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Contraception, reproduction and demography of free-ranging Etosha lions (*Panthera leo*)

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The use of long-acting contraceptives as an effective population control mechanism for free-ranging lions was investigated during a three-year study in the Etosha National Park on five lion prides. Lions were immobilized with ketamine hydrochloride and xylazine hydrochloride. Following immobilization, lionesses were weighed, measured and aged, while serum steroid hormone levels were analysed and vaginal smears were obtained. Physical condition and sexual state were assessed. Individuals were used as control animals or given melengestrol acetate (contraceptive) implants, branded and released; the animals were observed for possible changes in behaviour, birth rate and mortality. Ten treated lionesses were recaptured at irregular intervals to reassess weight and steroid hormone levels, while three lionesses had their implants removed to determine if their fertility would return. The contraceptives prevented pregnancy, were reversible when removed and did not alter lion behaviour significantly, except that sexual behaviour was not recorded in treated lionesses.

Contents

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Introduction

Lions were formerly distributed throughout South-West Africa/Namibia (Shortridge, 1934) but now occur only in the northern parts and occasionally in the south-east, adjoining the Kalahari Gemsbok National Park. Most lions occur in the Etosha National Park. A game count in Etosha in 1926 estimated a lion population of 200 (Berry, 1980). The lion population increased and estimates of 260 in 1975, 400 in 1980 and 500 in 1981 have been made (Gaerdes, 1975; Berry, 1980), while the numbers of hyaena, wild dog, cheetah and leopard have decreased significantly (Berry, 1980, unpubl. data; Orford, 1987). The possibility exists that an increase in lion numbers may have contributed to the decline of other predators.

Berry (1980), investigating a marked decline in the wildebeest population in the Etosha National Park, concluded that the principal factor involved was boundary fencing which prevented seasonal migrations. Furthermore, the building of numerous artificial waterpoints created new permanent water sources for game while the building of tourist roads resulted in numerous gravel pits in the limestone beds of Etosha. The water in these alkaline pits formed an ideal medium for anthrax transmission which caused 62% of wildebeest mortality during the period 1974 to 1978.

The artificial waterpoints, abundance of anthrax carcasses and failure of the game to migrate resulted in an increased lion survivorship, numbers and number of prides (Berry, 1980).

Attempts to control the density of free-ranging lion populations in national parks have not been particularly successful. The natural control of lion populations is usually a consequence of inadequate food supplies and social factors (Schaller, 1972; Bertram, 1973). Jewell, Harwood, Beddington, Laws & Holt (1979) have speculated on controlling populations of large mammals artificially in parks by various methods, including the addition of sterilizing chemicals to drinking water.

Smuts (1978) culled lions in the Kruger National Park but lion numbers rapidly returned to previous levels on ending the cull (Smuts, 1982). The prides' cohesive structure and the behaviour of the individuals was disrupted and Smuts (1982) documented the risks of disturbing predator-prey relationships. Culling at Umfolozi Game Reserve has resulted in extended pride male tenure which may result in incestuous matings (Anderson, 1980). The indirect disruption of natural selection may have serious genetic consequences.

Contraceptives have been effective in regulating populations of feral cats, white-tailed deer and wild mustangs (MacDonald, 1980; Turner & Kirkpatrick, 1982; Levenson, 1984); the latter experiment resulted in an 80% decline in mustang foals without adverse changes in adult behaviour.

As part of a planned programme to retain genetic diversity in large captive carnivores, Seal *et al.* (1975, 1978) investigated the use of long-acting progesterone contraceptives in lions and other felids. They treated 217 cats and only 2% became pregnant. No abnormal behaviour or serious

physiological complications were recorded and on removal of the implant the contraceptive effect was reversed.

The protection that national parks give to lions has often resulted in marked increases in their numbers. The management dilemma that results from this increase has on occasions led to large mammals being killed in considerable numbers in the very areas set aside for their preservation (Jewell *et al.*, 1979). Since culling has practical, ethical and aesthetic objections, and to find an alternative management tool to culling, the use of contraception in free-ranging lions of the Etosha National Park was tested. The study created an ideal opportunity to investigate aspects of the lions' reproductive physiology, demography and social behaviour.

