

CHAPTER 4.

CHARACTERISTICS OF HOME-RANGE ESTABLISHMENT AND HABITAT USE IN REINTRODUCED LIONS AND CHEETAHS.

Lions and cheetahs display far greater degrees of sociality than most other felids and this has important implications for their ranging dynamics. As the only cat species which lives in extended family groups, lions exhibit complex patterns of territoriality which have fundamental implications on their spatial organisation. Related females live in stable social groups which may occupy the same range for generations and generally exclude unrelated females (Hanby *et al*, 1995). Coalitions of males associate with the female groups and attempt to defend from other males an area which encompasses one or more prides (Pusey & Packer, 1994; Hanby *et al*, 1995). In cheetahs, females appear to be non-territorial and may occupy home-ranges as large as 1500km² (Caro, 1994; Marker-Kraus *et al* 1996). Male cheetah ranging behaviour, however, resembles patterns observed in lions in that, where possible, coalitions of males establish exclusive territories and defend them from other males in occasionally fatal clashes (Caro & Collins, 1986; Caro, 1994; Hunter & Skinner, 1995; Appendix III).

The main factor determining establishment and spatial characteristics (particularly size) of territories and home-ranges in felids is resource availability (Sandell, 1989; Kitchener 1991; Caro, 1994; Mizutani & Jewell, 1998). The size of female home-ranges is generally determined by prey density, availability and distribution, and will also be affected by the availability and spacing of suitable den sites for rearing cubs (Sandell, 1989; Caro, 1994; Bothma *et al*, 1997). Male home-ranges are usually larger and may overlap a number of female ranges, presumably to increase mating opportunities (Sandell, 1989; Bailey, 1993).

Considerable variation has been observed in lion and cheetah range size due to these factors. Hanby *et al* (1995) demonstrated that lion ranges on the Serengeti Plains where food supplies were ephemeral and den sites for cubs were widely scattered averaged almost five times as large as ranges in superior habitat in Ngorongoro Crater where density of food and den-sites was greater and more evenly distributed. Similarly, Van Ordsol (1982) and Van Ordsol *et al* (1985) demonstrated that range size underwent a reduction when there was an increase in lean season biomass in good years. Stander (1991) reported pride size in the arid Etosha National Park may be as large as 2075km², presumably due to migratory movements and low density of ungulates.

In cheetahs, Serengeti females followed migratory gazelles and had home ranges larger than 800km² (Durant *et al*, 1988). In Namibia, female ranges were almost twice that size (Morsbach, 1986). Amongst male Serengeti cheetahs, the average size of territories was 37.4km² (Caro, 1994) whereas for non-territorial males (usually singletons unable to defend a territory), home-range size averaged 777km². The main determinants of territory location were a combination of adequate cover and adequate densities of Thomson's gazelles (Caro, 1994).

Very few data are available on home-range and territory characteristics for reintroduced felids. Ruth *et al* (1993) considered three translocated mountain lions to have established home ranges after six months constant use of an area, but few additional details are provided. Similarly, Hamilton (1981) established that one translocated female leopard 'eventually settled' at the release site but further details are unknown. Although there have been numerous successful efforts to re-establish lynx in some European countries (Breitenmoser & Breitenmoser-Wursten, 1990; Yalden, 1993), there are very few data on their movements following release and the process by which they establish home ranges. While lion and cheetah spatial patterns have been well-studied in established populations in numerous ecosystems, they are not known from translocation or reintroduction scenarios.

A reintroduction project such as at Phinda offers opportunities to explore aspects of felid spatial patterns which would not be possible in established populations. There were no resident or, even transient lions or cheetahs at Phinda, so the movements and behaviour of released individuals were not constrained by the presence of conspecifics. Available habitat was highly heterogeneous (Fig. 5, Chapter 2) so that felids had a 'choice' of suitable habitats in which to settle. Finally, ungulates were non-migratory and existed in high densities in all habitats in approximately even distributions throughout the reserve (Chapter 7) so that felids may not have had to make large movements in order to secure prey.

In the previous chapter, I examined the movement patterns of reintroduced felids immediately following release. In this section, I examine the home-range and movement characteristics of lions and cheetahs over the entire duration of the study. I present details of the home-range patterns of reintroduced lions and cheetahs. I attempt to explore the process of home-range establishment by felids in an environment in which some factors affecting spatial patterns in established populations were absent or minimal. I examine differences in seasonal ranges and the presence of young cubs on female ranging behaviour. Finally, I include some management and technical considerations pertaining to lion and cheetah ranging patterns and habitat use which may assist future reintroduction efforts.

METHODS

Lions and cheetahs were located by radio-telemetry and their positions recorded as specified in Chapter 2. Radio-collared cats were located as frequently as twice daily, though this generally varied from between daily to every third day. I also recorded all opportunistic sightings of non-telemetred cats which, naturally, were not as frequent (Table 6). Mindful of the problem of autocorrelation of data (Rooney *et al*, 1998), I took the minimum time interval between fixes for all analyses as one day. Autocorrelation of tracking data is the phenomenon whereby the position of an animal at time $t + \Delta t$ is not independent of its position at time t (Rooney *et al*, 1998). If data are highly autocorrelated, the estimation of home range size can be underestimated (Swihart & Slade, 1985) and interpretation of range utilisation can be erroneous (Cresswell & Smith, 1992). The simplest way to deal with the problem assumes that the time to independence between successive locations (i.e. the shortest time between two data points which are not autocorrelated) will be the time it takes an animal to traverse its home range. Accordingly, as lions and cheetahs could and often did cross their home range easily within one day, that was the minimum frequency at which I subsampled the data for analysis. If cats were stationary for more than one location, such as when feeding on a kill or mating on consecutive days, only the first location was included in the analysis. Daily locations have been used previously for similar analyses in large felids with meaningful results (Mizutani & Jewell, 1998).

All location points were plotted and analysed using ArcView Geographical Information System (GIS) software (version 3.0). I used a recently developed extension package for ArcView which analyses animal movements and ranges (Hooge & Eichenlaub, 1998) in conjunction with the Spatial Analyst facility of ArcView. I adopted the kernel utilisation distribution as the method of home range analysis for my data. The kernel method is a probability density estimation which calculates the home range of an animal in terms of the relative amount of time that an animal spends in different areas of the range (Worton, 1987, 1989, 1995; Seaman & Powell, 1996). In other words, the density of points at any location is an estimate of the amount of time spent there. This is potentially very revealing about patterns of location use and preference (Worton, 1995; Seaman & Powell, 1996), and has been demonstrated to be an accurate method to meaningfully calculate range size (Worton, 1995; Seaman & Powell, 1996). It was suited for data from Phinda in which animal ranging patterns were constrained by boundary fences which less sophisticated estimators of home ranges such as the widely used minimum convex polygon

(Kenward, 1987) and Jennrich-Turner (Jennrich & Turner, 1969) methods do not easily accommodate. Kernel methods are increasingly being adopted due to their advantages over more traditional methods (Worton, 1995) and have been used formerly for analysis of home range patterns in large carnivores (Seaman & Powell, 1996; Bothma *et al.*, 1997; Powell *et al.*, 1998.)

For all monitored animals, I have presented the 50% and 95% utilisation distributions for the entire time for which they were monitored following release. I have termed this the total home range. The 50% and 95% probabilities are generally considered the most robust estimators of an animal's centre of activity (or 'core area') and total range size excluding excursions or 'outliers' (Mizutani & Jewell, 1998) respectively. For interest's sake, I have also included the 75% probability distribution in the total home range estimations.

I also examined factors which may reasonably be expected to influence range size. In the case of females which may reduce range size when lactating (Sandell, 1989; Laurenson, 1995b), I analysed home range sizes for the periods in which they had young cubs. For the sake of this analysis, I took young cubs as being four months old. Although both lion and cheetah cubs often emerge from den-sites younger than this, they are frequently left hidden while the mother hunts. After the age of four months or thereabouts, cubs of both species are capable of accompanying the mother(s) all the time (Caro, 1994; Laurenson, 1995b; *pers. obs.*, this study).

I also examined seasonal differences in range sizes, comparing the dry winter (April to September) to the wet summer (October to March: see Chapter 2). Van Ordsol *et al.* (1985) demonstrated expansion in lion range size during summer when herbivore distribution was far more widespread than in winter. At Phinda, its small size, total enclosure by fences and presence of artificially maintained sources of water may moderate this effect. Finally, I analysed some data to look at the effect of certain stochastic events on ranging patterns, in particular, the death of companions or of neighbours, and movements following territory take-overs or expulsions. I provide specific details of these factors in the relevant sections.

Finally, I also made some estimation of reintroduced lion and cheetah habitat use. I calculated the density of locations for each animal in different habitat types and compared this to random distribution by a chi-squared analysis. I calculated the 'expected' habitat use (i.e. the distribution of 'available' habitats) separately for each animal, rather than simply adopt the distribution of habitat types for the entire reserve (see Fig. 5, Chapter 2). Although cats could easily traverse the entire reserve (and in some cases, did so), some individuals never visited certain areas. Accordingly, they may never have used certain

habitat types or areas simply by virtue of not knowing they existed. Therefore, I derived a minimum convex polygon which encompassed *every* location point (including all excursions) for each individual, and within that area, I calculated the area of each habitat type. In other words, available habitat figures were derived only for areas that each individual had visited and therefore, of which it might reasonably be expected to have some knowledge.

RESULTS

LIONS

Total home range

Total home range estimations for all monitored lions are presented in Figures 9 - 14. Lion home ranges (95% Kernel) ranged from 27.56km² for the lone lioness LF2 to 130.20 km² for a 3-male coalition (LMs11-13). Mean home-range size of lionesses (one, two or three individuals) was 52.83 km² ± 35.68 km² (range: 27.56km² - 105.60km², n = 3). Prior to associating permanently till their deaths with LFs1-2 (see Table 6), the brothers LMs 3-4 had a home range of 35.27 km². Core areas (50% Kernel) averaged 6.78 km² ± 5.21 km² for females (n = 4) and 15.18 km² ± 14.03 km² for male coalitions (n = 2).

Seasonal home ranges

Kernel estimations for seasonal home ranges of lions are presented in Table 7. For all lionesses combined, mean winter home range (95%) was 27.58km² ± 18.31 km² compared to mean summer range of 47.25 km² ± 19.97 km² which was significantly different (t = -1.83, p = 0.048, df = 11). Mean core areas (50%) for lionesses shrank from 7.48 km² ± 4.98 km² in the summer to 3.12 km² ± 2.68 km² in the winter (t = -1.91, p = 0.04, df = 11). For males, mean 95% range size in the summer was 126.85 km² ± 9.29 km² compared to 84.10 km² ± 50.51 km² in the winter which was not significantly different (t = -1.64, p = 0.09, df = 3). Mean core area (50%) for males was 37.73 km² ± 0.93 km² in the summer and 17.73 km² ± 16.08 km² in the winter which was significantly different (t = -2.49, p = 0.04, df = 3).

Animal	Total number of fixes used.	Monitoring period		Notes
		start	finish	
LIONS				
LF1* & LF 2	543	23/06/92	28/03/94	LF1 radio-collared. LF2 accompanied her until LF1's death 28/03/94.
LF2* alone	278	13/05/94	19/08/95	LF2 radio-collared 13/05/94. Unaccompanied by other females from this date.
LF5*, LF6, LF7	762	30/05/92	21/08/95	LF5 radio-collared & accompanied by LF6 entire time. LF7 joined them 08/11/92.
LM3*, LM4*, LF7	131	15/05/92	09/11/92	Accompanied by LF7 until 08/11/92. LM3 & LM4 joined LF1 & LF2 09/11/92.
LF8*, LF9, LF10	55	27/02/93	22/04/93	All destroyed 23/04/93: see Chapter 5.
LM11, LM12*, LM13	612	27/02/93	20/08/95	LM12 joined LFs5-7 following deaths of coalition mates: see Chapter 5.
CHEETAHS				
CF3*	649	01/04/93	22/08/95	
CF4*	132	27/12/92	08/11/93	Fixes based on opportunistic sightings.
CF5*	145	12/05/94	20/08/95	Fixes based on opportunistic sightings.
CF25*	137	29/01/95	22/08/95	Accompanied male siblings CM23-24 from 20/08/94 - 18/05/95.
CM1 & CM2*	746	19/10/92	27/04/95	
CM7*, CM8, CM9	98	27/11/92	27/05/93	CM7 killed 28/08/93: CMs8-9 unmonitored following his death.
CM13*, CM14*	17	15/06/94	30/06/94	
CM23*, CM24	165	20/08/94	30/08/95	Accompanied by their female sibling CF25 from 20/08/94-18/01/95.

