

CHAPTER 5.

POPULATION CHARACTERISTICS OF REINTRODUCED LIONS AND CHEETAHS AND PERSISTENCE OF REINTRODUCED CARNIVORE POPULATIONS.

Reintroduction of large carnivores as a viable method for species repatriation 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, (Childes, 1988; Hamilton, 1981; Kruger, 1988; Pettifer, 1981; Mills, 1991; Linnell *et al* 1998). Such failures have led many authors to conclude that the factors affecting success are not well enough understood to justify relocation as a method for conserving and managing large carnivores (Panwar & Rodgers, 1986; Wemmer & Sunquist, 1988; Mills, 1991). One critical factor in assessing the success of these projects is the demography of reintroduced populations. In particular, reproduction, mortality and population growth are crucial to understanding population dynamics (Kleiman *et al*, 1989; Stanley-Price, 1989). Furthermore, analyses and predictions about viable population sizes and the persistence of populations are typically produced using such demographic data (Lacy 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 perfections have improved success of reintroduction efforts (Clark & Reading, 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-felids 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 translocated with the mother suffered increased mortality, giving rise to recommendations that females with young cubs were poor candidates for translocation (Rogers, 1986). 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 (Brannon, 1987; Miller & Ballard, 1982). Only one study to date has accurately documented the ability of translocated female bears to reproduce (Blanchard & Knight, 1995), which, perhaps more than post-release survival, is a better indication of project success (Clark & Reading 1996; Linnell *et al*, 1997). Among canids,

reintroduced grey wolf females had a tendency to abandon pups which usually perished (Fritts, 1992), although wolves in general appear more successful at post-release reproduction than bears (Bangs *et al*, 1996; Bangs & Fritts, 1996; Koch *et al*, 1995).

The information available for felids is less detailed. Two female mountain lions produced cubs within 2 years of release in New Mexico despite a high mortality rate for the project (Ruth *et al*, 1993). Eurasian lynx releases within Austria, France, Slovenia and Switzerland appear to have successfully established populations (with the exception of Austria) though specific details about mortality and reproduction are largely unknown (Breitenmoser & Breitenmoser-Wursten, 1990; Yalden, 1993). Among African felids, published data is even more scant. Numerous efforts to reintroduce cheetahs in South Africa have apparently failed and were largely unmonitored so there is little post-release data available on demographic parameters (Rowe-Rowe, 1992, and see Table 2, Chapter 2). In the well-documented study by Hamilton (1981) on translocated leopards in Kenya only one female of 12 released individuals eventually settled in the release site and potentially reproduced. Translocation of lions has been largely unsuccessful for numerous reasons mostly related to dispersal from the release site and past projects have not provided any demographic data (Van den Meulen, 1977; Stander, 1990). An important exception occurred in Namibia, where lions which left Etosha National Park were returned to their original range and usually remained there (Standen, 1990). However, while useful, this provides no indication of demographic processes which affect the re-establishment of felids.

Clearly, there is very little information available on the demographics of reintroduced felids. In this chapter, I present the mortality and reproductive characteristics of reintroduced lions and cheetahs. These data originates from daily observations from May 1992-September 1995 and episodic data collection on 12 field trips between September 1995 and June 1998.

The specific objectives of this section are to:

1. document the post-release survival of reintroduced lions and cheetahs and attempt to determine important causes of mortality;
2. document patterns of reproduction of reintroduced lions and cheetahs;
3. use the above data as input parameters to model population viability estimations;
4. make methodological recommendations based on the data and population projections to enhance the success of large felid reintroduction efforts.

METHODS

Daily radio-monitoring of felids allowed me to observe patterns of oestrous and mating behaviour in female lions and cheetahs, and anticipate and document births. Lionesses have very conspicuous oestrous and mating bouts which I noted. Following matings, I attempted to observe lionesses daily to record any resumption of oestrus and determine if they were pregnant. Lionesses generally showed obvious signs of pregnancy 3-6 weeks prior to birth which, in conjunction with dates they last mated, allowed me to predict fairly accurately when they would give birth. All lionesses were telemetred prior to giving birth or their daily locations ascertained via association with telemetred individuals. As a result I was able to record all births of lions at Phinda (with the possible exception of one litter: see Results).

This level of monitoring was not possible in cheetahs. Phinda management was reluctant to permit radio-collaring of female cheetahs, (see Appendix II), so aside from two telemetred females, I relied on opportunistic sightings to gather information. Mating behaviour in cheetahs is extremely rarely observed due to their apparent shyness during consorts and the brief nature of matings (Caro, 1994). I never observed matings but I often saw consortships between males and females. I noted when males and females were in association, after which I attempted to regularly locate these females until their predicted birth date, assuming they had conceived. Whereas I knew the birth dates of all lion cubs to within a 3-4 day period, most cheetah litters were aged after emergence and so birth dates presented here are accurate to within about 1-3 weeks, depending on the level of monitoring possible with the mother. Incidental sightings of unmonitored cheetahs with cubs indicated additional litters to those I recorded: however, these females were often very shy and specific details are generally poorly known.

Most litters of both species were counted after emergence at approximately 6-8wks so mortality while still in the natal lair is largely unknown. Accordingly, my figures represent the minimum numbers of cubs born at Phinda for the study period. However, partial loss of litters prior to emergence appears to be rare (Laurenson, 1996; Packer *et al*, 1988) so my figures are probably close to the actual number of cubs born, particularly for lions.

Most post-release mortalities of reintroduced felids were documented within 24h of an animal's death. Accordingly, the cause and date of death was apparent in most cases. For some post-mortems, I consulted the regional veterinarian for the Natal Parks Board. For non-collared cheetahs where sightings were opportunistic, I calculated post-release survival based on the date these individuals were last sighted. However, it should be noted

this represents a minimum survival time: some of these animals were rarely sighted when living and certainly in some cases would have been alive beyond the date I last saw them. I also present survival data on animals which are still alive (as at 30/06/98) or which have been translocated to other reserves.

To attempt some estimation of the persistence of lion and cheetah populations following reintroduction, I used the population viability analysis software VORTEX, a simple stochastic simulation of population change and extinction. VORTEX is one of the most widely used population models and has been used to simulate changes in lion and cheetah populations in other regions and contexts (Berry *et al*, 1997; Zank, 1997). I used my specific demographic data from the lion and cheetah populations at Phinda as the input parameters for the population viability analysis. For some parameters (e.g. cub survival and age at first reproduction), my data probably represent a 'best case scenario' (in comparison to established populations) which may only apply in the early years following a reintroduction. Therefore, I explored the effect of varying these parameters in subsequent simulations within observed variation from established populations. Where VORTEX required data which I did not have specific to Phinda (for example, age of reproductive senescence), I used data from the published literature. I present details of all the parameters in the Results.

RESULTS

Mortality

Most reintroduced lions and cheetahs survived the early post-release stage of 3 months (Chapter 3) and generally survived for considerably longer (Table 12). For cats which died during my study, the mean post-release survival time was generally longer than a year.

The survival time of animals other than those which were confirmed dead is presented in Table 13. All these lions survived a minimum of almost 4 years post-release. Some of these animals are still living at Phinda after more than 6 years. Survival time of some unmonitored cheetahs is less clear due to sporadic observations, but females generally appeared to live longer than males. As indicated in the Methods, these individuals almost certainly survived longer than to the date they were last seen.

		Known deaths	All animals
LIONS:	both sexes	346 ± 259 (n = 8)	991 ± 893 (n = 13)
	females	214 ± 319 (n = 4)	1128 ± 1030 (n = 8)
	males	478 ± 97 (n = 4)	772 ± 662 (n = 5)
CHEETAHS:	both sexes	596 ± 612 (n = 10)	657 ± 582 (n = 14)
	females	832 ± 701 (n = 4)	972 ± 596 (n = 6)
	males	439 ± 552 (n = 4)	422 ± 476 (n = 8)

Table 12. Mean ± SD post-release survival time (days) of reintroduced lions and cheetahs. “Known deaths” presents the survival time only of animals which definitely died during the study. “All animals” includes known deaths, individuals which were still alive as at 30/06/98, translocated animals and individuals where the last date sighted was taken as date of death.

	Fate	Days since release
LIONS		
adult female, LF2	Translocated 09/05/96	1455
adult male, LM12	Still living*	1947
adult female, LF5	Still living*	2237
adult female, LF6	Still living*	2237
adult female, LF7	Still living*	2237
CHEETAHS		
adult male, CM7	last seen 10/06/93	203
adult male, CM17	last seen 09/97	536
adult female, CF6	last seen 03/02/95	1070
adult female, CF5	last seen 01/02/96	1432

Table 13. Minimum survival time of animals still living, translocated or whose fate was uncertain. *Still living, as at 30/06/98.

Mortality in re-introduced lions and cheetahs fell into two main categories: deaths related to human activities and those from natural causes (Table 13). Human-mediated mortality accounted for all post-release deaths of lions and three, possibly four, deaths of cheetahs. Seven deaths were the result of wire snare poaching. Three lionesses were destroyed following an incident in which they killed a tourist in one of the rest camps at Phinda. A female cheetah with three year-old cubs born at Phinda left the reserve through a security gate inadvertently left open and disappeared into farmland where they were almost certainly shot. A female cheetah was found dead near a public road through Phinda and appeared to be the result of being hit by a vehicle.

