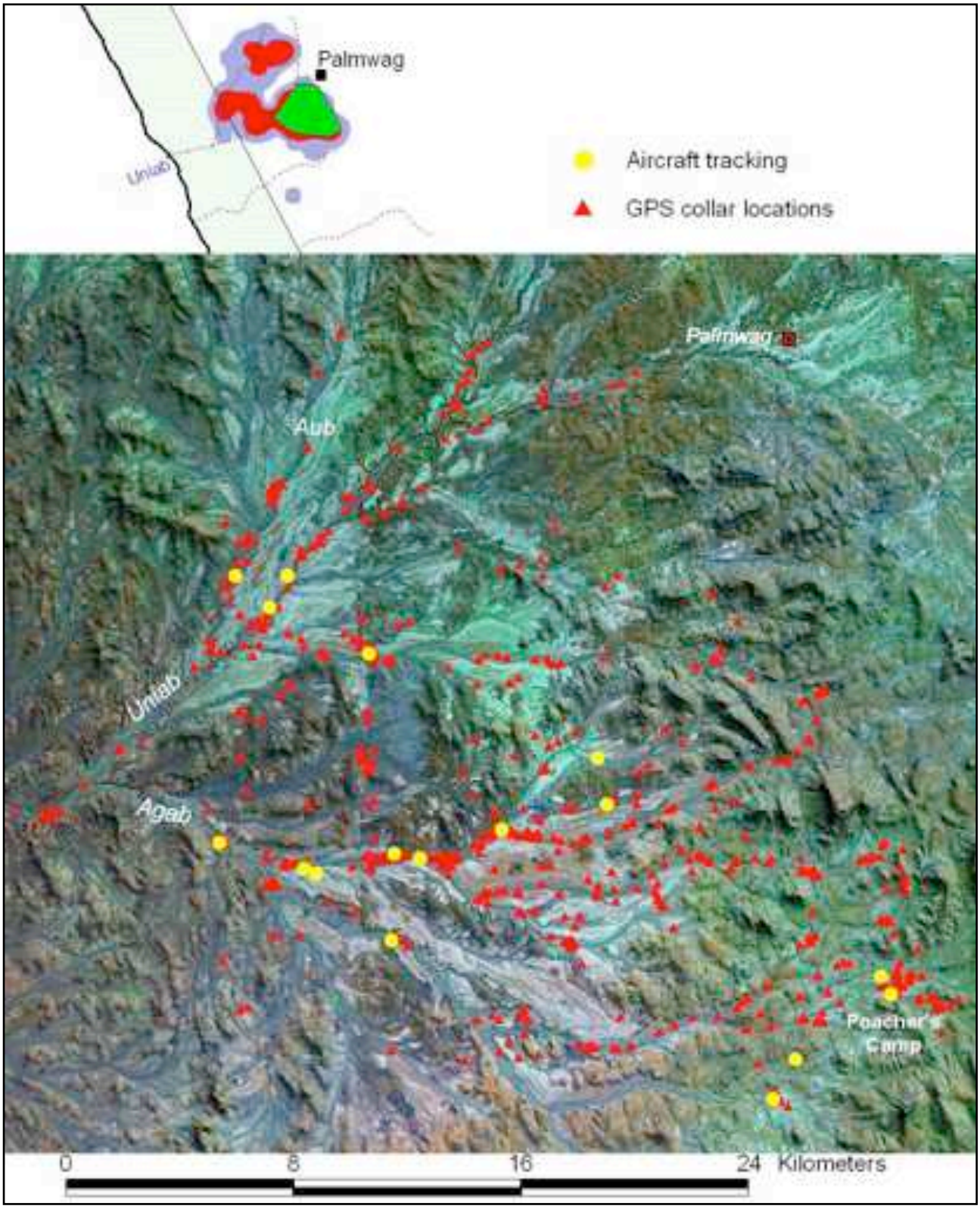
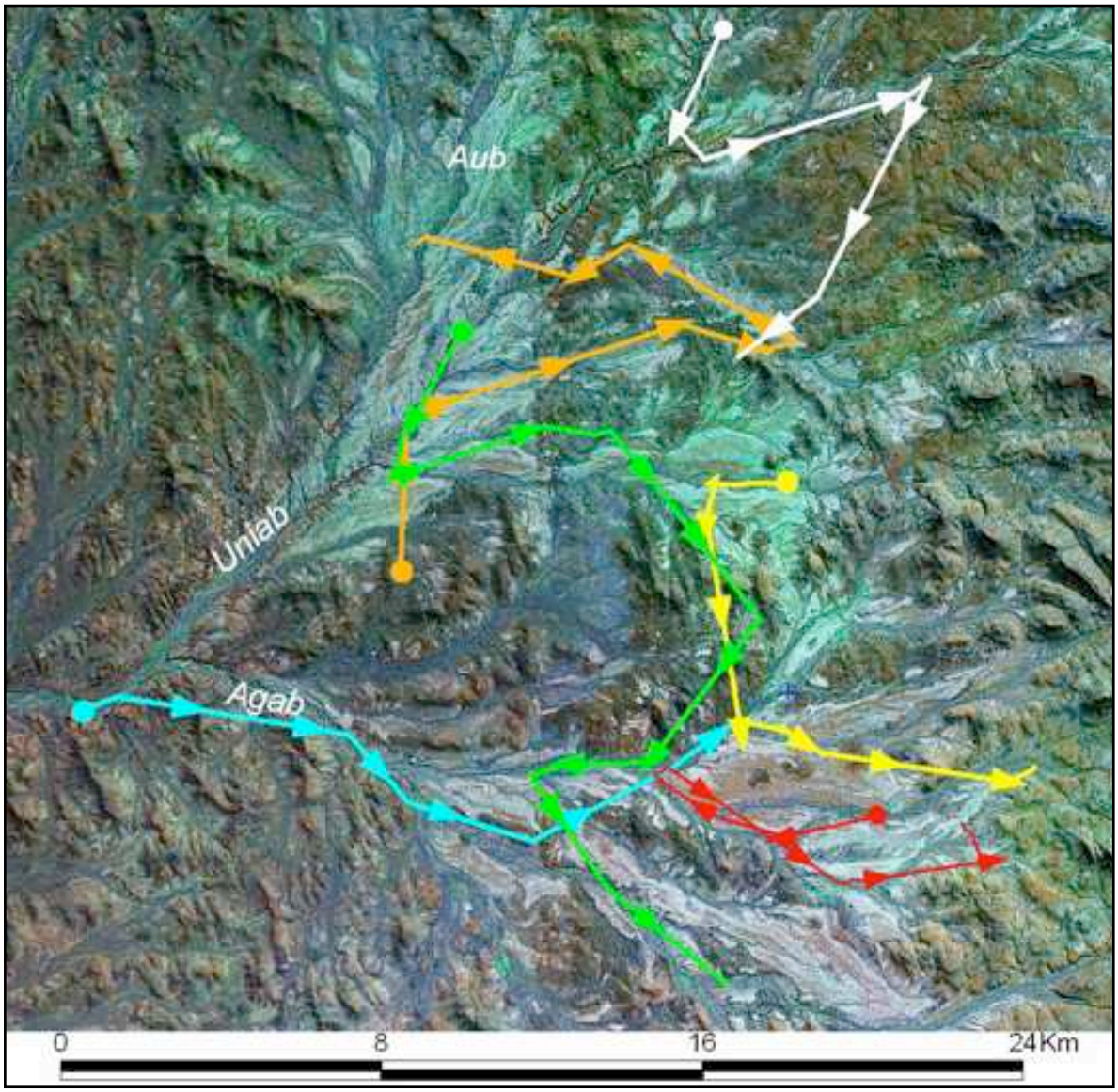