Table 6. Details of monitoring periods for home-range estimations for reintroduced lions and cheetahs at Phinda. Monitoring period represents entire study duration from which I calculated total home range size. I sampled further from these data for specific analyses, details in text. * Radio-collared individual.

Individual	Win '92	Sum '92-3	Win '93	Sum '93-4	Win '94	Sum '94-5	Win '95
FEMALES							
LF1 50%	1.06km ² (72)	6.68km ² (158)	2.08km ² (159)	11.39km ² (168)			
95%	19.19km ² (72)	41.62km ² (158)	18.16km ² (159)	56.18km ² (168)			
LF2 50%					1.02km ² (60)	1.63km ² (118)	8.25km ² (73)
95%					8.77km ² (60)	18.78km ² (118)	34.58km ² (73)
LF5 50%		7.25km ² (151)	4.19km ² (101)	3.06km ² (172)	4.33km ² (126)	14.88km ² (136)	0.96km ² (59)
95%		32.07km ² (151)	34.51km ² (101)	71.30km ² (172)	62.86km ² (126)	63.57km ² (136)	15.03km ² (59)
MALES							
LM3 50%	5.12km ² (92)						
95%	37.21km ² (92)						
LM12 50%			4.00km ² (163)	37.17km ² (137)	24.52km ² (109)	38.50km ² (124)	37.30km ² (45)
95%			43.95km ² (163)	133.43km ² (137)	122.40km ² (109)	120.28km ² (124)	132.85km ² (45)

Table 7. Seasonal home-range estimations for lions. Animal code in 'Individual' column is the radio-collared animal of each group: refer to Table 6 for entire group composition. Figure in parenthesis is the number of locations used to derive each estimate.

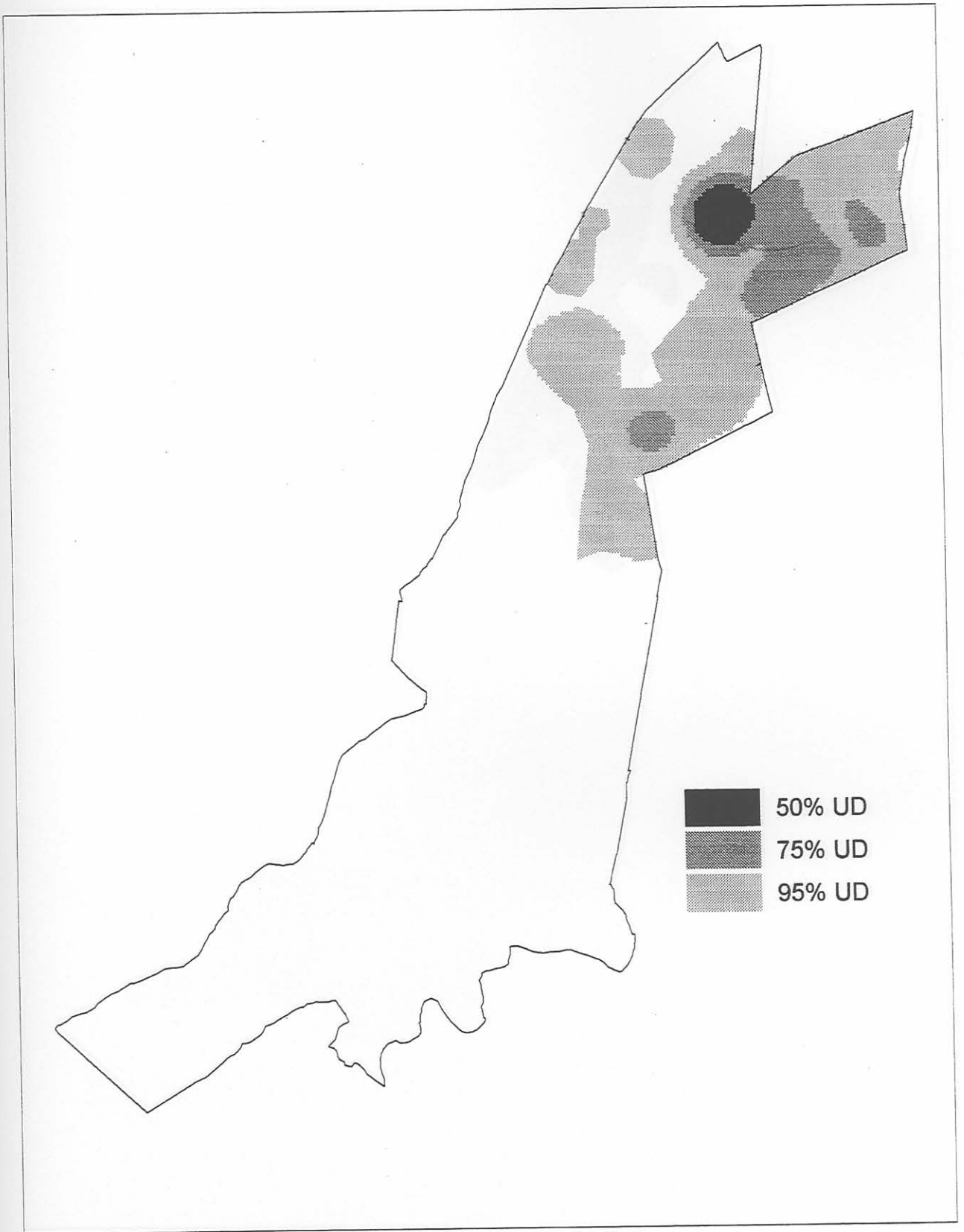


Figure 9. Kernel estimation (50%, 75% and 95% probability) of the home range of the lionesses LF1 and LF2 .

Areas: 50%: 1.79 sq.km, 75%: 10.10 sq.km, 95%: 42.23 sq.km.



Figure 10. Kernel estimation (50%, 75% and 95% probability) of the home range of the lioness LF2.

Figure 10. Kernel estimation (50%, 75% and 95% probability) of the home range of the lioness LF2.

Areas: 50%: 2.78 sq.km, 75%: 8.70 sq.km, 95%: 27.56 sq.km.



Figure 11. Kernel estimation (50%, 75% and 95% probability) of the home range of the lionesses LF5, LF6 and LF7.

Areas: 50%: 11.76 sq.km, 75%: 51.06 sq.km, 95%: 105.60 sq.km.



Figure 12. Kernel estimation (50%, 75% and 95% probability) of the home range of the lionesses LF8, LF9, and LF10.

Areas: 50%: 10.36 sq.km, 75%: 19.99 sq.km, 95%: 35.93 sq.km.



Figure 13. Kernel estimation (50%, 75% and 95% probability) of the home range of the lions LM3, LM4.

Areas: 50%: 5.23 sq.km, 75%: 15.09 sq.km, 95%: 35.27 sq.km.

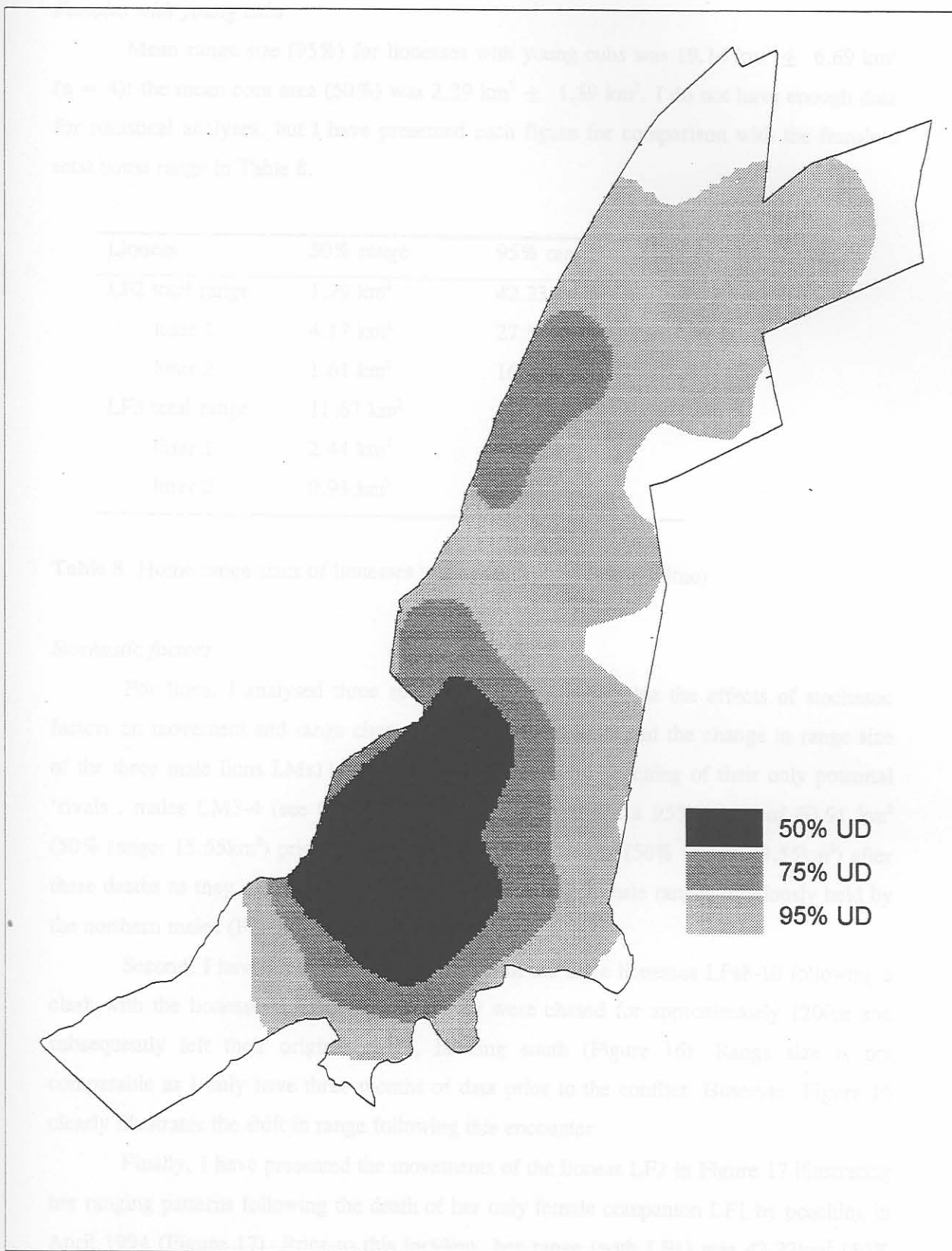


Figure 14. Kernel estimation (50%, 75% and 95% probability) of the home range of the male lions LM11, LM12 and LM13.

Areas: 50%: 25.10 sq.km, 75%: 53.13 sq.km, 95%: 130.20 sq.km.

Females with young cubs

Mean range size (95%) for lionesses with young cubs was $19.14 \text{ km}^2 \pm 6.69 \text{ km}^2$ ($n = 4$): the mean core area (50%) was $2.29 \text{ km}^2 \pm 1.39 \text{ km}^2$. I do not have enough data for statistical analyses, but I have presented each figure for comparison with the female's total home range in Table 8.