Natural causes accounted for the deaths of six re-introduced cheetahs, all of them the result of conflict with other large carnivores. Lions killed two males, leopards killed two females and territorial clashes between male cheetahs resulted in the deaths of two males. In the latter case (both incidents), the victorious animals cannibalised the carcasses (Hunter & Skinner, 1995: Appendix III). In the case of the four deaths by lions and leopards, the killed cheetahs had been resident at Phinda for a minimum of 879 days (Table 14). They were not eaten by lions or leopards (Chapter 6).

	Cause of death	Days since release
LIONS		
adult female, LF8	destroyed	55
sub-adult female, LF9	destroyed	55
sub-adult female, LF10	destroyed	55
adult male, LM3	wire snare	398
adult male, LM4	wire snare	399
adult male, LM11	wire snare	519
adult male, LM13	wire snare	596
adult female, LF1	wire snare	692
CHEETAHS		
adult male, CM14	wire snare	8
adult male, CM13	cheetahs	15
adult female, CF11	vehicle	73
adult male, CM7	wire snare	129
adult male, CM8	cheetahs	189
adult female, CF4	left reserve, shot(?)	619
adult female, CF10	leopard	879
adult male, CM2	lions	1139
adult male, CM1	lions	1153
adult female, CF3	leopard	1756

Table 14: Causes of mortality of re-introduced lions and cheetahs.

Reproduction

A minimum of 43 lions in 14 litters (mean litter size: 3.07 ± 0.91) and 48 cheetahs in 11 litters (mean litter size: 4.36 ± 0.92) were born at Phinda between 1992 and 1997 (Table 15.). The figure for lions represents all litters born at Phinda with the possible exception of one litter born to LF1: she mated on the 5th-8th July 1993, followed by anoestrus for 110 days (the typical gestation period). She then remained at one location in dense vegetation for 8 days before emerging and leaving the area. These events suggest that she gave birth, though I could not find any evidence of cubs, living or dead, when I searched her 'den-site' after she left. As indicated in the Methods, the number of cheetah cubs born is a minimum estimate and I knew of at least three additional litters born to shy, unmonitored females about which I have no accurate data.

Patterns of reproductive behaviour for five reintroduced lionesses are presented in figures 27 - 31. The inter-litter interval for females which had more than one litter during my study averaged 601.5 days ($SD = \pm 119.8$ days), with a range of 504 - 854 days. Three females of known age had their first conception at age 32-33mo which is considerably younger than recorded elsewhere in wild lions (Smuts, 1978; Pusey & Packer, 1987). Five male lions sired cubs at the age of 26-28 months old which accords well with the age males are known to begin producing spermatazoa (26 months old; Smuts, 1978). I do not have data for cheetahs.

Survivorship of monitored cubs of both species has been high relative to recorded survivorship for established populations. 85% of lion cubs survived the first 12 months and survived a minimum of 20 months (the minimum age at which 'independent' sub-adults were translocated). 75% of cheetah cubs survived the first 12 mths and 62% reached independence (Table 15: Note that a portion of the deficit is due to some cubs still being dependent upon mothers at the time of writing: I have excluded them from the percentage reaching independence, though the chances that some will are high). Where the causes of cub mortality are known, most are due to natural causes: however, human activity is a factor in some losses. For example, five lion cubs from two litters were lost to infanticidal males during pride take-overs which occurred after the cubs' sires were killed by poachers. The opportunity for intrusion by foreign males may not have arisen if the pride males had survived. Additionally, the first litter of cheetahs born to a re-introduced female was lost when they left the reserve as a result of poor boundary security (see Mortality section). Other causes of cub mortality are largely unknown: cubs mostly simply disappear and are never found. Lions were observed to kill one cheetah cub at 11 months old and a 5month

old cheetah cub was separated from its mother and never reunited. It survived and was apparently feeding for at least 23 days on its own after which it disappeared. Five cubs of cheetah litter 17 were orphaned at 7 months old. One disappeared at 8 months old and one was killed by a leopard at 9 months old. The remaining three survived to a minimum of 24 months old.

Information on mortality of young adults after independence indicates high survival. Aside from the six cubs which died before they were 12 months old (Table 15) only one other lion born at Phinda has died, a 3 year old male killed in a snare in May, 1998. 29 lions born at Phinda have been captured and translocated to other reintroduction sites: all were aged 20mo and older at the time of translocation with the exception of two 14mo cubs translocated with grown pride members. A 16 month old male cheetah was killed by spotted hyaenas after sustaining a leg injury two months after separation from its mother. A 14mo female cheetah left the reserve through a hole in the boundary fence and was still being sighted at a property 20km away 12 months later. However, as she is probably the only cheetah on that property, her chances of breeding are slight unless she returns to the Phinda population. Two young males, both singletons, were killed in two separate clashes with a three-male coalition of cheetahs (*NB*: these incidents are separate to the two deaths of reintroduced individuals from intra-specific conflict detailed in Table 14 and Appendix III). Excepting these losses, all the cheetahs born at Phinda for which I have good data are still alive at the time of writing. Four grown individuals (2:2) and two dependent cubs all born at Phinda have been translocated to other re-introduction sites.

Table 15: Details of lion and cheetah cubs born at Phinda

Lions of Phinda-born females. All other lions are those of singly reintroduced females.

* Surviving cubs still dependent on mother at time of writing.

* Three cubs still alive at 12mo when they left reserve with mother and disappeared.

* This litter orphaned at 7mo. Three survived at least to 24 mo.

Litter	Born	Litter size	When counted	Survived to independence
LIONS				
1	05/93	2	emerged	0
2	11/93	2	emerged	2
3	01/94	3	emerged	2
4	01/94	3	emerged	3
5	03/94	3	in lair	0
6	08/94	3	emerged	3
7	04/95	5	emerged	5
8	05/95	4	emerged	4
9	06/95	2	emerged	2
10	01/97	4	emerged	4
11	01/97	2	emerged	[2] ^d
12 ¹	05/97	4	emerged	[4] ^d
13	08/97	3	emerged	[3] ^d
14 ¹	10/97	3	emerged	[3] ^d
Total number lion cubs: 43				
CHEETAHS				
15	11/92	3	emerged	0*
16	07/93	5	in lair	3
16	05/94	5	emerged	4
18	06/94	5	emerged	5
19	10/94	4	emerged	4
20	10/94	5	in lair	3
21	06/96	6	emerged	3 [†]
22	06/96	4	emerged	3
23 ¹	08/96	4	emerged	2
24 ¹	04/97	3	emerged	[3] ^d
25 ¹	05/97	4	in lair	[3] ^d
Total number cheetah cubs: 48				

Table 15: Details of lion and cheetah litters born at Phinda.

¹ Litters of Phinda-born females. All other litters are those of originally re-introduced females.

^d Surviving cubs still dependent on mother at time of writing.

* Three cubs still alive at 12mo when they left reserve with mother and disappeared.

[†] This litter orphaned at 7mo. Three survived at least to 24 mo.