Fig. 25. Layout of nocturnal movements of Xpl-18 (Agab Pride) during six nights (see Table 5).



In order to demonstrate these findings, a sub-set of six nocturnal movements, is presented (Fig. 25). The movements of Xpl-18 were often erratic, as she crossed over mountains, and between different tributaries of the ephemeral river systems. With the exception of 23 July 2005 (blue line), there were frequent and considerable changes in the direction of movements. The distance between one day-time-resting-spot and the next, is substantially less than the actual distance moved during the night, as recorded by the GPS collar (Table 6). Conventional radio-tracking techniques (daytime locations) clearly produce inadequate data on movements and habitat use, when compared with the GPS collar data.

Table 6. Summary of distances moved during six nights by Xpl-18 (Agab Pribe), as recorded by a GPS radio collar between 11 July and 22 October 2005.

Date	Colour	Distances (km)		Proportion[3]
		GPS data[1]	Day resting[2]	
23-Jul-05	Blue	16.0	14.8	93%
19-Aug-05	White	15.7	7.3	46%
23-Aug-05	Yellow	17.3	9.4	54%
16-Sep-05	Red	16.2	2.2	14%
28-Aug-05	Green	22.2	17.4	78%
29-Jul-05	Orange	24.1	7.2	30%

[1] Total distance moved during the night, calculated by joining all the GPS fixes.
[2] Distance between one day-time-resting-spot and the next (point-to-point).
[3] Day resting distance[2] as a percentage of the total distance moved (GPS data[1]).