Lioness	50% range	95% range
LF2 total range	1.79 km ²	42.23 km ²
litter 1	4.17 km ²	27.87 km ²
litter 2	1.61 km ²	16.05 km ²
LF5 total range	11.67 km ²	105.60 km ²
litter 1	2.44 km ²	20.37 km ²
litter 2	0.93 km ²	12.26 km ²

Table 8. Home range sizes of lionesses when with young cubs (<4mo).

Stochastic factors

For lions, I analysed three specific incidents to examine the effects of stochastic factors on movement and range characteristics. First, I examined the change in range size of the three male lions LMs11-13 following the deaths by poaching of their only potential 'rivals', males LM3-4 (see Chapter 5). LMs11-13 occupied a 95% range of 60.91 km² (50% range: 15.55km²) prior to these deaths and 142.84 km² (50% range: 39.55km²) after these deaths as they moved northwards to encompass the female ranges previously held by the northern males (Figure 15).

Second, I have presented the movements of the three lionesses LFs8-10 following a clash with the lionesses LFs1-2 in which they were chased for approximately 1200m and subsequently left their original range, heading south (Figure 16). Range size is not comparable as I only have three months of data prior to the conflict. However, Figure 16 clearly illustrates the shift in range following this encounter

Finally, I have presented the movements of the lioness LF2 in Figure 17 illustrating her ranging patterns following the death of her only female companion LF1 by poaching in April 1994 (Figure 17). Prior to this incident, her range (with LF1) was 42.23km² (50% range: 1.79 km²: see Figure 9): following the death of LF1, her range was 27.56 km² (50% range: 2.78 km²: see Figure 10).

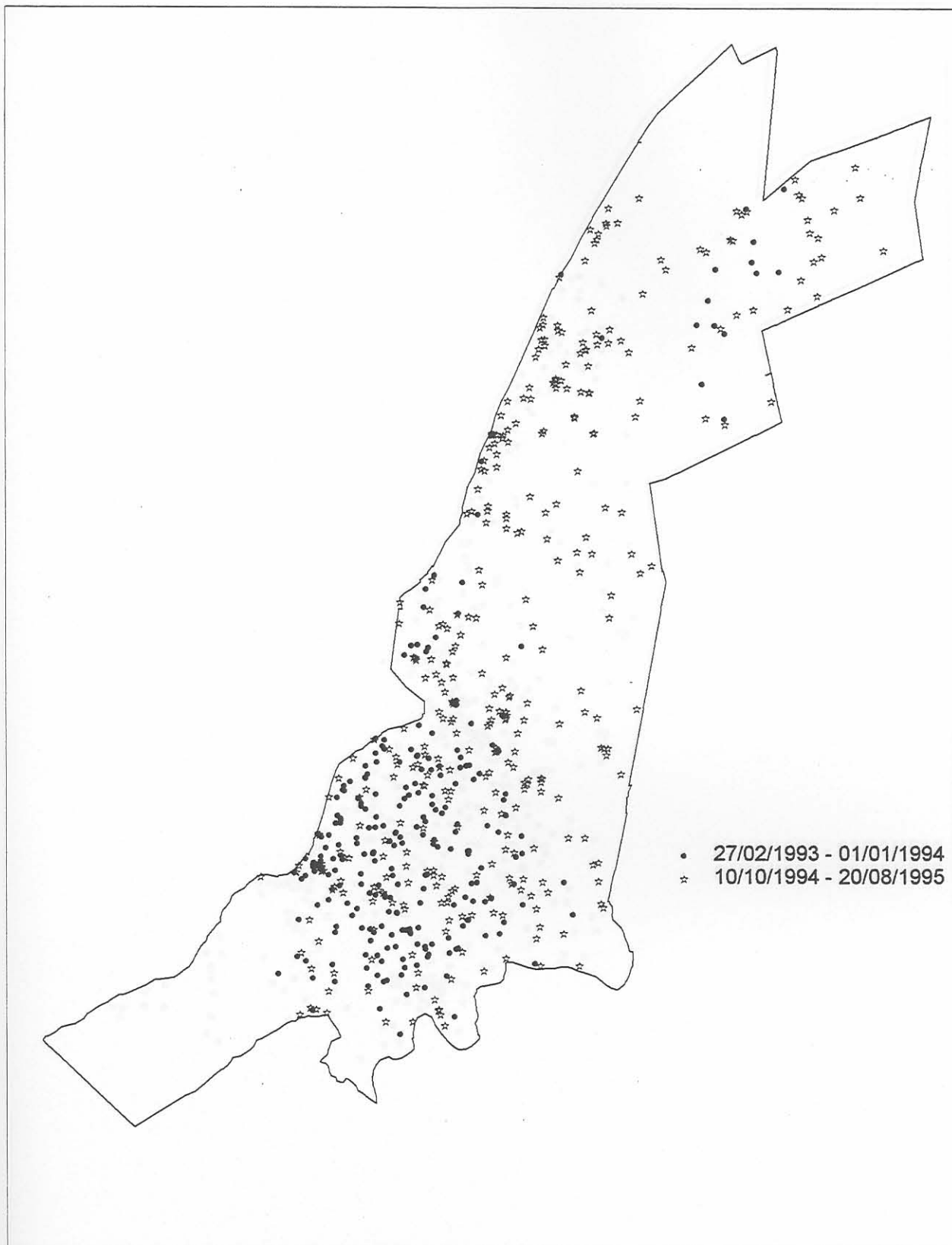


Figure 15. Distribution of location points for the lion males LM11, LM12 and LM13

following the deaths of the males LM3 and LM4 . See text for details

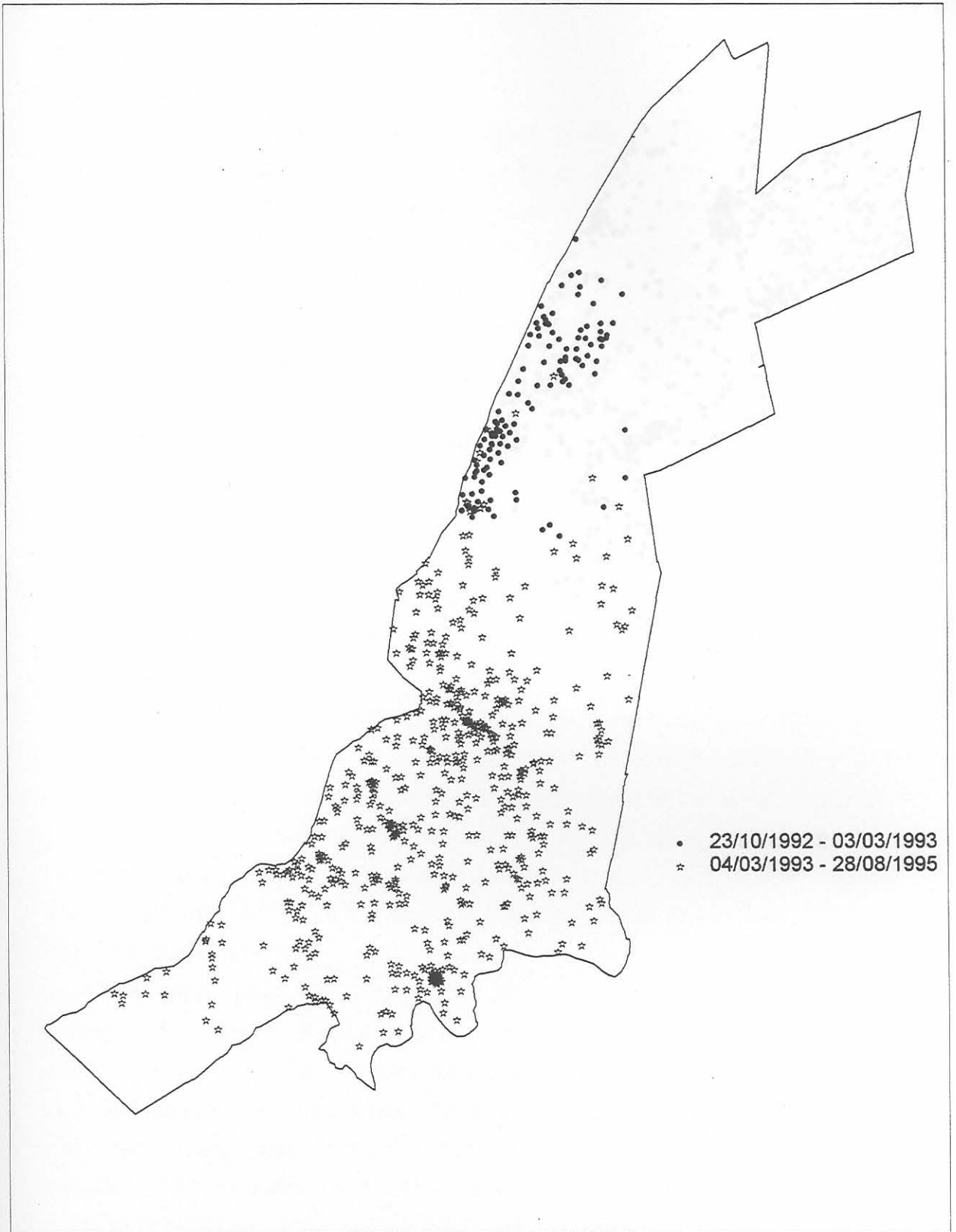


Figure 16. Distribution of location points for the lionesses LF5, LF6 and LF7 following expulsion from their original home range on 03/03/1993. See text for details