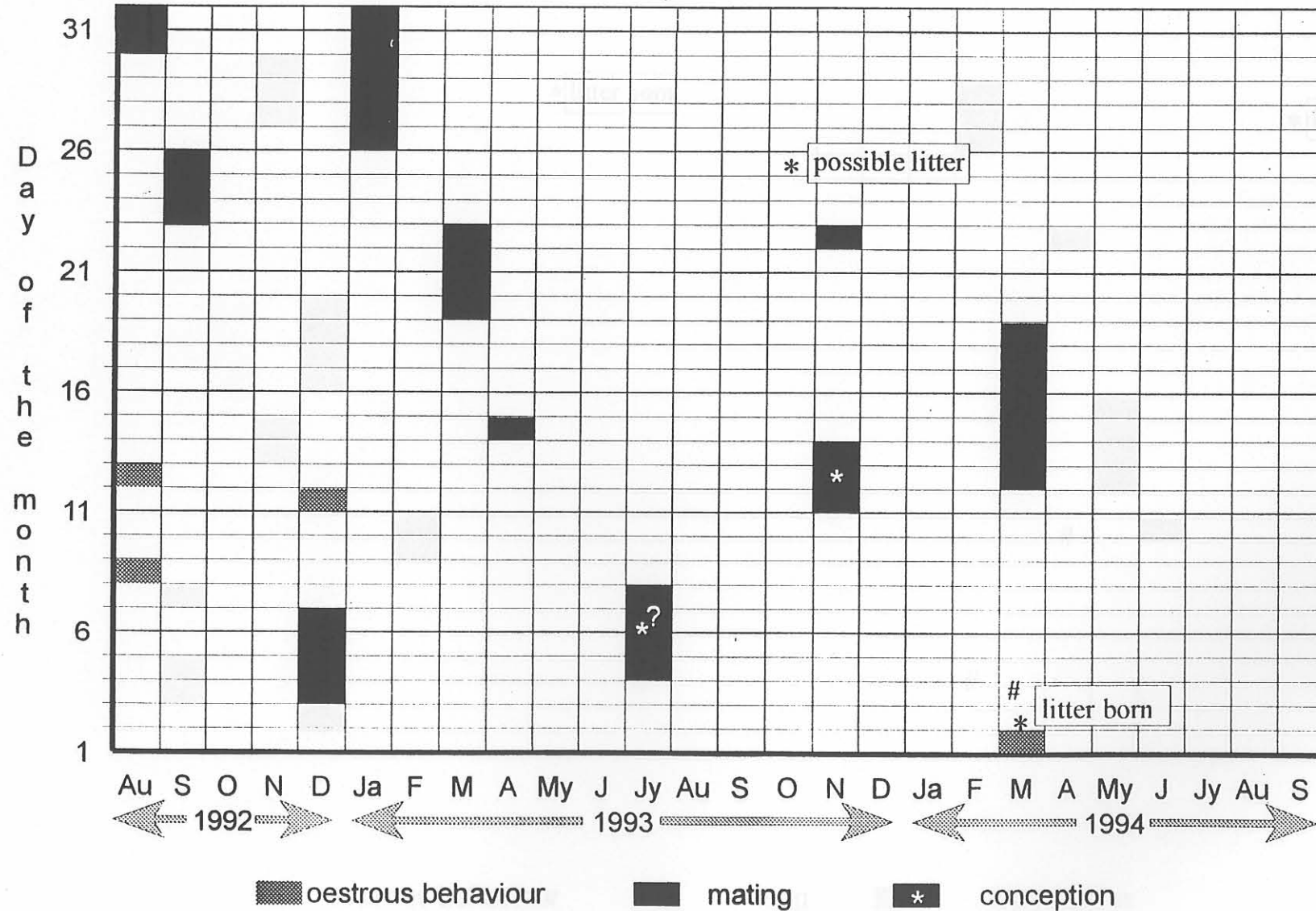


Figure 27. Reproductive behaviour for the lioness LF1. Her first litter was killed by infanticidal males one day after birth, marked #. See Results regarding possible litter born October 1993.

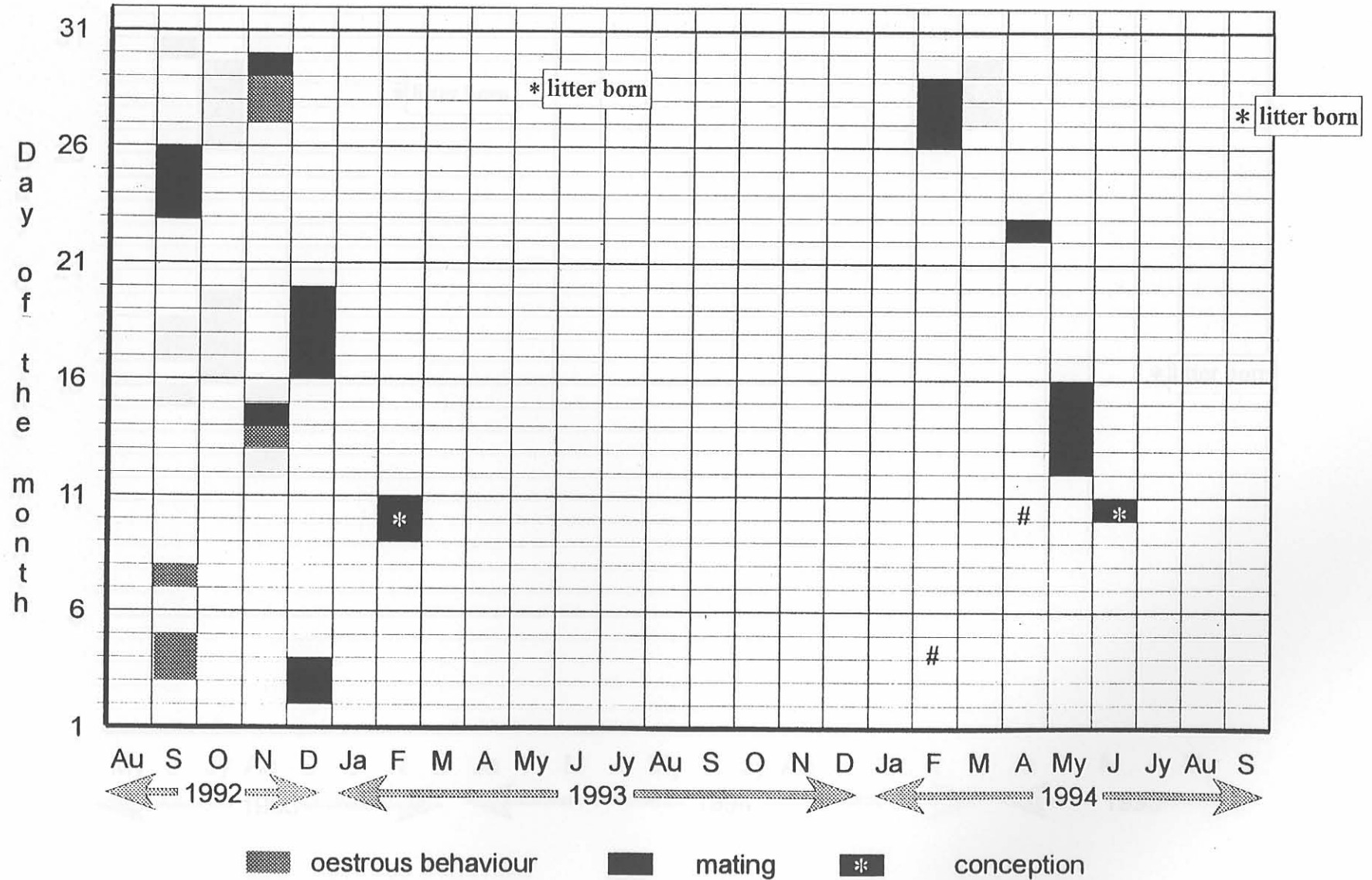


Figure 28. Reproductive behaviour for the lioness LF2. Both cubs of her first litter were killed by infanticidal males, marked #. Note. Litter#3 born approximately 20/05/96 (not illustrated).

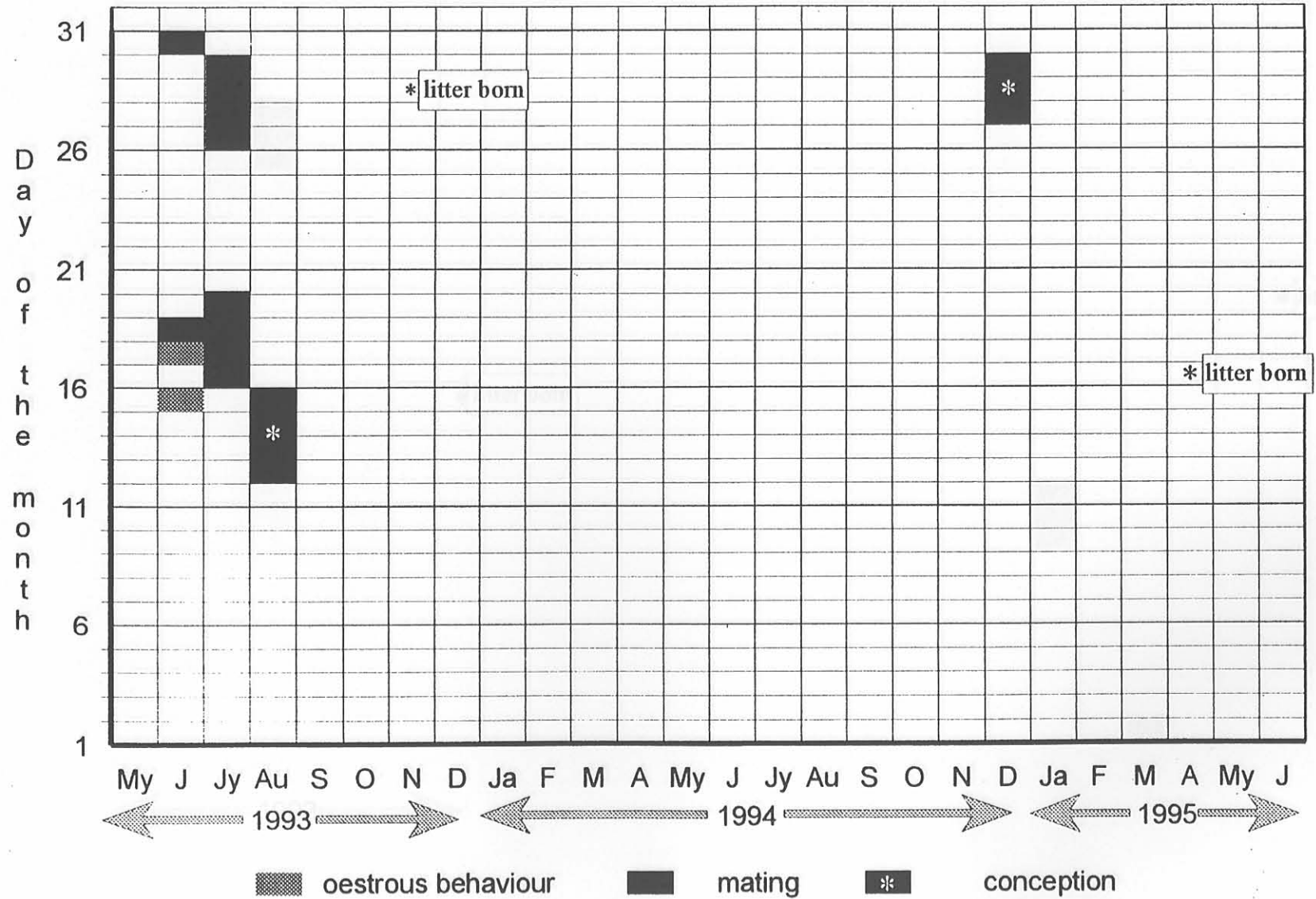


Figure 29. Reproductive behaviour for the lioness LF5.