Materials and methods

Study area and lion prides

The Etosha National Park, referred to here as Etosha, was fenced in 1973 and enclosed 22,270 km^2. Etosha lies in northern South-West Africa/Namibia and its coordinates centre at 19° South and 16° West. The Park extends 295 km east-west and 65-110 km north-south.

The major feature of the Park is a vast, flat, saline depression known as the Etosha Pan, with an area of 4,590 km^2. The study area was confined to 5 lion pride territories along the south-western edge of the pan surrounding the Okondeka, Okaukuejo, Ondongab, Gemsbokvlakte and Ombika waterholes, and covered approximately 660 km^2.

There are 3 seasons at Etosha, i.e. wet and hot (January to April), dry and cool (May to August) and dry and hot (September to 31 December) (Walter, 1973). Minimum and maximum temperatures (-1 ° to $+40$ °C) and mean monthly rainfall (0 to 117 mm) were recorded at Okaukuejo between July 1981 and June 1985.

Immobilization, marking and sampling

Fifty six lions were immobilized between April 1981 and September 1984 using 8·0 mg/kg ketamine hydrochloride and 3·2 mg/kg xylazine hydrochloride (Van Wyk & Berry, 1986). Following immobilization, each lion was weighed, and then mensural data, blood samples and vaginal smears were taken. All lions were permanently and individually marked with a hot brand and aged by examining the eruption, wear and discoloration of their teeth (Smuts, Anderson & Austin, 1978*a*). Each lion was allocated to one of the following age classes: small cubs (0-1 year), large cubs (1-2 years), sub-adults (2-4 years) and adults (4 plus years) (Schaller, 1972).

Blood samples were collected from the external jugular vein and the plasma separated within 4 hours of collection; plasma was stored temporarily at -20 °C. The lionesses were subjectively placed into reproductive categories depending on their behaviour prior to immobilization and subsequent examination.

The assignation of reproductive categories to lionesses (except for those lactating) proved to be difficult, and the method is not considered reliable. Vaginal smears were collected from each lioness with a sterile cotton-tipped applicator.

Plasma samples were analysed by the S.A. Institute for Medical Research to obtain baseline values of gonadal steroid hormones by employing radio-immunoassay techniques.

Administration of the contraceptive

A long-acting progesterone contraceptive was administered to 10 lionesses between January 1981 and July 1982. The melengesterol acetate (MGA) implants were inserted into the neck muscle of lionesses, 10 cm antero-lateral to the left shoulder. A 4 cm incision was made in the skin and the muscle was incised

longitudinally to allow insertion of the implant; the sheath and skin were closed with interrupted vicryl sutures. Four lionesses were recaptured 22 months after treatment and their implants were removed.

Three lionesses had natural markings which allowed individual recognition and were used as uncaptured controls. The remaining lionesses and large female cubs were captured and treated in exactly the same way as the treated lionesses except for the fact that no contraceptive was administered to these lionesses.

Behaviour recording

Behaviour records of treated and untreated lionesses comprised resightings, focal animal studies and instantaneous group scans. 'Focal animal' studies recorded specified actions (or interactions) of a known individual for a predetermined period of time, while 'Instantaneous scans' of a group recorded the activity of each individual at preselected moments and thus measured states, not events (Altmann, 1974; Berry, 1980).

Schaller (1972) categorized lions into 'residents' that remain from a year to their whole lives within the pride area, where they associate with each other to form prides, and 'nomads', that wander widely often following migratory herds of game. These definitions were used in this study.

The behavioural data were collected according to a strict procedure. The data, time, season, climatic conditions, surrounding habitat, group size, activity and relationship to other lions, and prey species were recorded on each occasion. Thirteen activities were used for the focal animal studies and 9 for the group scans. All positive resightings of the lions in the 5 study prides were recorded.

A standard sampling period of 15 min (900 sec) every alternate 15 min was employed; the time devoted to each activity was measured with a stop-watch. A group scan involved one scan of group activity every 5 min, followed by a 15-min observer rest period.