CHEETAHS

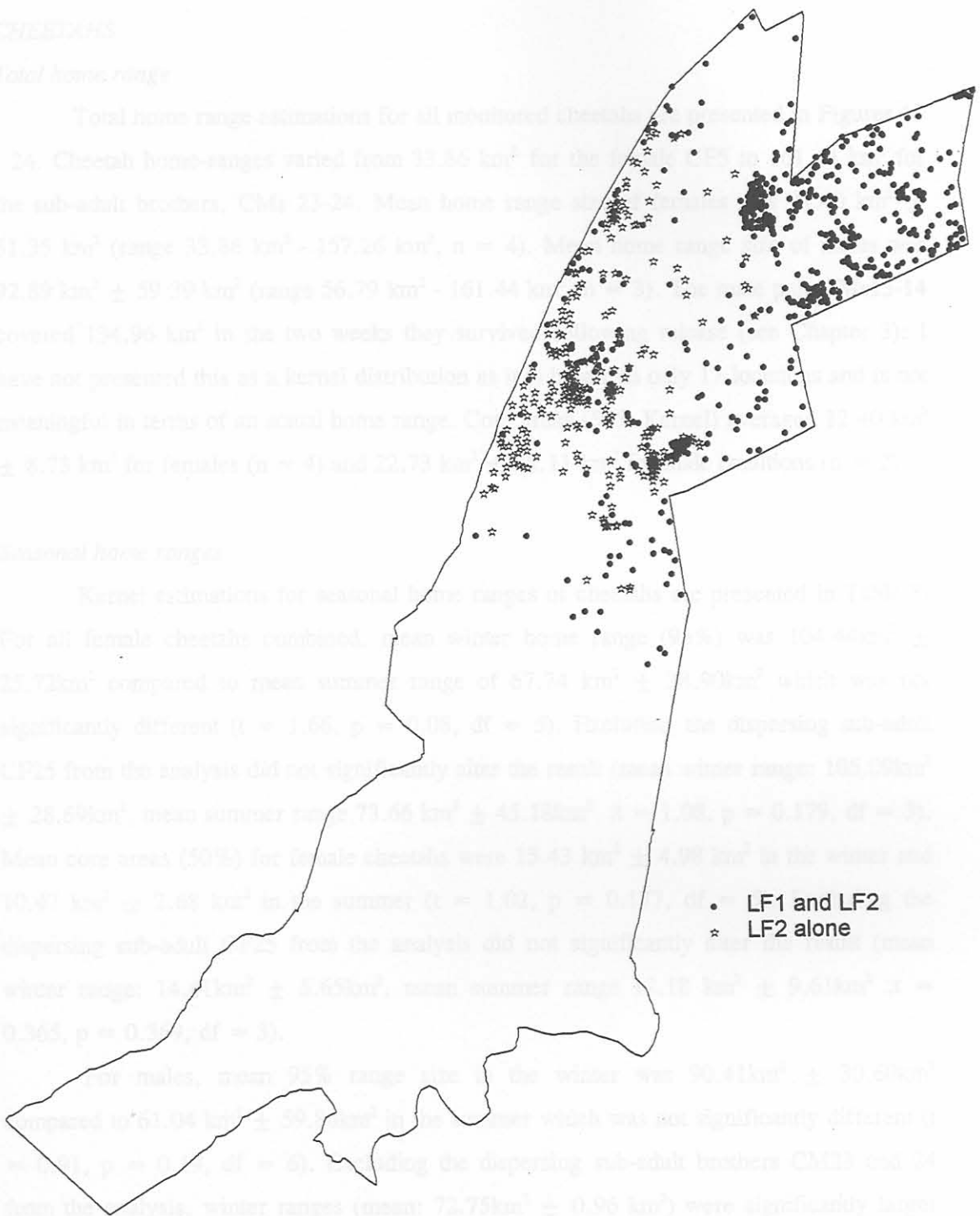
Total home range

Total home range estimations for all monitored cheetahs are presented in Figure 17. Cheetah home-ranges varied from 33.86 km² for the dispersing sub-adult brothers, CMs 23-24. Mean home range was 92.85 km² ± 39.39 km² (range 36.79 km² - 161.44 km², n = 24) compared 134.96 km² in the two weeks they survived. We have not presented this as a kernel distribution as it was not meaningful in terms of an actual home range. Core area was 22.79 km² ± 8.73 km² for females (n = 4) and 22.79 km² for males (n = 4).

Seasonal home ranges

Kernel estimations for seasonal home ranges of the dispersing sub-adults are presented in Figure 18. For all female cheetahs combined, mean winter home range was 104.96 km² ± 25.72 km² compared to mean summer range of 67.74 km² ± 28.59 km² which was significantly different (t = 1.66, p = 0.18, df = 3). However, the dispersing sub-adult CM25 from the analysis did not significantly alter the result (winter range: 165.05 km² ± 28.64 km², mean summer range: 71.66 km² ± 45.10 km², t = 1.06, p = 0.175, df = 3). Mean core area (50%) for female cheetahs were 13.43 km² ± 4.96 km² in the winter and 10.47 km² ± 2.65 km² in the summer (t = 1.61, p = 0.17, df = 3). For the dispersing sub-adults from the analysis, winter ranges (mean: 14.07 km² ± 8.65 km², mean summer range: 11.18 km² ± 9.61 km², t = 0.365, p = 0.72, df = 3).

For males, mean 95% range size in the winter was 96.41 km² ± 30.07 km² compared to 61.04 km² ± 50.08 km² in the summer which was not significantly different (t = 0.91, p = 0.47, df = 3). Including the dispersing sub-adult brothers CM23 and 24 from the analysis, winter ranges (mean: 72.75 km² ± 0.96 km²) were significantly larger than summer ranges, (mean: 35.48 km² ± 26.56 km², t = 3.61, p = 0.02, df = 3). Mean core area (50%) for males was 17.58 km² ± 8.30 km² in the winter and 21.6 km² ± 22.68 km² in the summer which was not significantly different (t = 0.17, p = 0.87, df = 3).



- LF1 and LF2
- * LF2 alone

Figure 17. Distribution of location points for the lioness LF2, following the death of her companion LF1. See text for details

CHEETAHS

Total home range

Total home range estimations for all monitored cheetahs are presented in Figures 18 - 24. Cheetah home-ranges varied from 33.86 km² for the female CF5 to 161.44 km² for the sub-adult brothers, CMs 23-24. Mean home range size of females was 94.40 km² ± 51.35 km² (range 33.86 km² - 157.26 km², n = 4). Mean home range size of males was 92.89 km² ± 59.39 km² (range 56.79 km² - 161.44 km², n = 3). The male pair CMs13-14 covered 134.96 km² in the two weeks they survived following release (see Chapter 3): I have not presented this as a kernel distribution as it is based on only 17 locations and is not meaningful in terms of an actual home range. Core areas (50% Kernel) averaged 12.40 km² ± 8.73 km² for females (n = 4) and 22.73 km² ± 28.11 km² for male coalitions (n = 2).

Seasonal home ranges

Kernel estimations for seasonal home ranges of cheetahs are presented in Table 8. For all female cheetahs combined, mean winter home range (95%) was 104.44km² ± 25.72km² compared to mean summer range of 67.74 km² ± 38.90km² which was not significantly different (t = 1.66, p = 0.08, df = 5). Excluding the dispersing sub-adult CF25 from the analysis did not significantly alter the result (mean winter range: 105.09km² ± 28.69km², mean summer range 73.66 km² ± 45.18km² :t = 1.08, p = 0.179, df = 3). Mean core areas (50%) for female cheetahs were 15.43 km² ± 4.98 km² in the winter and 10.47 km² ± 2.68 km² in the summer (t = 1.02, p = 0.177, df = 5). Excluding the dispersing sub-adult CF25 from the analysis did not significantly alter the result (mean winter range: 14.41km² ± 5.65km², mean summer range 12.18 km² ± 9.61km² :t = 0.365, p = 0.369, df = 3).

For males, mean 95% range size in the winter was 90.41km² ± 30.60km² compared to 61.04 km² ± 59.86km² in the summer which was not significantly different (t = 0.91, p = 0.19, df = 6). Excluding the dispersing sub-adult brothers CM23 and 24 from the analysis, winter ranges (mean: 72.75km² ± 0.96 km²) were significantly larger than summer ranges, (mean: 35.48km² ± 26.56km² :t = 3.61, p = 0.02, df = 3). Mean core area (50%) for males was 17.58km² ± 8.30km² in the winter and 20.64km² ± 37.89km² in the summer which was not significantly different (t = -0.17, p = 0.43, df = 1). Excluding the dispersing sub-adult brothers CM23 and 24 from the analysis did not alter this result (winter ranges mean: 13.44 km² ± 5.89 km², summer ranges, mean: 3.72km² ± 1.98 km² :t = 2.26, p = 0.13, df = 1).

Individual	Sum '92-3	Win '93	Sum '93-4	Win '94	Sum '94-5	Win '95
FEMALES						
CF3 50%		6.81km ² (156)	18.68km ² (137)	22.35km ² (126)	16.72km ² (127)	15.54km ² (100)
95%		103.48km ² (156)	97.33km ² (137)	149.67km ² (126)	102.10km ² (127)	92.33km ² (100)
CF4 50%		12.10km ² (95)				
95%		108.50km ² (95)				
CF5 50%					1.14km ² (97)	15.26km ² (50)
95%					21.56km ² (97)	71.47km ² (50)
CF25 50%					5.36km ² (38)	20.54km ² (99)
95%					49.97km ² (38)	101.21km ² (99)
MALES						
CM1 & CM2 50%	1.26km ² (156)	17.63km ² (147)	3.03km ² (130)	9.27km ² (138)	5.66km ² (130)	
95%	17.31km ² (156)	73.43km ² (147)	20.00km ² (130)	72.07km ² (138)	44.17km ² (130)	
CMs7-9 50%	4.91km ² (98)					
95%	60.45km ² (98)					
CM23 & 24 50%					88.36km ² (88)	25.88km ² (75)
95%					163.29km ² (88)	125.74km ² (75)

Table 9. Seasonal home-range estimations for cheetahs. Figure in parenthesis is the number of locations used to derive each estimate.



Figure 18. Kernel estimation (50%, 75% and 95% probability) of the home range of the cheetah CF3.
Areas: 50%: 24.16 sq.km, 75%: 76.16 sq.km, 95%: 157.26 sq.km.



Figure 19. Kernel estimation (50%, 75% and 95% probability) of the home range of the cheetah CF5.

Areas: 50%: 4.49 sq.km, 75%: 12.04 sq.km, 95%: 33.86 sq.km.

Areas: 50%: 13.77sq.km, 75%: 35.31 sq.km, 95%: 105.33 sq.km.

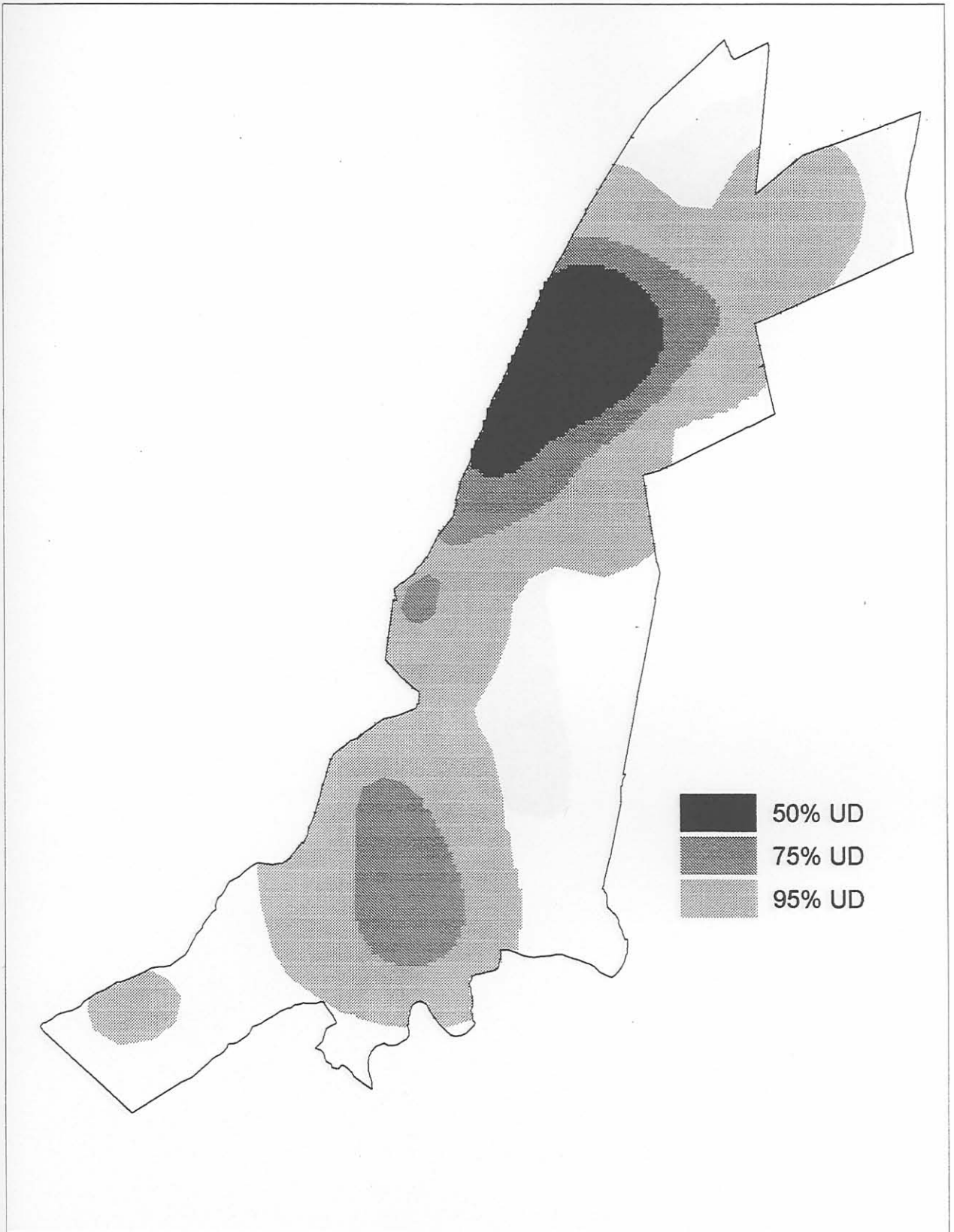


Figure 21. Kernel estimation (50%, 75% and 95% probability) of the home range of the cheetah

Figure 20. Kernel estimation (50%, 75% and 95% probability) of the home range of the cheetah CF4.