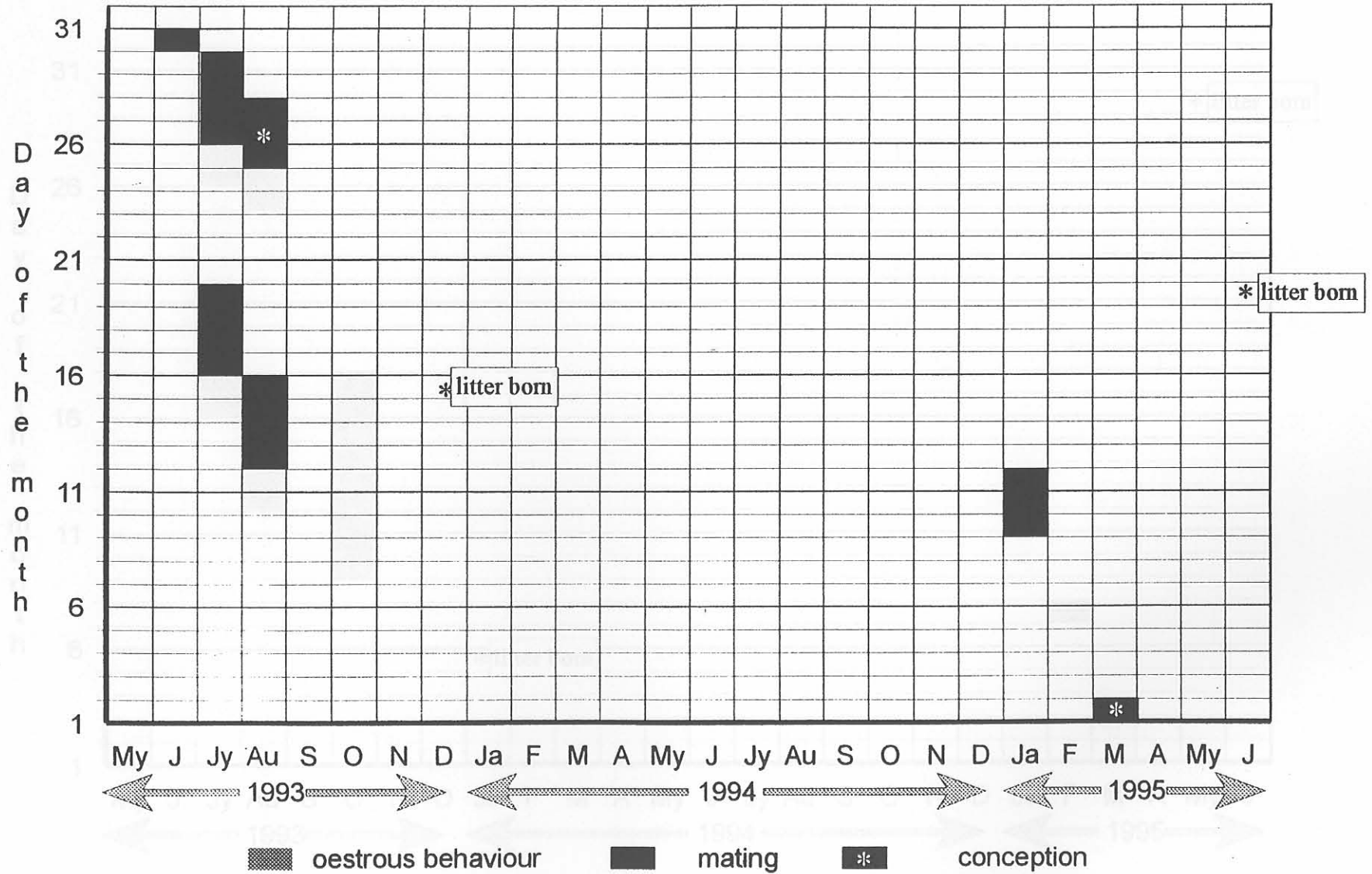


Figure 30. Reproductive behaviour for the lioness LF6.

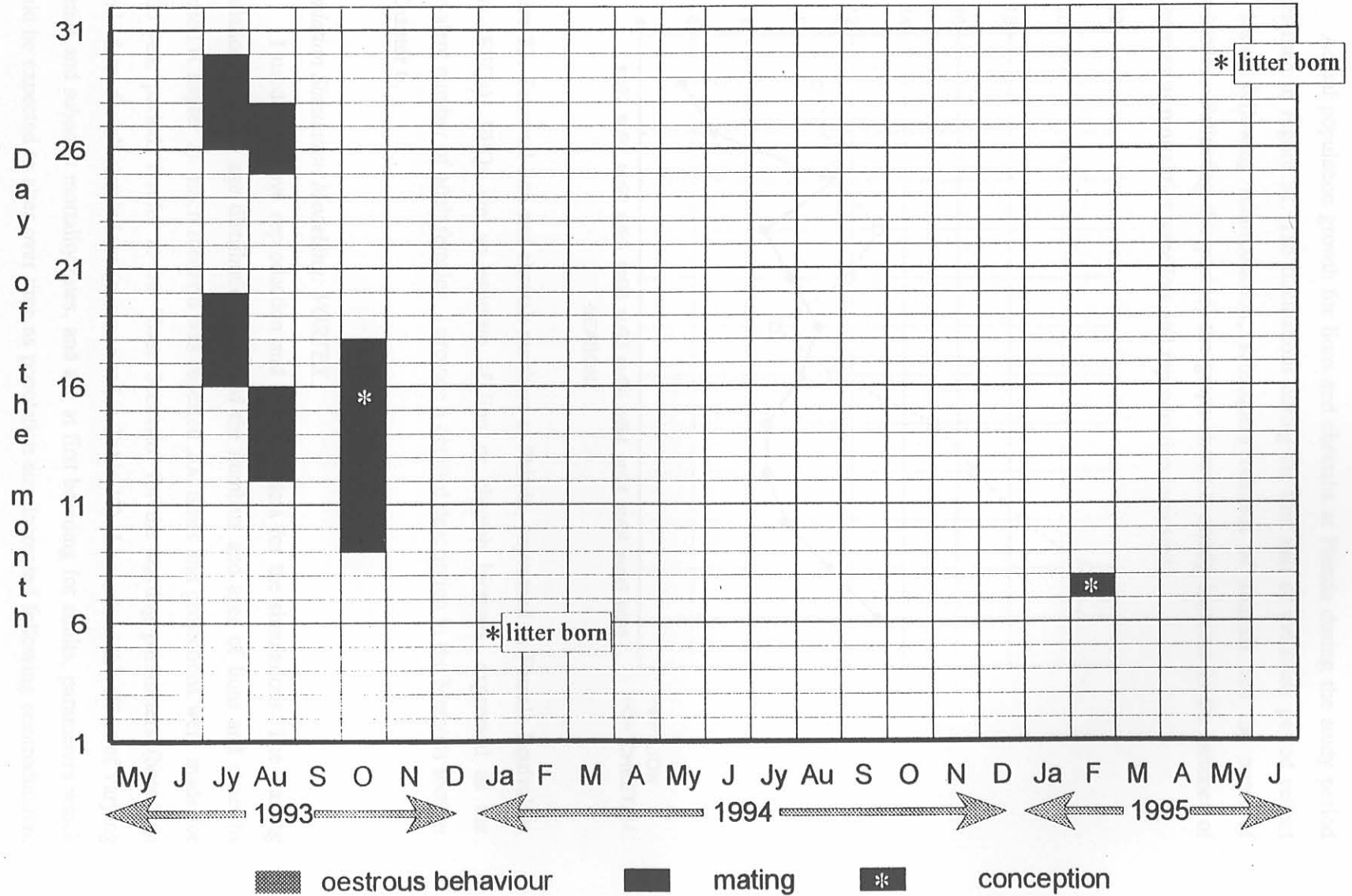


Figure 21. Reproductive behaviour for the lioness LE7

Age at first reproduction and breeding system

Actual population growth for lions and cheetahs at Phinda during the study period is presented in Figure 32. The fluctuations during the first half of the study period reflect high losses following reintroduction, subsequent releases of animals and the onset of reproduction. Following this period, the graph shows a steady increase in the number of both species as mortalities were low and reproduction increased.