Habitat expansion and dispersal

Habitat expansion

With the rapid growth of the Kunene lion population in the core study area, especially between 2000 and 2004, dispersal of individual lions and the expansion of the range of the population are expected. Intensive monitoring, between 2000 and 2005, of habitat utilisation (Fig. 26) by the core study group of 18 radio-collared lions and their offspring, initiated in 1999, illustrates a striking increase in their range. Reliable estimates of the size of this lion population were calculated, independently of the habitat data, at the end of each year. An analysis of these data show that there is a significant relationship between the number of lions and the size of the habitat they occupy (Fig. 27). Range size can be expressed as a linear function of lion numbers. This finding has important relevance to conservation strategies and when developing human-lion conflict management plans.

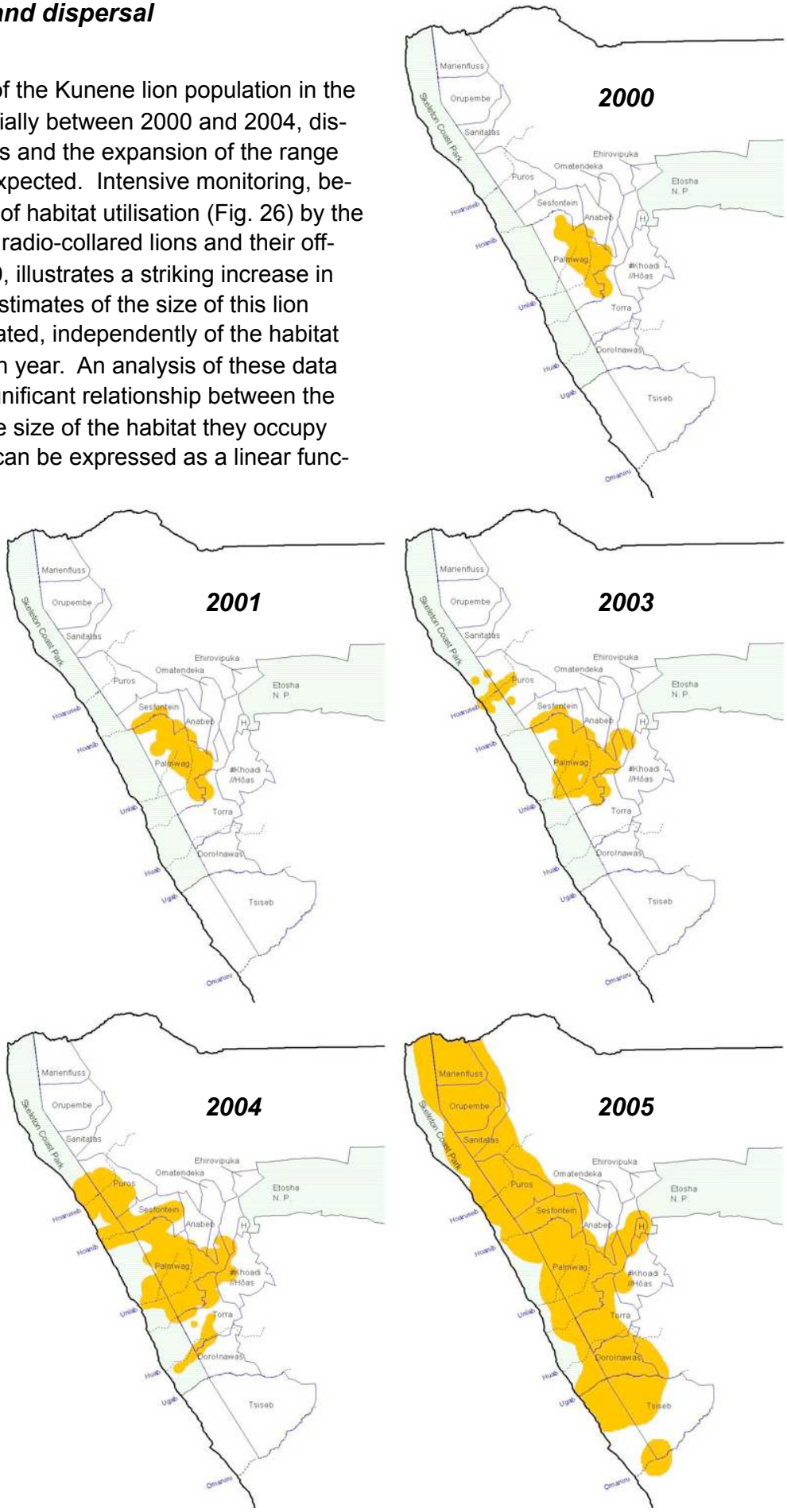
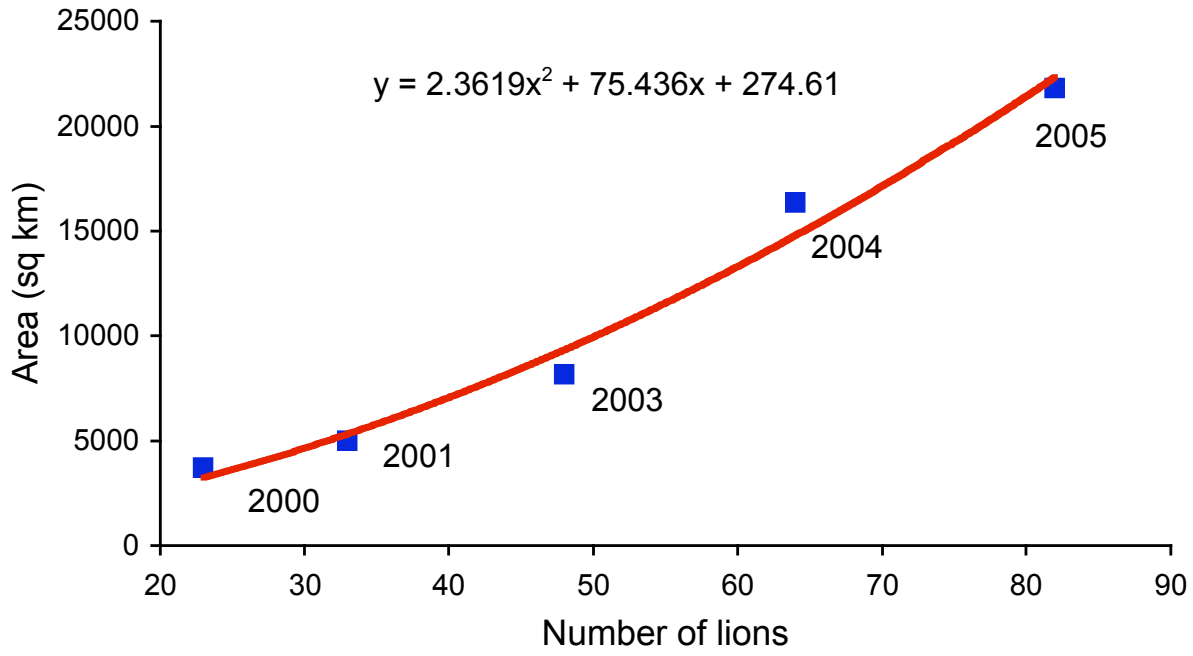