Areas: 50%: 13.71sq.km, 75%: 35.31 sq.km, 95%: 105.33 sqkm.

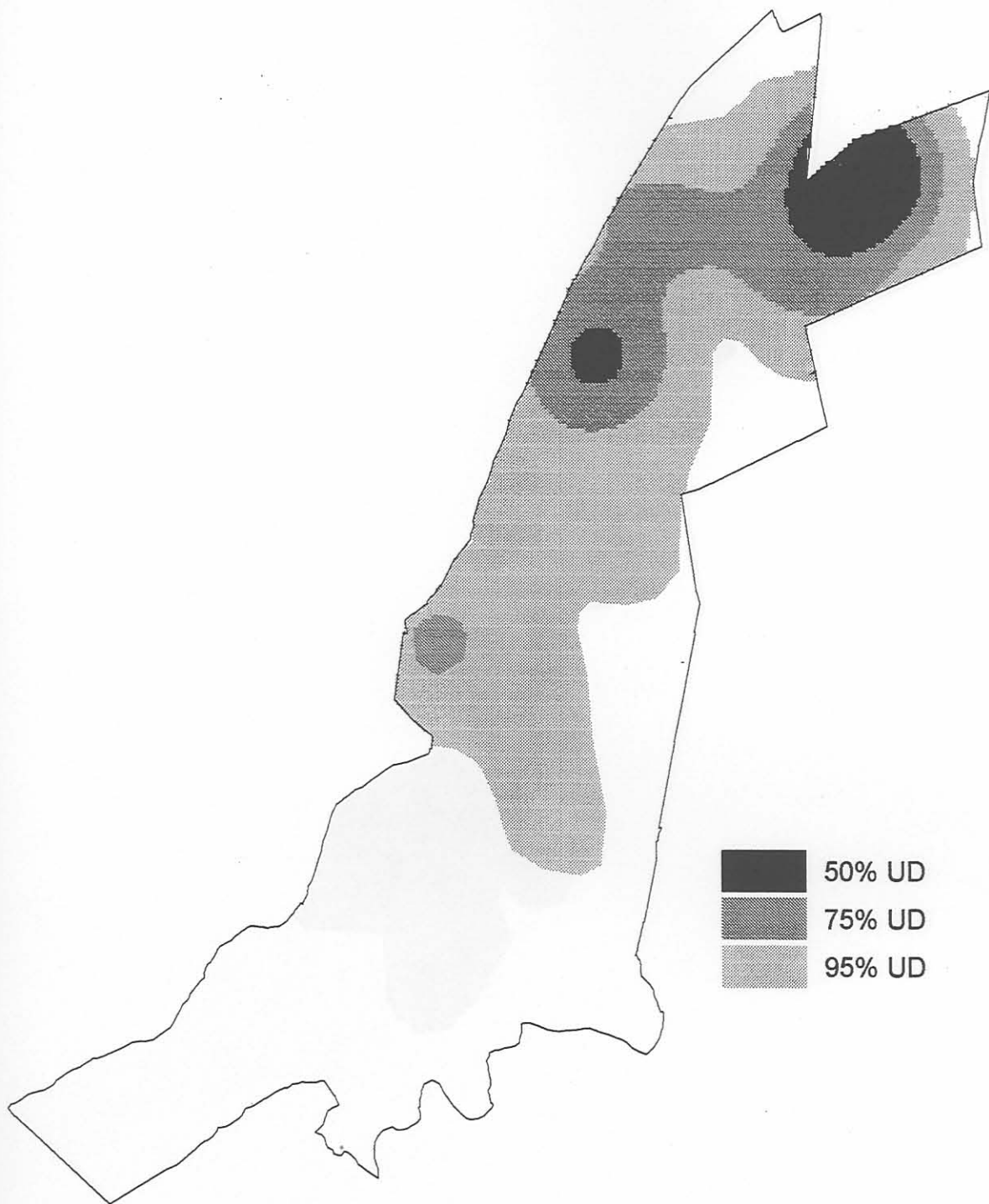


Figure 21. Kernel estimation (50%, 75% and 95% probability) of the home range of the female cheetah, CF25.

Areas: 50%: 7.27 sq.km, 75%: 29.27 sq.km, 95%: 81.18 sq.km.

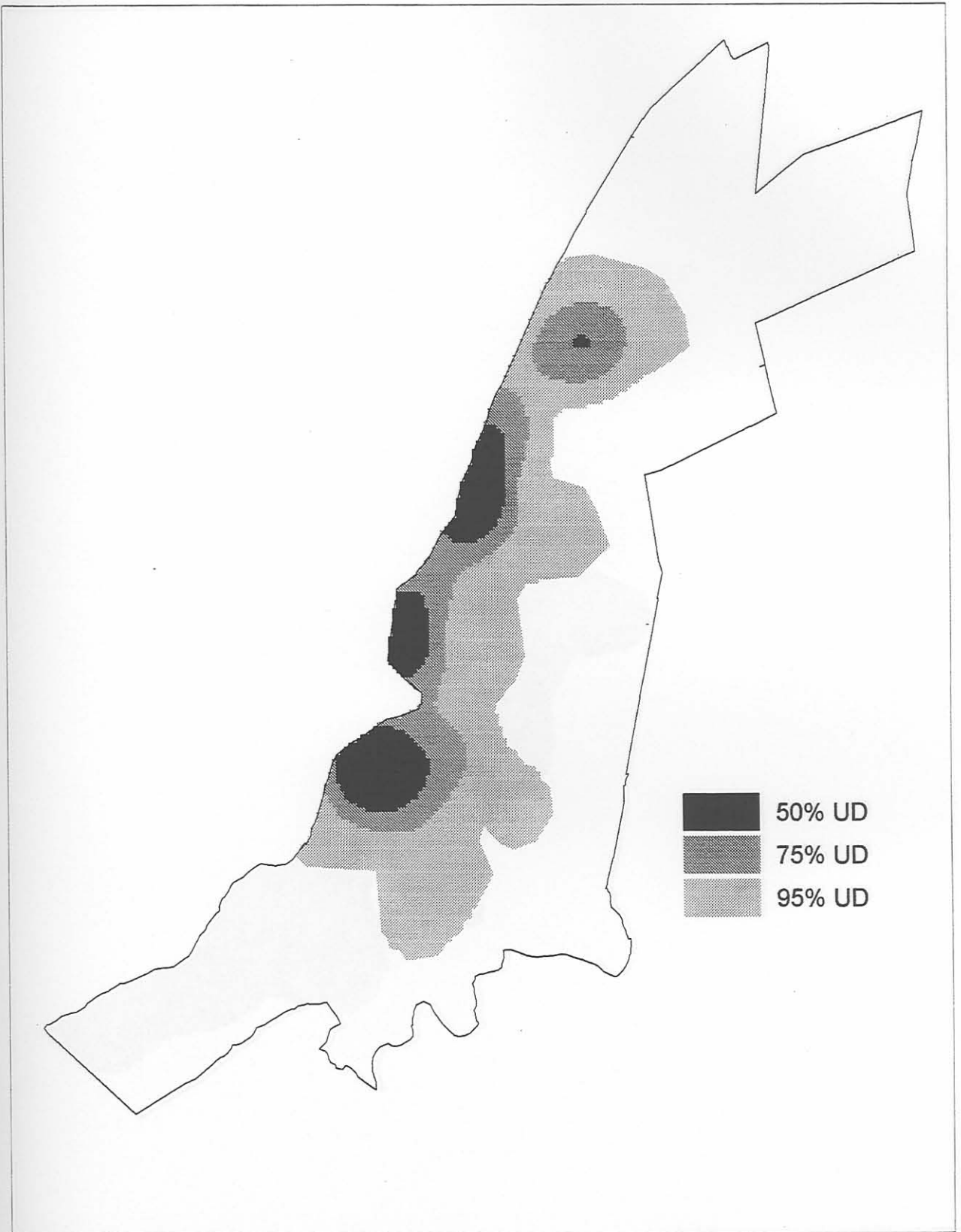


Figure 22. Kernel estimation (50%, 75% and 95% probability) of the home range of the male cheetahs, CM1 and CM2 .

Areas: 50%: 8.15 sq.km, 75%: 20.71sq.km, 95%: 56.79 sq.km.

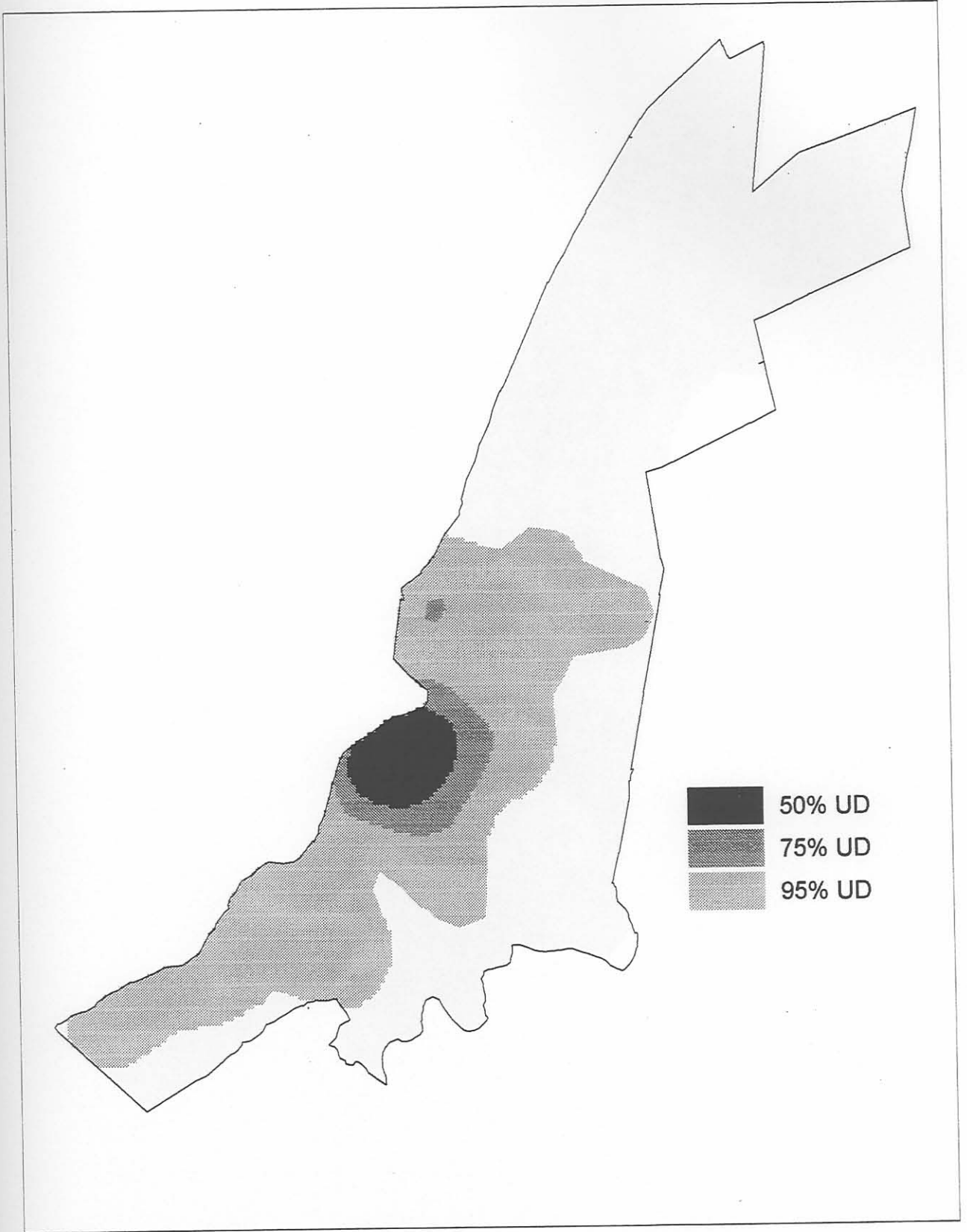


Figure 23. Kernel estimation (50%, 75% and 95% probability) of the home range of the male cheetahs CM7, CM8 and CM9.