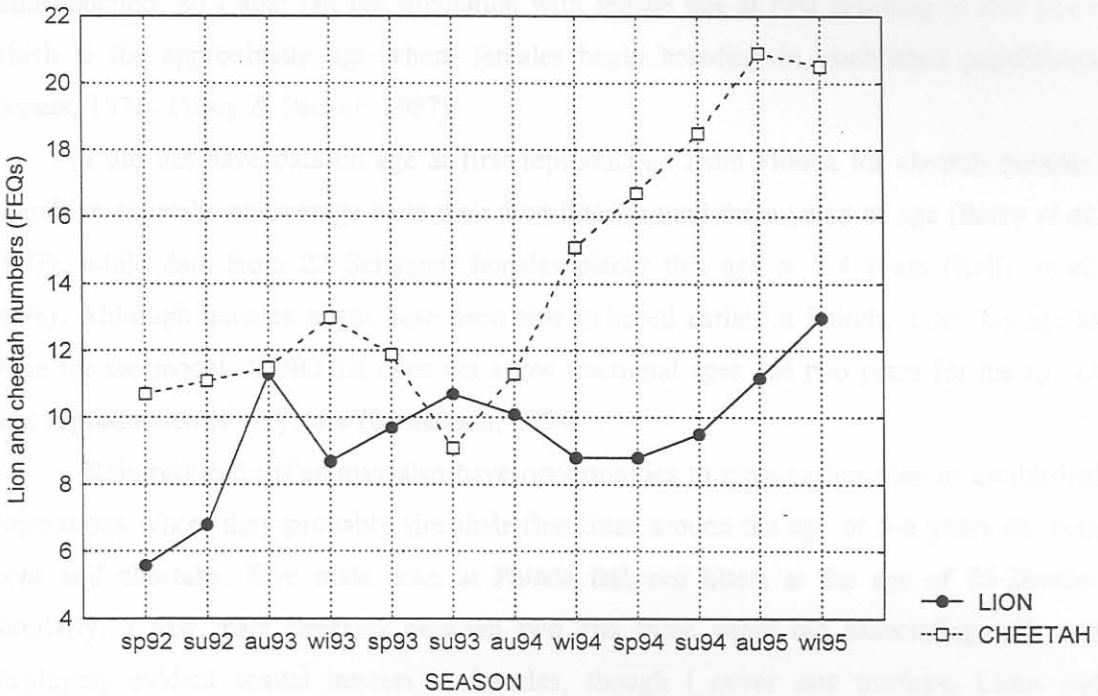


Figure 32. Seasonal lion and cheetah numbers at Phinda, expressed as Female Equivalent Units (FEQs). FEQs are an estimate of lion or cheetah biomass, expressed as the equivalent number of adult females. I provide a detailed description in the Methods section of Chapter 6.

Population Simulation Modelling: VORTEX.

I used the above reproduction and mortality data for the simulations. The starting population size and age distribution reflected the numbers and ages of lions and cheetahs released (Chapter 2). Each scenario was repeated 200 times and projections were made for a 100 year period. I refer to the ‘Base Scenario’ for the starting parameters (based on Phinda data) for all simulations (summarised in Table 17). I examined the effect of varying juvenile and subadult mortality rates, and age at first breeding for adults, parameters which would be expected to alter over time as population size increased following reintroduction. I present specific details in each section.

Age of first reproduction and breeding system.

VORTEX defines breeding as the age when young are born, not the age of sexual maturity. The opportunity to breed earlier than in established populations may exist in reintroduced populations. Three lionesses at Phinda conceived at age 32-33 mths which is generally earlier than other populations. Accordingly, I set this age for the model at three years. However, opportunities for early breeding may only exist in the early years after reintroduction, so I also ran the simulation with female age at first breeding at five years which is the approximate age where females begin breeding in established populations (Smuts, 1978; Pusey & Packer, 1987).

I did not have data on age at first reproduction from Phinda for cheetah females. Namibian cheetahs on average have their first litter around three years of age (Berry *et al*, 1997). while data from 22 Serengeti females places this age at 2.4 years (Kelly *et al*, 1998). Although females might have been able to breed earlier at Phinda, I set this age as three for the model. VORTEX does not allow fractional ages and two years for the age of first reproduction is very rare (Laurenson, 1994).

Reintroduced males may also have opportunities to mate earlier than in established populations where they probably sire their first litter around the age of 5-6 years for both lions and cheetahs. Five male lions at Phinda fathered litters at the age of 26-28mths. Similarly, I saw male cheetahs between two and three years old associating with and displaying evident sexual interest in females, though I never saw matings. Lions and cheetahs have a polygynous mating system so populations must be extremely small for male reproductive age to have a significant demographic effect in the model (Berry *et al*, 1997). Given the very small starting population size at Phinda, I ran the simulation with male reproductive age at three years and at five years for both species.

Cub production

VORTEX requires data on the number of cubs per litter, interval between litters and the proportion of females producing cubs per year. Mean litter size for lions was 3.1 (range 2-5) and for cheetahs was 4.4 (range 3-6). Average interval between litters for Phinda lionesses was 601.5 days which is lower than other populations where it is usually two to four years. Given the very small sample here, I opted for the lower estimate of this figure from elsewhere, i.e. two years. An inter-litter interval of two years translates to 50% of females not producing a litter each year.

I do not have these data for Phinda cheetahs, though one female which had three litters during my study period had an inter-litter interval of 16.5 months. Data from the Serengeti and Namibian populations places this interval at 15 to 24 mths which means that

between 20% and 50% of females do not produce a litter each year. For this simulation, I assumed a third of females did not produce a litter in a given year (i.e. an inter-litter interval of 18mths). I set the sex ratio at birth at 0.5 for both species which assumes equal numbers of males and females at birth as has been reported from wild populations (Berry *et al.*, 1997).

Age of Senescence.

This was set at 12 years for cheetahs and 14 years for lions (Berry *et al.*, 1997).

Mortality

Mortality in VORTEX was entered as the percentage of cubs (birth to 12 months old) surviving and the percentage of each sex of sub-adults (12 months old to age at first reproduction in the model) and adults older than age at first reproduction in the model) dying each year. I did not include translocations (which would influence survivorship of some animals, e.g. by creating spaces in the population) as ‘mortalities’ and therefore have calculated annual mortality rates only for the period between release to when translocations began (April 1996 for lions and December 1995 for cheetahs). Mortality rates from the Phinda data for lions and cheetahs are presented in Table 16.

	Cubs (0-12mths)	Subadults	Adults
Lions	15%	males 0%	males 20.0%
		females 0%	females 12.5%
Cheetahs	25%	males 12.5%*	males 17.85%
		females 10.0%*	females 12.5%

Table 16. Annual mortality rates for cubs, subadults and adults used as input parameters for VORTEX ‘base scenario’ simulations. * I did not have sufficient data on sub-adult survival in cheetahs and have adopted figures used by Berry *et al.* (1997).

I also compared population projections under increased mortality regimes for juveniles and subadults. As indicated in the Methods, mortality rates of these cohorts were lower than in most established populations during my study. Such levels would be unlikely to persist in the population once numbers increased (see Discussion). VORTEX does not allow these parameters to change during a simulation which would probably give the best approximation of what might be expected to occur in a recolonising population over time.

Therefore, I ran separate simulations to compare the effect of increased juvenile and subadult mortality rates as presented in Table 17.

Catastrophes.

VORTEX enables the user to model the effects of a catastrophe (such as a disease outbreak) by assigning a probability of occurrence and a severity factor reflected by increased mortality or decreased reproduction. No data are available on the frequency of such catastrophes in wild felid populations but Berry *et al* (1997) speculate that severe disease epidemics in felids might be expected to occur once in 20 years with perhaps 20-35% of the population dying and with no effect on reproduction in the survivors. Accordingly, I modelled the effect of a 5% chance of a catastrophe in 100 years with 25% reduction in survival on reintroduced lion and cheetah populations. I did not include an effect on reproduction following a catastrophe.

Inbreeding Depression.

VORTEX allows the user to model the effects of inbreeding depression. Given the very small population size, the potential for a high rate of heterozygosity loss by drift or by random is very high. Loss of heterozygosity is thought to have additional effects on juvenile mortality and so I ran the simulation including inbreeding depression as a factor. There are no published estimations of this for wild felids so I set the level at the mammalian median of 3.14 lethal equivalents per individual, comprising 1.57 recessive lethal alleles, and 1.57 lethal equivalents not subject to removal by selection.

Carrying Capacity.

The carrying capacity ('K') option in VORTEX defines an upper limit for population size, above which additional mortality is imposed proportionally across age classes to return the population to the value set for K. I set a value for K of 50 adults for both species which probably represents an absolute maximum population size for Phinda. 50 is also the minimum number of animals suggested necessary to maintain genetic variance in the short term (Soule, 1980: but see Lacy & Clark, 1989; Yalden, 1993).