Fig. 26. A schematic layout of the range occupied by Kunene lions, between 2000 and 2005.

Fig. 27. The relationship between lion numbers and the size of the range (km²) they occupied, 2000 - 2005.



Dispersal

Dispersal of individual lions, and small groups, is an important mechanism in the ecology and self-regulation of the Kunene lion population. Following a sharp population growth between 2000 and 2004, several individual lions, and some small groups, dispersed from their natal prides in 2004 and 2005, presumably in search for new habitats (Table 7). Radio-collared lions were monitored and 12 incidents of dispersal were recorded. During five events, lions moved deep into unknown territory (*N* = 176 km, range 92-343) to established new home ranges.

Table 7. Dispersal by 12 lions during 2004 and 2005 in the Kunene Region.

Group	Composition	Distance (km)	Time period
Secumib	6 SA males	343	7 months
Hobatere	2 A males	92	4 months
Huab/Ugab	1 A male	136	5 months
Huab/Ugab	1 A male	164	3 months
Hoanib	2 A males	145	3 months

CONCLUSION

The desert adapted and coastal roaming lions of Namibia were believed to have dwindled to alarmingly low numbers after a low rainfall period in the 1980's when many were killed by pastoralists. Improved rainfall patterns during the 1990s and 2000s, and successful conservation programmes, such as the emergence of Communal Conservancies, have seen a significant increase in wildlife numbers. This study presents data on the population status and demography of lions that are in line with, and complement, the trends and recent conservation achievements. Kunene lions live in the most rugged and arid of environments, yet they demonstrated remarkable success, with high survivorship, rapid growth rates, and dispersal. Conflict between lions and the local communities remain the most important ecological, conservation, and economic problem. Developing conservation strategies for the Kunene lions is, among many ecological parameters, dependent on a sound understanding of the factors that drive the distribution, dispersion, and regulation of the population. This research report presents scientific data on key ecological characteristics of the lion population. The study, and its results, is aimed at providing a sound technical and ecological foundation for the development and implementation of long-term and successful conservation strategies.

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