Areas: 50%: 4.91 sq.km, 75%: 9.95 sq.km, 95%: 60.45 sq.km.

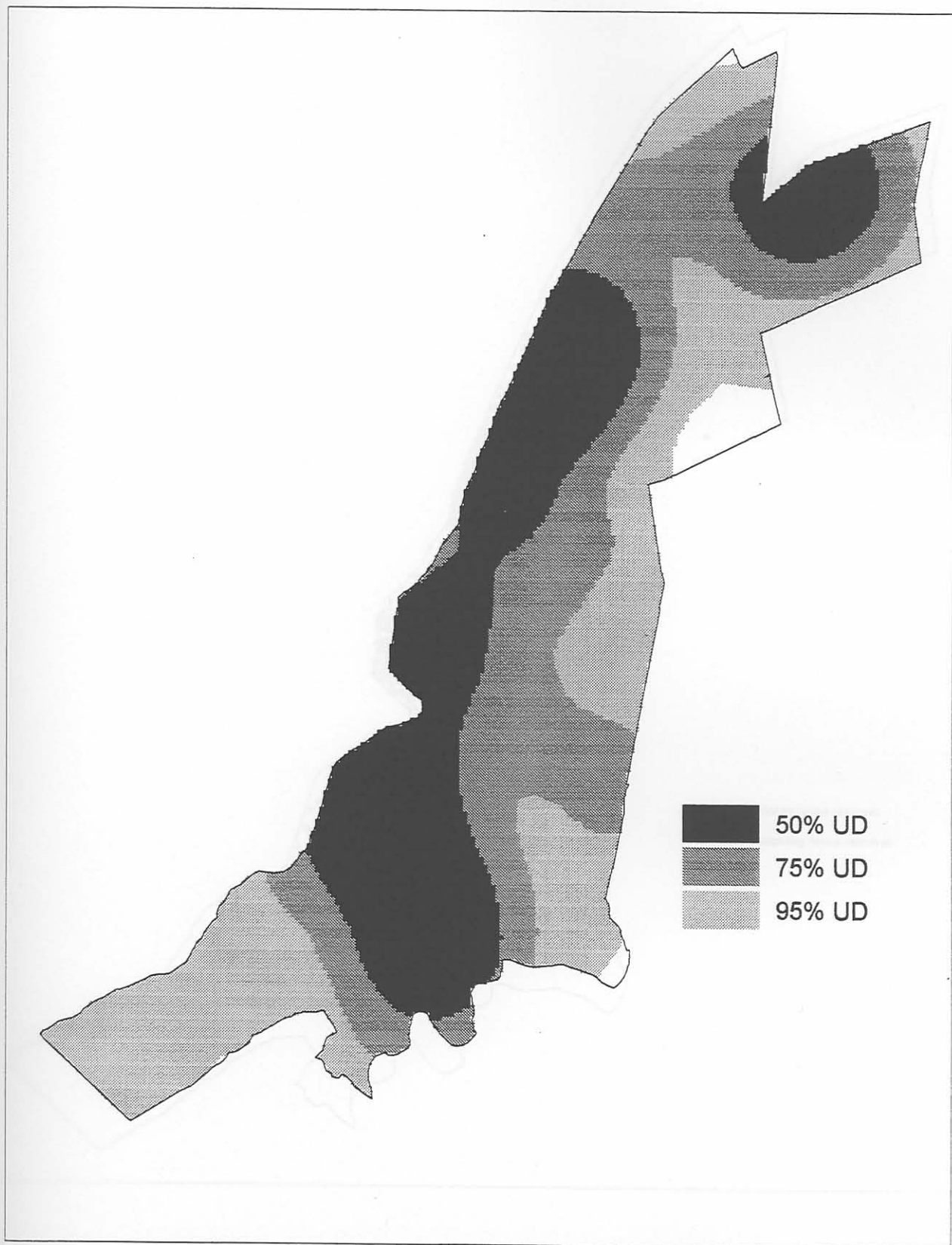


Figure 24. Kernel estimation (50%, 75% and 95% probability) of the home range of the male cheetahs CM23 and CM24. on 01/03/93. See text for details.

Areas: 50%: 55.15 sq.km, 75%: 109.20 sq.km, 95%: 161.44 sq.km.

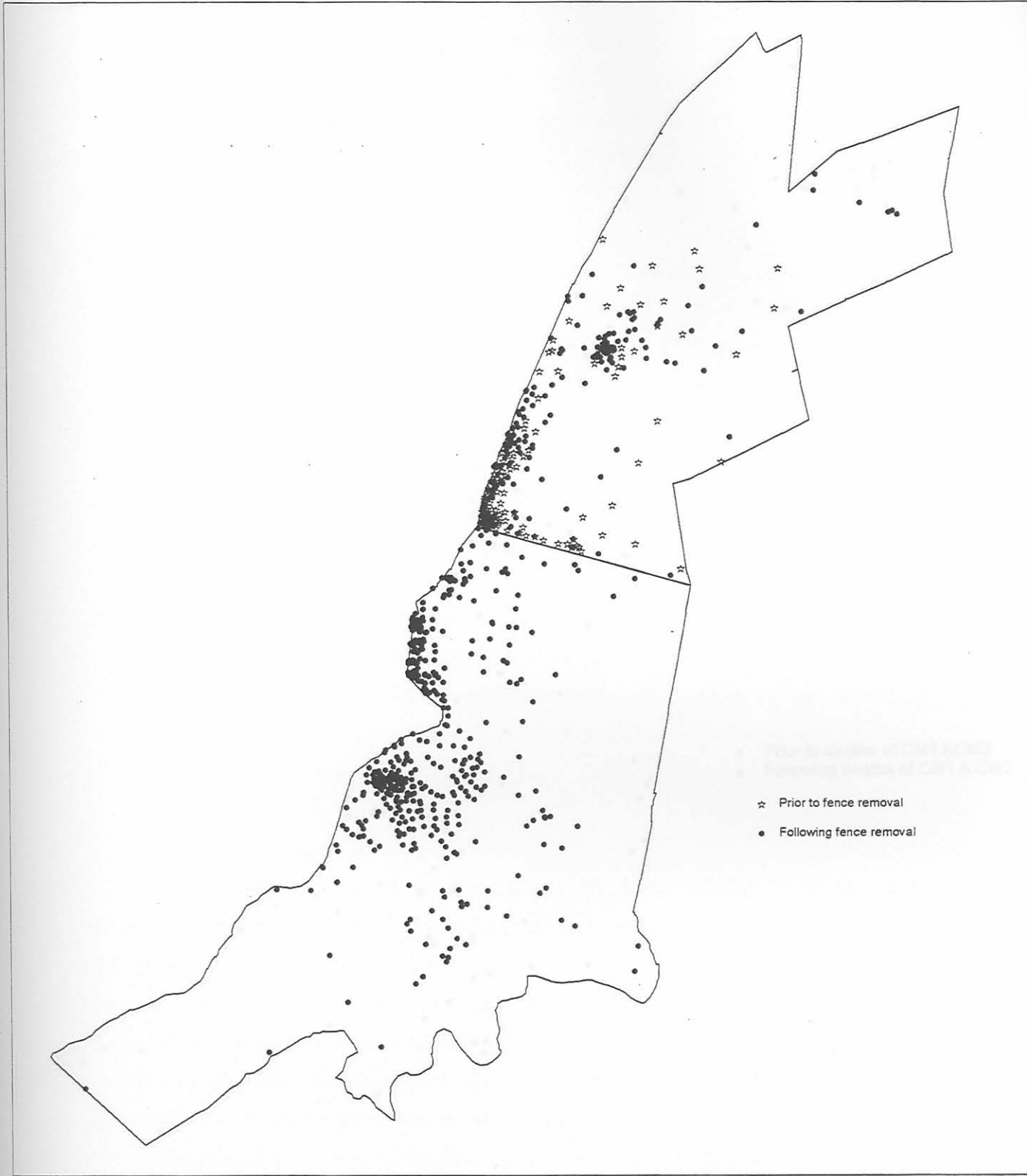


Figure 25. Distribution of location points for the male cheetahs CM1 and CM2, following the removal of an internal fence (line) on 01/03/93. See text for details.

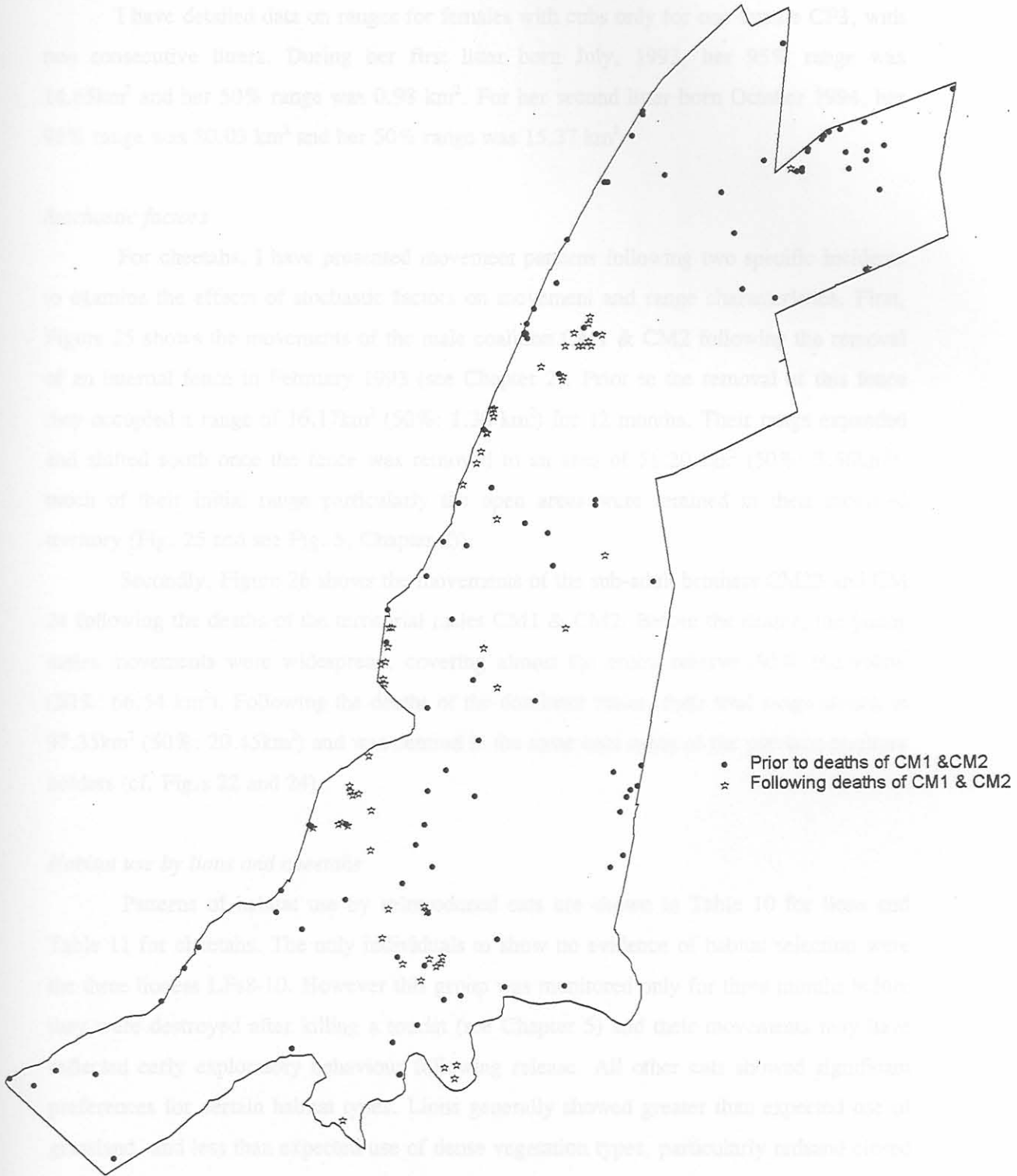


Figure 26. Distribution of location points for the male cheetahs CM23 and CM24 following the deaths of the territorial males CM1 and CM2. See text for details.