VORTEX parameter	Lions	Cheetahs
Age at first reproduction.	Females 3 years, males 3 years. (Females 5 years, males 5 years).	Females 3 years, males 3 years. (Females 3 years, males 5 years).
Litter size.	mean = 3.1, range 2 -5.	mean = 4.4, range 3 -6.
Inter-litter interval.	2 years.	18 months.
Mortality.	Base Scenario as in Table 17 (high juvenile mortality = 50%) (high subadult mortality = 15%)	Base Scenario as in Table 17 (high juvenile mortality = 45%) (high subadult mortality = 25%)
Catastrophe.	5% chance in 100 years, 25% reduction in survival.	5% chance in 100 years, 25% reduction in survival.
Carrying capacity	50 adults	50 adults
Age of Senescence.	14 years	12 years
Inbreeding depression.	Number of lethal alleles = 3.14.	Number of lethal alleles = 3.14.

Table 17: The ‘Base Scenario’ parameters for VORTEX population simulations. Parentheses indicate where I varied parameters for subsequent simulations. Note that I refer to increased mortality rates as ‘high’ in comparison to figures from Phinda: however, they are well within the bounds of observed mortality rates in established populations.

The results of the VORTEX simulations are depicted in Figures 33 - 36. Under the ‘base scenario’ using Phinda data, both lion and cheetah populations reached carrying capacity within the first decade and returned very low probabilities of extinction for the 100 year period. Increasing the age at first reproduction slightly reduced the rate of population growth, more so for lions than for cheetahs. Similarly, increased juvenile or increased subadult mortality rates slowed population growth, particularly for lions. Projected population changes for lion under a normal breeding regime with 15% juvenile mortality and 15% subadult mortality returned a 25% chance of extinction (Table 18). The most severe effects for both species were under a normal breeding regime with combined increased juvenile and subadult mortality. In this scenario, the lion population had a 94.5% chance of extinction and for the cheetah population, it was 19.5%.

VORTEX scenario	Lions		Cheetahs	
	Early breeding	Normal breeding	Early breeding	Normal breeding
base scenario	0.005	0.01	0.000	0.01
high juvenile mortality	0.08	0.075	0.000	0.005
high subadult mortality	0.005	0.25	0.005	0.025
high combined mortality	0.495	0.945	0.07	0.195

Table 18. VORTEX predictions of the probability of extinction for the Phinda lion and cheetah populations under different mortality and reproduction regimes. Early breeding refers to age of first reproduction at 3 years (both species, both sexes). Normal breeding refers to age of first reproduction at 3 years for female cheetahs and 5 years for male cheetahs and lions (both sexes).

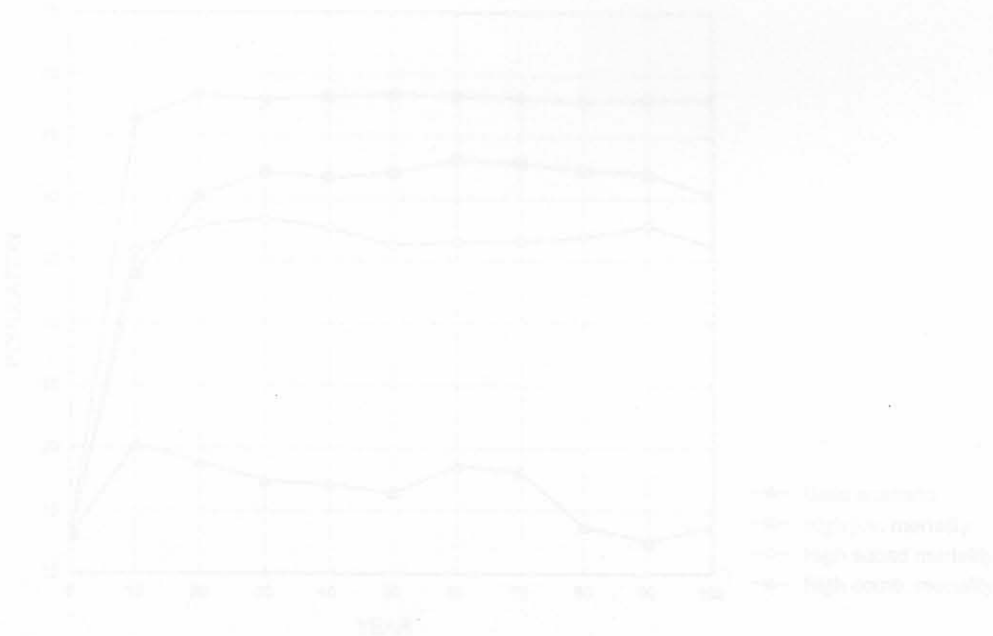


Figure 34. Lion population size predictions at 10 year intervals for 100 years, for different levels of cub and subadult mortality, and age of first reproduction for females and males at 3 years. All other parameters as for Base Scenario.

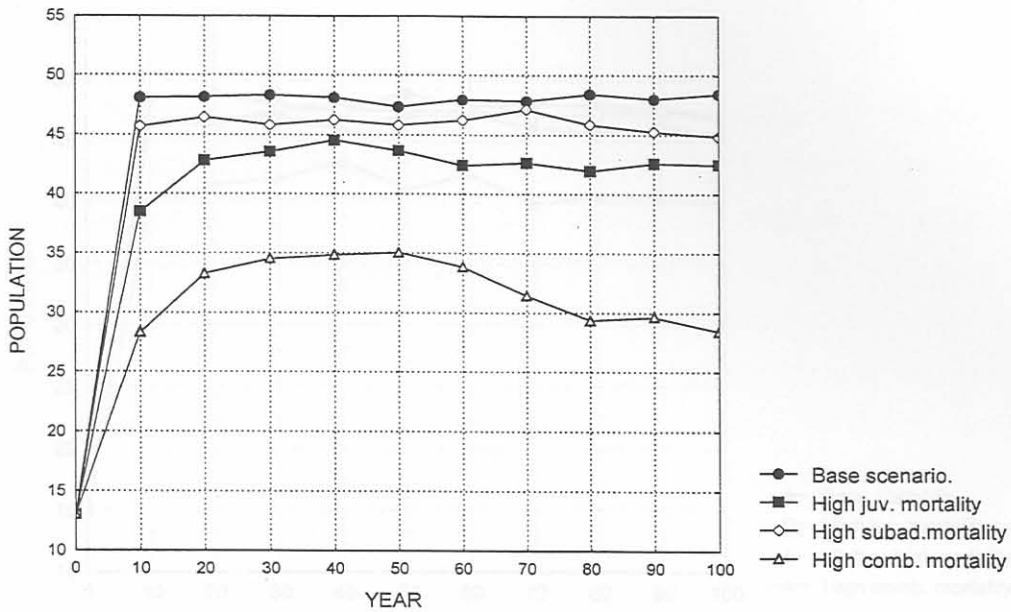


Figure 33. Lion population size projections at 10 year intervals for 100 years, for different levels of cub and subadult mortality, and age of first reproduction for females and males at 3 years. “High comb. mortality” refers to combined high juvenile and high subadult mortality. All other parameters as for Base Scenario.

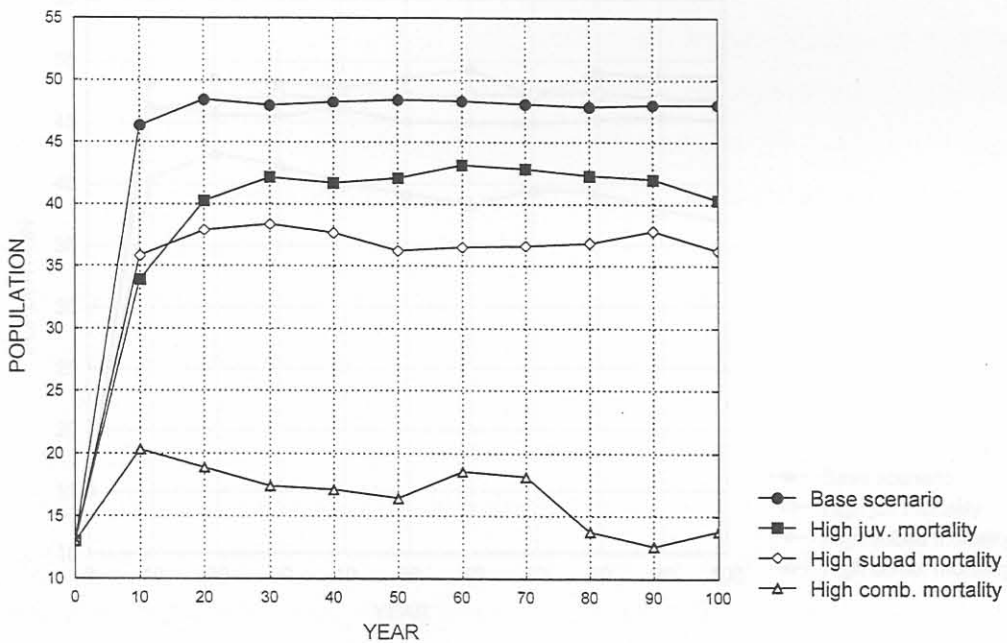


Figure 34. Lion population size projections at 10 year intervals for 100 years, for different levels of cub and subadult mortality, and age of first reproduction for females and males at 5 years. All other parameters as for Base Scenario.

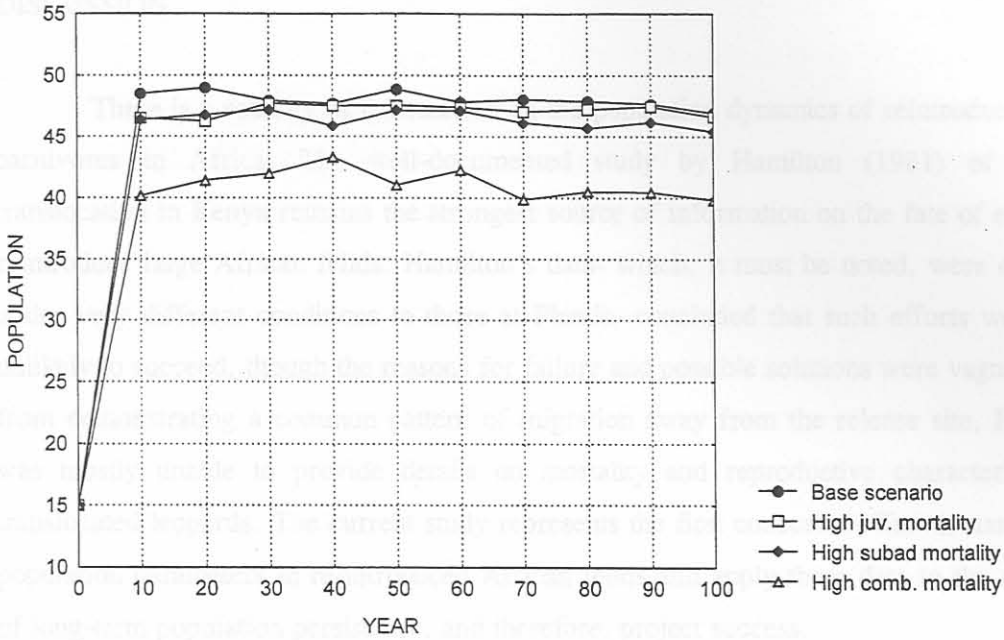


Figure 35. Cheetah population size projections at 10 year intervals for 100 years, for different levels of cub and subadult mortality, and age of first reproduction for males at 3 years. All other parameters as for Base Scenario.

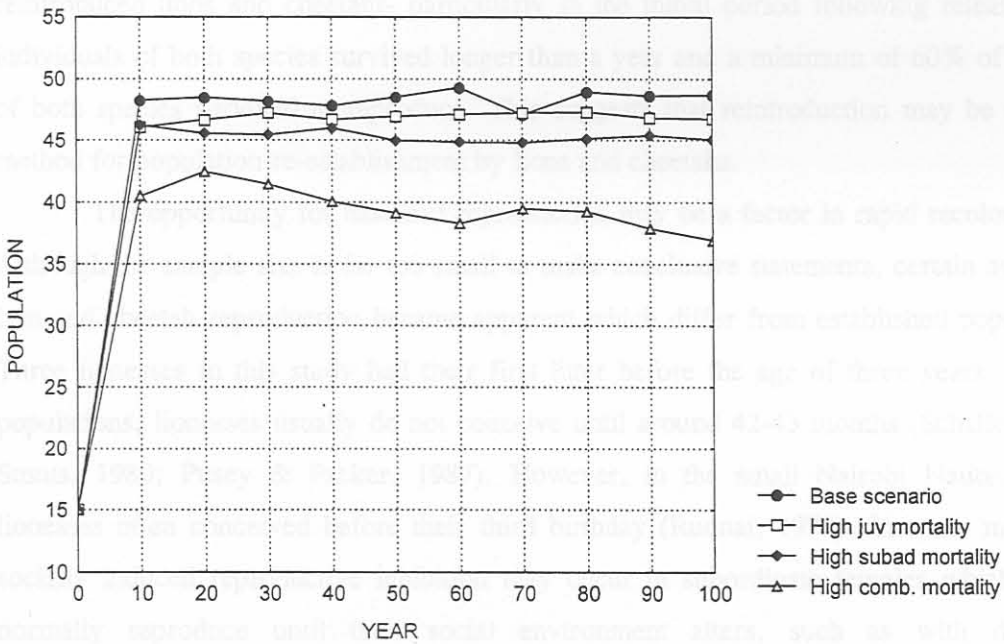


Figure 36. Cheetah population size projections at 10 year intervals for 100 years, for different levels of cub and subadult mortality, and age of first reproduction for males at 5 years. All other parameters as for Base Scenario.

DISCUSSION

There is a scarcity of information on the population dynamics of reintroduced large carnivores in Africa. The well-documented study by Hamilton (1981) of leopard translocation in Kenya remains the strongest source of information on the fate of efforts to reintroduce large African felids. Hamilton's data- which, it must be noted, were collected under very different conditions to those at Phinda- concluded that such efforts were very unlikely to succeed, though the reasons for failure and possible solutions were vague. Apart from demonstrating a common pattern of migration away from the release site, Hamilton was mostly unable to provide details on mortality and reproductive characteristics of translocated leopards. The current study represents the first concerted effort to assess such population parameters in re-introduced African felids and apply these data to the appraisal of long-term population persistence, and therefore, project success.

Lion and cheetah populations at Phinda displayed rapid growth during the study period. The population viability projections indicated that numbers of both species would reach 50 (the carrying capacity for the model) within the first decade. Together, these observations and simulations suggest that both species are amenable to swift re-establishment, at least in the short term. Despite relatively high mortality rates of reintroduced lions and cheetahs- particularly in the initial period following release- most individuals of both species survived longer than a year and a minimum of 60% of females of both species survived to reproduce. This suggests that reintroduction may be a viable method for population re-establishment by lions and cheetahs.

The opportunity for hastened reproduction may be a factor in rapid recolonisation. Although the sample size is far too small to make conclusive statements, certain aspects of lion and cheetah reproduction became apparent which differ from established populations. Three lionesses in this study had their first litter before the age of three years. In other populations, lionesses usually do not conceive until around 42-43 months (Schaller, 1972; Smuts, 1980; Pusey & Packer, 1987). However, in the small Nairobi National Park, lionesses often conceived before their third birthday (Rudnai, 1973). In some mammals, socially induced reproductive inhibition may occur in subordinate females which do not normally reproduce until their social environment alters, such as with dispersal, immigration or the death of dominant group members. Where such social factors appear to regulate reproduction, reduced population density may result in a change in age-specific fecundity where subordinate females have the chance to reproduce earlier (Macdonald &

Moehlman, 1982; Van Aarde, 1987 a,b; Creel & Waser, 1991). Although reproductive suppression is well known from many social carnivores such as dwarf mongooses (Creel, 1996), Eurasian badgers (da Silva *et al*, 1994), and African wild dogs (Fuller *et al*, 1992), there is no evidence that it occurs in lions. Lions do not display the typical alpha-pair mating system characteristic of species in which reproductive suppression occurs and they are well known for their highly polygynous mating system. However, there is some evidence that females born to prides in which males have prolonged tenure conceive for the first time later than for females in prides where male tenure is shorter, (C. Packer *pers comm*¹). This may function to reduce the possibility of females conceiving to related males. Although the sample size here is very small, young lionesses may have been responding to a lack of related pride males and as a result, conceived earlier than if there was a normal pride structure in place. Creel (1996) has suggested that lion society shares many features of carnivore sociality common to species displaying some form of socially-induced reproductive control. In established, stable lion populations, such controls may not be readily apparent. With the recent proliferation of projects attempting to re-establish lions in South Africa, the opportunity to determine such patterns (if they exist) across a number of different sites may be a rewarding avenue for future research. Where possible, the effect of nutrition and the availability of food resources is one aspect which should be examined (Rudnai, 1973; Smuts *et al*, 1978). The early breeding of females observed in Nairobi National Park was possibly a reflection of reduced competition for resources (Rudnai, 1973) which may hasten reproduction (Smuts *et al*, 1978).

The lack of established prides also affected patterns of male reproduction, permitting male lions at Phinda to sire litters far younger than elsewhere. Similar opportunities were probably available for male cheetahs though I do not have direct evidence. Five male lions here fathered offspring at 26-28 months old. Post-mortems by Smuts and co-workers (1978) on 158 male lions revealed that the onset of spermatogenesis occurs at the age of 26 months old. In a normal social situation, males of this age are approaching the period when they are typically expelled from the natal pride by mature males of the pride. Presumably, the lack of adult males at Phinda permitted young males to consort with oestrous females and begin mating around the age of 21-23 months old. A lowered first age for reproduction in males is less likely than accelerated breeding in females to have a demographic effect at the population level (Lacy, 1993). Nonetheless, the

¹ Packer, C., Dept of Ecology, Evolution & Behavior, Univ. Minnesota, St Paul, MN 55108, USA.
email: packer@biosci.cbs.umn.edu

VORTEX simulations suggested that lowered male reproductive age slightly increased the rate of population growth and significantly lowered the probability of extinction. Furthermore, from a management point of view, practitioners of lion reintroduction need to assume that males in the artificial and often unusual social circumstances of re-establishing populations can begin fathering cubs when little more than two years old and therefore have a potential reproductive lifespan of more than 10 years.