Females with young cubs

I have detailed data on ranges for females with cubs only for one female CF3, with two consecutive litters. During her first litter born July, 1993, her 95% range was 14.65km² and her 50% range was 0.98 km². For her second litter born October 1994, her 95% range was 80.03 km² and her 50% range was 15.37 km².

Stochastic factors

For cheetahs, I have presented movement patterns following two specific incidents to examine the effects of stochastic factors on movement and range characteristics. First, Figure 25 shows the movements of the male coalition CM1 & CM2 following the removal of an internal fence in February 1993 (see Chapter 2). Prior to the removal of this fence they occupied a range of 16.17km² (50%: 1.30 km²) for 12 months. Their range expanded and shifted south once the fence was removed to an area of 51.20 km² (50%: 5.56km²): much of their initial range particularly the open areas were retained in their modified territory (Fig. 25 and see Fig. 5, Chapter 2)).

Secondly, Figure 26 shows the movements of the sub-adult brothers CM23 and CM 24 following the deaths of the territorial males CM1 & CM2. Before the deaths, the young males movements were widespread, covering almost the entire reserve (95%:162.96km² (50%: 66.54 km²). Following the deaths of the dominant males, their total range shrank to 97.35km² (50%: 20.45km²) and was centred in the same core areas of the previous territory holders (cf. Fig.s 22 and 24).

Habitat use by lions and cheetahs

Patterns of habitat use by reintroduced cats are shown in Table 10 for lions and Table 11 for cheetahs. The only individuals to show no evidence of habitat selection were the three lioness LFs8-10. However this group was monitored only for three months before they were destroyed after killing a tourist (see Chapter 5) and their movements may have reflected early exploratory behaviour following release. All other cats showed significant preferences for certain habitat types. Lions generally showed greater than expected use of grassland, and less than expected use of dense vegetation types, particularly redsand closed bushveld and sandforest. Prides which had riparian forest in their ranges generally showed greater than expected use of this habitat type. Lions appeared to generally avoid dry mountain bushveld when it occurred in their range.

All cheetahs except for one male coalition showed a highly significant preference for grassland and a tendency to occupy open mixed bushveld and palmveld in most cases. All cheetahs avoided sandforest and redsand closed bushveld.

Individual/group	DMB	Grass	MBC	MBO	Palm	RSC	RSO	RF	SF	χ^2 Result
LF2										
available		10.41			4.38	175.55	41.89		41.56	$\chi^2 = 65.44,$ p < 0.000, df = 8
observed		25			3.0	133	79		34	
LF1(LF2)										
available		51.37	15.48	3.74	52.23	284.41	67.6		58.69	$\chi^2 = 110.86,$ p < 0.000, df = 8
observed		87	21	8	93	232	80		13	
LF5 (LF6,LF7)										
available	71.45	57.97	176.09	106.13	41.72	124.03	62.61	33.48	75.72	$\chi^2 = 164.22$ p < 0.000, df = 8
observed	44	102	207	166	36	64	63	49	18	
LF8 (LF9,LF10)										
available	9.13	3.66	27.78	9.83				3.59		$\chi^2 = 7.66,$ p < 0.467, df = 8
observed	2	5	33	9				5		
LM3, LM4										
available		6.44		0.009	5.52	87.43	21.76		7.8	$\chi^2 = 80.84$ p < 0.000, df = 8
observed		25		0	9	58	36		1	
LM12 (LM11,LM13)										
available	21.62	57.32	95.51	68.66	45.74	176.06	58.98	17.23	52.63	$\chi^2 = 232.52,$ p < 0.000, df = 8
observed	14	72	200	99	30	60	50	31	38	

Table 10. Habitat use by lions. The figure presented is the actual number of locations per habitat type ('observed'). The expected ('available') figure was calculated by multiplying the percentage of each habitat type occurring in the 100% minimum convex polygon of each individual (see Methods) by the total number of locations. Significant results at $p < 0.05$ are shown in boldtype.

Habitat types are described in Chapter 2: DMB = dry mountain bushveld; Grass = grasslands; MBC = closed mixed bushveld; MBO = open mixed bushveld; Palm = palmveld; RSC = closed red sand bushveld; RSO = open red sand bushveld; RF = riparian forest; SF = sandforest.

Individual/group	DMB	Grass	MBC	MBO	Palm	RSC	RSO	RF	SF	χ^2 Result
CF3										
available	41.08	55.46	124.41	65.95	48.59	174.13	56.35	22.13	47.76	$\chi^2 = 323.77$ $p < 0.000, df = 8$
observed	9	142	120	93	111	90	43	16	12	
CF4										
available	10.27	8.46	22.79	13.17	7.83	38.48	15.11	4.42	9.54	$\chi^2 = 188.6,$ $p < 0.000, df = 8$
observed	8.23	46	16	11	11	26	12	0	2	
CF5										
available	7.6	10.16	35.52	22.04	8.18	18.5	10.37	6.01	14.53	$\chi^2 = 90.41$ $p < 0.000, df = 8$
observed	4	23	56	41	2	1	0	5	1	
CF25										
available		13.04	2.85	9.19	12.42	58.25	18.42	3.68	16.09	$\chi^2 = 114.32,$ $p < 0.000, df = 8$
observed		48	0	2	14	44	19	2	5	
CM1 & CM2										
available	52.56	62.81	134.72	80.65	46.2	196.52	65.62	23.1	59.93	$\chi^2 = 1038.0$ $p < 0.000, df = 8$
observed	18	297	102	68	79	89	42	16	11	
CMs7-9										
available	14.8	5.35	27.6	15.47	5.55	8.02	6.49	4.79	2.85	$\chi^2 = 25.76,$ $p < 0.000, df = 8$
observed	12	6	22	28	11	4	0	5	3	
CMs23-24										
available	10.77	13.54	33.95	15.68	12.16	46.61	14.92	5.74	12.53	$\chi^2 = 218.26,$ $p < 0.000, df = 8$
observed	5	64	31	11	17	20	11	1	6	

Table 11. Habitat use by cheetahs. The figure presented is the actual number of locations per habitat type ('observed'). The expected ('available') figure was calculated by multiplying the percentage of each habitat type occurring in the 100% minimum convex polygon of each individual (see Methods) by the total number of locations. Significant results at $p < 0.05$ are shown in boldtype.

Habitat types are described in Chapter 2: DMB = dry mountain bushveld; Grass = grasslands; MBC = closed mixed bushveld; MBO = open mixed bushveld; Palm = palmveld; RSC = closed red sand bushveld; RSO = open red sand bushveld; RF = riparian forest; SF = sandforest.

DISCUSSION

Reintroduced lions and cheetahs at Phinda appeared to establish enduring home ranges with similar characteristics and patterns to that observed in other ecosystems. All individuals which survived the early post-release period (Chapter 3) remained at Phinda and settled in ranges within the reserve which were stable at least for the duration of monitoring. Lions (of both sexes) and male cheetahs were territorial whereas female cheetahs showed no signs of establishing territories and used (in some cases) the entire reserve as their home range. The long-term nature of some individual's ranges (i.e. those of the longest surviving animals) suggests that lions and cheetahs are amenable to establishing a home-range following translocation, and therefore, that reintroduction may be a viable method for re-establishing resident felids in areas of their former distribution.

Ranging and movement patterns in re-introduced lions followed the broad outline typical of the species from other regions. In general, small founding groups of lionesses established exclusive ranges and tolerated little overlap with other female groups. Male coalitions associated with these female groups and their ranging patterns reflected the distribution of females. For example, when the dominant male coalition in the north of the reserve (Fig. 13) was killed by poachers, a coalition of males from the south expanded their range to incorporate the female ranges in the north. As the only males in the reserve during the latter part of the study, this coalition's territory constituted 78.7% of the entire reserve, moving between non-overlapping female territories. Between February and December 1993 when there were two coalitions of males in the reserve, each remained in discrete territories of 42.23km² ('northern' males: Fig. 9) and 60.91km² ('southern' males: Fig. 14) which did not overlap.

Sizes of female territories were amongst the smallest recorded for the species. The 95% range of the lone lioness LF2 was 27.56km² which was approximately half the size of her range when she was permanently in association with the lioness LF1 until her death 23 months after they were released. During most of this period, the males LMs7 and 8 were in constant association with these females. Sample size is clearly too small to make robust conclusions but the range of these four adult lions (42.23km²) is comparable to pride range size in the 'optimal' habitat of Ngorongoro Crater which has very high, densities of prey species which vary minimally year round. Ngorongoro contains one of the highest densities of lions (and incidentally, spotted hyaenas) in studied populations anywhere and competition for space is intense (Hanby *et al*, 1995). Lions at Phinda were not under the same social pressures so it is difficult to predict the minimum size required by lions in the

reserve and therefore, the maximum lion density a small enclosed reserve such as Phinda could maintain. Prey density is approximately six times as great in Ngorongoro (11,693 - 12000kg/km²; Hanby *et al*, 1995) compared to Phinda (1996.3 kg/km²; Chapter 7) so lion densities at Phinda would never be able to reach the levels in similarly-sized Ngorongoro. It would be interesting to establish the minimum spatial requirements of lions in the long-term as they underwent population growth following re-introduction. However, the prospect for such research is slim, at least in many of the small reserves in South Africa where large felids have been reintroduced or where it is planned. Predation in enclosed reserves can have considerable impact on prey populations (Chapter 7) and as a result, the lion population at Phinda has been heavily managed with frequent removals since 1996 (Chapter 5). In Hluhluwe-Umfolozi Game Reserve, the pressure of increasing lion numbers forces many dispersing sub-adults out of the reserve and similar population control measures have been implemented there (Maddock *et al*, 1996). Most small reserves reintroducing lions will probably have to implement similar management action and ultimately, the ranging patterns of reintroduced lions in small areas will always be affected by such measures.

Despite the relatively uniform distribution of ungulates and a lack of migratory movements of prey (Chapter 7), some lionesses at Phinda reduced their home ranges in winter to almost half their summer range. Van Ordsol *et al* (1985) demonstrated an increase in lean season biomass resulted in a subsequent reduction in range size in a number of lion populations, although there was no clear evidence of seasonal fluctuation. The observed patterns at Phinda may have reflected restricted and artificial availability of water during the dry winter. Phinda management artificially supplied water to some dams and pans in winter, particularly during 1992-1994. The strongest pattern of reduced winter ranges was observed for the lionesses LFs1&2 whose ranges were centred around these water sources. Indeed, the very small range of this pride during LF2's first litter of cubs (Table 8) reflects their almost exclusive use of a core area of 4.17 km² surrounding one such waterhole. These lionesses moved the cubs from their birth site approximately 6km to the water source where they essentially remained for six months until summer rains. During this period, I often saw these lions lie in wait at the waterhole and I observed them make 27 kills of ungulates at the waterhole less than 300m from the den-site of the cubs.

Although predators will naturally seek high concentrations of available prey (Durant *et al*, 1988; Caro, 1994) and the pattern observed at Phinda may arise naturally during water shortages, the management of resource availability in small reserves is clearly

an issue which requires careful consideration. The provision of artificial sources of water may substantially influence ungulate behaviour and movements (Mills & Retief, 1984; Knight *et al*, 1998). In small reserves, the opportunity for herbivores to escape predation may be very limited (Chapter 7). Managers need to be aware of exacerbating that problem by their placement of artificial water sources. The waterhole around which the lionesses LFs1&2 centred their activities was the only source of water in their home range during this period and probably concentrated ungulate activity in that area. I do not have sufficient data to establish whether this increased ungulate vulnerability to predation or whether predation rates were increased. However, intuitively, the potential for such effects would be reduced by providing water at multiple sites so that herbivores had a 'choice.' While financial and logistic restrictions invariably limit the numbers and distribution of such waterpoints, planning with this in mind is an important aspect of predator-prey management in small reserves.

Cheetah males established relatively small, exclusive territories. In two cases, I observed male coalitions kill single males which were caught intruding into these territories (Hunter & Skinner, 1995, Appendix III). Interestingly, all the males released at Phinda originated from Namibia (see Chapter 2) where they apparently have very large home ranges of between 800 to 1500km² which are probably not defended as territories (Marker-Kraus *et al*, 1996). Unfortunately I do not have specific data on any of the males before they were translocated to Phinda: it would be extremely interesting to compare the ranging patterns of known males from Namibia before and after they were translocated to a very different region such as Phinda. Presumably, the high density of non-migratory game at Phinda (see Chapter 7) facilitated the establishment of territories by males at Phinda. Caro (1994) demonstrated that Serengeti males established territories averaging 37.4km² in areas with high concentrations of Thomson's gazelles and sufficient cover which were favoured by females for hunting. By locating their territories in areas with high rates of visitation by females, males increased their chances of encountering females, and, presumably, therefore opportunities to mate.

I do not have strong enough data to establish how males made decisions about where to locate territories at Phinda. Female cheetahs at Phinda generally used the entire reserve or a considerable portion of it and it was difficult to determine factors which may have increased their use of a specific area. In the Serengeti, very localised rainfall patterns and differences in soil quality gives rise to considerable spatial and temporal variation in the flush of grass growth, causing Thomson's gazelles to form temporary localised concentrations (Caro, 1994). Female cheetahs move over large areas searching for these

resource patches. At Phinda, although the distribution of ungulates varied in different habitats, herbivore density was high in all areas (Chapter 7) and I believe females did not have to cover large areas in search of ungulate aggregations. However, suitable habitat for hunting, rather than the prey itself, may have been the 'patchy' resource which gave rise to cheetah movements. Open habitat, particularly grasslands, were heavily favoured by cheetahs at Phinda (Table 11) and was the preferred habitat for hunting by cheetahs (Table 30: Chapter 6). Yet grasslands constituted only 8.6% of available habitat and were distributed as small, discreet, widely spaced patches (Fig. 5; Chapter 2). The core areas of the males with the longest tenure at Phinda (CMs1&2) were centred in regions with the most extensive grasslands. All monitored females at Phinda used these same grasslands extensively: in the case of the female CF5, her home range for 15 months was only 33.86 km² and was centred in an area of grassland and open mixed bushveld (Fig. 19 and see Fig. 5, Chapter 2). Her range was entirely enclosed by CMs1&2's territory for 12 of those months until their deaths in April 1995. Following their deaths, the two brothers CMs23&24 centred their activities in the same region. Furthermore, although I do not have good data after the end of 1995, when these two males were captured and translocated elsewhere (see Chapter 5), a coalition of three males born at Phinda (CMs31-33) have apparently established the core area of their range in the same grasslands and open regions (Walker, *pers comm*¹).

The importance of such key areas to territory establishment by male cheetahs following reintroduction is an area which requires further research. This is particularly so in highly heterogeneous ecosystems such as at Phinda which is dominated by *Acacia* woodlands and has relatively small areas of 'typical' cheetah habitat. I saw two fatal fights, between male cheetahs, both occurring in these grasslands and two other single males were killed in the same areas by a territorial three-male coalition during 1997-8 (Chapter 5). This suggests there is considerable competition for such areas. From a management perspective, the suitability of habitat for cheetahs in a reintroduction project requires careful consideration. Much of the region where Phinda is located (and indeed many areas presently being 'reclaimed' as wildlife land in South Africa) suffers from the removal of bulk grazers and browsers such as elephants and rhinoceros which may facilitate the maintenance of open savannah (Dublin, 1995). Their expatriation, combined with high densities of livestock has resulted in extensive areas of 'bush encroachment' in some areas (Moll, 1981). Phinda has adopted an aggressive scheme of selective bush-clearing of such areas, which aims to open up dense stands which were formerly open savannah (based on

¹ Walker, C. Phinda Resource Reserve, Private Bag 6001, Hluhluwe, 3960. tel: 035 562 0271.

aerial photographs). The impact of such procedures on cheetah ranging dynamics would be a productive topic to explore as more open habitat becomes available.

Despite extensive overlap between lions and cheetahs, cheetahs appeared to be relatively free of pressure from lions and were still successful in establishing home ranges in the same areas as lions. I saw 29 occasions when cheetahs encountered lions, 11 of them involving female cheetahs with young cubs: on two of those occasions, I saw female cheetahs pursue lions for distances up to 70m in defence of their cubs (Chapter 5). In three encounters between the two species, lions killed cheetahs, an 11 month old cub which was separated from its mother and two adult males which had been resident at Phinda for over three years at the time of their deaths (CM1 & CM2; fig 22). Interestingly, lions and cheetahs displayed similar habitat preferences, showing high use of grasslands and generally avoiding very dense habitat types (Tables 10 & 11). However, the pattern of kills made in different habitat types differed markedly, illustrating that while lions often utilised more open areas, they made more kills in dense bush (Chapter 6). As well as their preference for open habitats for hunting, the use of such regions by cheetahs probably assists them in avoiding lions due to increased visibility. On the three occasions lions killed cheetahs, they were caught in thick vegetation after having moved from more open areas. While heterogeneous habitat may provide advantages to females for raising cubs and avoiding predation on juveniles (Laurenson, 1995b; Durant, 1998 and see Chapter 5), the widespread distribution of small patches of open habitat may have increased the encounter rate between lions and cheetahs at Phinda. Given that both species used these areas extensively and that they generally occurred as isolated patches surrounded by much denser habitat (Fig 5; Chapter 2), the potential for greater conflict and more cheetah deaths by lions than observed here was high. In Nepal, McDougal (1998) documented high rates of leopard mortality by tiger predation where habitat suitability favoured high densities of tigers. At Phinda, Cheetahs may only have avoided increased pressure due to the relatively low density of lions (Chapter 5). The balance between areas of suitable habitat and pressure from competitors is a critical factor in the success of reintroduction attempts of cheetahs and is an area where future efforts should devote extensive investigation.

There is clearly still considerable information to be gathered on the range and movement patterns of reintroduced felids. The patterns observed at Phinda were subject to considerable disruption by management practices, deaths of cats and other stochastic events

following their release. Reintroduced felids showed considerable variation in ranging characteristics, though they generally conformed to the patterns observed for their species in other regions. Small sample size is an aggravating factor here, given that only two or three individuals of each species' sex/age class could be monitored. This is probably inevitable in most reintroduction projects of large cats in South Africa which typically involve a small number of founding animals which are mostly sourced opportunistically (Chapter 2). Ultimately, long-term monitoring of many such efforts will provide a clearer picture of home-range patterns of reintroduced felids.

The present study illustrated that felid reintroduction into small areas entails extensive management. Ultimately, the question most managers will seek to answer is how many individuals of lions and cheetahs small reserves can sustain. At Phinda, with its relatively high density of prey species, lions and cheetahs (particularly males) were able to occupy small home-ranges and, in conjunction with the observed rapid reproduction (Chapter 5), relatively high densities of both species were theoretically possible. During the present study, lions and cheetahs reached a maximum number of the equivalent (in terms of biomass) of 13 and 21 adult females respectively (see Chapter 5). Even with these relatively low densities, there was considerable impact on some ungulate species as a result of predation (Chapter 7). Accordingly, small reserves should perhaps ask the question how many lions or cheetahs does the reserve 'need' rather than how many it can sustain. For example, at Pilanesberg National Park, the main objective of lion reintroduction has been for 'eco-tourism' (Van Dyk, 1997). Therefore, an important aspect of lion monitoring at Pilanesberg is tourist surveys in an attempt to establish the 'ideal' density of lions to enhance tourist sightings of lions (Van Dyk, 1997). Clearly, such a management plan needs to operate in conjunction with monitoring of prey species to establish the impact of lions on prey populations. The 'result', in terms of lion numbers will have to consider these elements and balance the advantages and disadvantages of both.

Range characteristics of lions and cheetahs at Phinda were heavily influenced by human activity which may prove to be a useful management tool for reserves attempting to re-establish 'sustainable' populations of large felids. The respective propensities of cheetahs to centre their ranges in open habitat and lions to do likewise around artificial waterholes are useful considerations for management of these species in small reserves. Although active manipulation of lion and cheetah ranging patterns was not attempted during the present study, subsequent projects may benefit from applying these observations. The strategic positioning of key landscape features valued by lions and cheetahs could enhance the success of a reintroduction project and diminish the level of management required in the longer-term. As efforts to restore large felids in small reserves in South Africa proliferate,

ongoing research across numerous sites will be very valuable to quantify further the important elements contributing to lions and cheetahs' ranging behaviour. Analysis of data from different reserves and the experimental manipulation of key factors (such as the location of artificial waterpoints) will be crucial to refine these ambitious projects.

Reintroduction of large carnivores as a viable method for species regeneration is still a very controversial subject. Although large carnivores are frequent subjects for re-introduction efforts, post-release monitoring of such attempts in the past has been poor, particularly in Africa, and where it has occurred, the success of projects has been limited (Calkins, 1988; Houlden, 1981; Kruger, 1988; Penfider, 1961; Mills, 1991; Lichtenstein, 1980). Such failures have led many authors to conclude that the factors affecting success are not well enough understood to justify re-introduction as a method for conserving and restoring large carnivores (Parker & Rodgers, 1986; Weinger & Suggart, 1984; Muth, 1981). One critical factor in assessing the success of these projects is the demographic characteristics of reintroduced populations. In particular, reproduction, mortality and population growth are crucial to understanding population dynamics (Kleinman et al. 1999; Storer-Pruitt, 1986). Furthermore, analyses and predictions about viable populations (i.e. the persistence of populations) are typically produced using such demographic data (Clay, 1987; Lacy & Clark, 1993; Berry et al. 1997). Few studies have been able to collect detailed data of this sort for reintroduced carnivores. As a result, while certain technical perfection have improved success of reintroduction efforts (Clark & Beeding, 1996), insight into important demographic parameters which may contribute to carnivore re-establishment is still poor.

In North America and Europe, observation largely from projects on non-felis has yielded some important data regarding the factors influencing survival and reproduction of reintroduced carnivores. For example, in one study, black bear cubs younger than a year associated with the mother suffered increased mortality, giving rise to recommendations that females with young cubs were poor candidates for translocation (Peters, 1966). Similarly, translocated brown bear cubs and subadults suffered increased mortality rates even when the mother survived, and adult females apparently had a reduced chance of reproducing the following year (Brannan, 1967; Miller & Ballard, 1982). Only one study in fact has accurately documented the ability of translocated female bears to reproduce (Stewart & Knight, 1995), which, perhaps more than post-release survival, is a better indication of project success (Clark & Beeding 1996; Linzell et al. 1997). Among canids,