High rates of cubs and subadult survival also contributed to rapid population growth for Phinda lions and cheetahs. On the short-grass plains of the Serengeti, Laurenson (1995) estimated that 95% of cheetah cubs die before independence mostly as a result of predation by other carnivores. In Serengeti lions, depending on the habitat, male take-overs and low prey availability kill between one and two thirds of cubs before one year of age (Packer *et al.*, 1988). At Phinda, increased cub survival is probably due to low density of established predators (conspecifics and competing species) and a high density of non-migratory game (Chapter 7). In the case of cheetahs, the availability of refuges for cubs probably has a significant effect on their survival. I saw 10 incidents in which mothers with cubs less than 6 months old encountered lions. In all cases, the cubs scattered into thick bush while the mother attempted to distract the lions. Although lions were often persistent in their search for cheetah cubs, spending up to an hour trying to locate them, they were unsuccessful on all observed occasions and no cubs were killed. The only incident of cub predation by lions of which I was aware (and observed) occurred at night when a lioness separated an 11-month cub from its family and caught it as it attempted to re-join its siblings. Laurenson (1995) has suggested the extremely high rate of predation on cheetah cubs in the Serengeti may be due in part to a paucity of available refuges for cubs and their extreme vulnerability on the short-grass plains. Durant (1998) recently demonstrated that environmental heterogeneity, particularly with respect to the distribution of prey and predators, provides cheetahs in the Serengeti with refugia from competition. The current study suggests that habitat heterogeneity may do likewise, particularly for mothers with small cubs (see Chapter 4).

Low mortality rates for cubs and subadults may be critical for the re-establishment of re-introduced felids. VORTEX simulations in which these parameters were increased to moderate-to-high levels (but certainly not the highest recorded for populations elsewhere) significantly increased the predicted probability of extinction (Table 18) when all other parameters were constant. Although such simulations are crude and must be interpreted cautiously, this suggests that high juvenile or subadult mortality in the early years of a reintroduction effort may increase the chance of project failure. Crooks *et al.* (1998)

recently modelled the impact of increasing rates of mortality on eight different age classes of cheetahs and concluded that the influence of juvenile survivorship on population growth rate is small and that adult survivorship is the most important factor contributing to population increase. They concluded that ‘even a slight decrease in adult survivorship outside of protected areas... may counteract any benefits of even complete elimination of predation-related mortality in juvenile stages.’ Crooks and co-workers’ models were based on data from the established Serengeti population, rather than re-colonising populations as at Phinda: nonetheless, the current study suggest that population growth is strongly affected by juvenile survival in re-establishing populations. While adult survival is clearly important, the relatively high rates of adult mortality seen at Phinda argues that populations can sustain considerable losses in the adult cohort and still increase rapidly where there is low cub and sub-adult mortality.

This has important implications for the planning of such programmes. At Phinda, cheetahs and lions were released over the same 18 month period (Chapter 2). In some subsequent projects, lions were already established when the release of cheetahs was attempted and indications are that they have not been as successful as at Phinda due to lion predation and competition (Van Dyk, *pers comm*²). Practitioners of multi-species re-introductions such as at Phinda should consider establishing vulnerable species such as cheetahs prior to the release of competitively dominant species such as lions. Although it is unclear from the present research precisely what duration between cheetah and lion releases would be effective, the high potential for reproduction by cheetahs freed of predation suggests that even a period of two to three years would improve the chance of project success. Importantly, cheetahs experiencing ‘predator release’ for longer periods may undergo such rapid population growth that converse management problems are presented. In the lion-free Suikerbosrand Nature Reserve 80km south of Johannesburg, seven cheetahs (4:3) released in 1975 gave rise to at least 40 cubs in the following five years (Cohen *et al*, 1978; Pettifer *et al* 1979, 1981 a,b). The increasing cheetah population was implicated in the reduction of some herbivore species (see Chapter 7) and capture and removal of all cheetahs was initiated in 1980. Similar attempts from other areas lacking competition for cheetahs such as Pilanesberg National Park (Anderson, 1980) and Itala Game Reserve (Rushworth, *pers comm*³) resulted in similar outcomes. Clearly, re-establishing large felids presents many management difficulties and should not be undertaken lightly.

² Van Dyk, G., North-west Parks Board, PO Box 4124, Rustenberg, 0300 South Africa.

³ Rushworth, I., Regional Ecologist North, Natal Parks Board, PO Box 662, Pietermaritzburg, 3200 South Africa. email: ianr@npb.co.za

Other aspects of this study illustrate where additional considerations may further facilitate the re-establishment process. Causes of mortality of re-introduced cats indicated that stochastic factors following the re-introduction process probably had little effect and human activity after release is the main contributory factor. All the deaths related to human activities occurred within a 16month period between March 1993 and July 1994 when allocation of resources shifted from issues of reserve and wildlife management to the tourism operation at Phinda. Subsequently, improved procedures for anti-poaching, boundary inspections and control of tourist movements have been implemented and no deaths as a result of human activities have occurred since July 1994, with the exception of a male lion (born at Phinda) killed in a snare in May 1998.

Increasingly, human activity is perceived as the single greatest factor likely to influence the success of reintroduction projects, especially with controversial species such as large carnivores (Peek *et al*, 1991; Reading & Clark, 1996; Linnell *et al*, 1997; Woodruffe & Ginsberg, 1998). Phinda was established entirely for 'eco-tourism' which provides the revenue for most of its running costs. Accordingly, the necessity of investing considerable resources in the tourism operation cannot be flawed. However, the extremely rapid pace at which development occurred at Phinda may ultimately have exacerbated the significant human-mediated mortality of cats seen here. The development of extensive infrastructure such as costly tourist lodges, airstrips and staff housing occurred in parallel with the felid reintroductions, and should perhaps have been staggered to reduce competition for resources. This can be a considerable challenge to newly established reserves where the tourism demand for large cats and fully operational facilities places significant pressure on projects.

Phinda is now in its sixth year since lions and cheetahs were re-introduced and while many lessons have been learned, the project faces long-term issues which, if ignored, will result in failure. Carnivore re-introductions are typically initiated with a small number of founders bringing genetic issues into question (Clark & Reading, 1996). A small population with few founders such as at Phinda may be subject to losses of genetic variability, reducing its ability to adapt to environmental changes and increasing chances of inbreeding and losses to disease outbreaks or other catastrophes (Soule, 1983; Lacy, 1987). Although the impact of reduced genetic heterogeneity is not well documented in populations of wild felids, two examples suggest it may have crucial effects. Lions in the Umfolozi-Hluhluwe Game Reserve originated from a maximum of five animals in the 1960s (Maddock *et al*, 1996). Although subsequent population growth was rapid, these lions now apparently suffer from an immunodeficiency syndrome possibly related to inbreeding and the population is in decline (Meltzer *et al*, 1997). Similarly, the south-eastern sub-species

of the mountain lion known as the Florida panther has been reduced to less than 50 animals and suffers from a suite of genetic problems including cryptorchidism, heart murmurs and high percentage of abnormal sperm (Roelke *et al.*, 1993). Small reintroduced populations arising from low numbers of founders such as at Phinda may well encounter similar problems in the future if left unmanaged.

Spatial considerations of sites in such projects are also threats to long-term success. Factors such as the degree of isolation from other potential release sites or established populations and whether the area is large enough to sustain enough individuals required to maintain demographic and genetic heterogeneity in the long term will impact the persistence of populations, exceedingly so for small founder groups typical of carnivore reintroduction (Gilpin, 1987; Clark & Reading, 1996). Minimum population sizes and the impact of these processes on restored populations are still largely unknown for large carnivores (Beier, 1993; Dinerstein *et al.*, 1997). Small reserves such as Phinda will act as ongoing experiments to establish some of these parameters and clearly will have considerable obstacles to long-term success. Increasingly, managers of such reserves in South Africa are realising the need to view small, isolated populations as a metapopulation (Gilpin, 1987). At the time of writing, Phinda management are involved in negotiations to consolidate 500km² of government and privately owned land into a single conservation area and exchanges and translocations of lions and cheetahs between Phinda and other developing reserves has been ongoing since 1995. While the population characteristics displayed by lions and cheetahs at Phinda are encouraging, continued data collection and intensive management of these issues will ultimately determine the long-term viability of reintroduced felid populations.

Similarly, the sexually variable system of cheetah sociality in which females are always solitary, and males may form coalitions or may remain alone (Caro, 1994) presents costs and benefits. Even the largest aggregation of cheetahs could probably not make up very large ungulates such as buffaloes and giraffes whose group size in lions plays a significantly beneficial role (Packer *et al.*, 1990). However, male cheetahs in coalitions can tackle larger animals than do single males or females, and hunting larger prey is one adaptation used by male cheetahs to cover the increased (collective) energetic demands of group living (Caro, 1994).