Using treatment data for observed values and control data for expected values is not strictly correct for chi-square tests. However, a modification of the chi-square tests can be used for such analyses. Neu, Byers & Peek (1974) described a statistical technique for calculating simultaneous confidence intervals for analysing utilization-availability data and the method was applicable to the day-time scan data recorded here for lionesses. The method was developed by Byers & Steinhorst (1984) who demonstrated that if a statistically significant difference is found between control and treatment data, further investigation using Bonferroni confidence intervals can be used to determine the expected probabilities of frequency of occurrence of different behaviours. Chi-square tests and Bonferroni analysis were used for the analyses of behaviour data.

Population composition

A total of two 545 resightings of known lions was made from which pride composition, natality, mortality and 'disappearances' were estimated.

Results

Age and body mass

The mean age of nomadic and pride males was greater than that of females. The oldest lions were the pride males, three of which died in their pride, one at the age of 14 years (Table I).

The heaviest male weighed 260 kg and the heaviest untreated female 165 kg. Male lions became significantly heavier than lionesses ($P < 0{\cdot}001$) when four years old (Table II).

Nutrition appeared to be adequate in Etosha for the lions were usually in good condition and in the three years 97% of the lions observed were classed as being in good or excellent condition. Subjective estimates of condition were supported by serum plasma studies of fat and nitrogen metabolism (Melton, Berry, Berry & Joubert, 1987).

TABLE I

Mean estimated age in years for adult lions in the five study prides in January 1982 and at death

	Age in January 1982			At death		
	mean	range	*n*	mean	range	*n*
Nomadic males	7	5–10	7*	9	8–10	3
Pride males	8	5–12	7	12	11–14	3
Pride females	5	4–8	18*	7	6–9	3

* Two nomadic male lions and 14 lionesses were aged under four years in January 1982 and are not included in these data

TABLE II

Mean mass (kg) of captured lions (±S.D.)

Age	*n*	Males	*n*	Females
0–2	5	99±14	5	84±17
2–4	3	181±28	14	126±15
4+	16	190±23	17	141±13

TABLE III

Composition of the five prides for various age and sex classes

	1982	1983	1984
Adult males	7	8	8
Sub-adult males	3	1	0
Large male cubs	0	0	2
Adult females	21	23	25
Sub-adult females	10	5	0
Large female cubs	0	0	3
Total cubs born	2	9	28
Total	43	46	66

Adult nomadic males were seen regularly in the study area and, despite deaths and emigrations, a constant number of six branded nomads was present during each year of the study. Two sub-adult male nomads were seen regularly in 1982 and 1983.

Demography

The number of adult lions and lionesses in the five prides changed annually owing to sub-adult maturation, emigration, and deaths of pride adults (Table III). The mean number of adults per pride was 1·5 (0-4) males and 4·8 (2-10) females. Changes in the number of lions was dependent on fluctuations in the sub-adult classes.

TABLE IV

Sex ratio of known lions of various age classes

Class	Male:Female ratio
Cubs born in study	1:0·8
Pride sub-adults	1:3·7
Pride adults	1:3·0
Nomads and pride adults	1:1·7
All known lions in study	1:1·5

TABLE V

Litters born to control lionesses, treated lionesses and to lionesses following removal of an implant

	n	Year 1	Year 2	Year 3	Year 4	Total
Captured control	15	1	2	7	1	11/15
Uncaptured control	3	0	1	1		2/3
MGA implant	10	0	0	0		0/10
Following implant removal	3	2	1			3/3

The sex ratio was calculated across the five prides for each age category (Table IV). For 33 cubs sexed during the study there was a preponderance of males; however, the ratio reversed with a bias towards lionesses amongst adult pride animals.

Natality

Thirty two adult/sub-adult lionesses were present in the five prides and ten of these were given MGA implants; 18 lionesses constituted the control group. Nineteen litters (39 cubs) were born during the study period; one litter in 1982, five in 1983 and 13 in 1984. Table V shows the number of litters born to the lionesses.

The ten lionesses that received MGA implants did not conceive during the study period. Three of these lionesses had their implants removed and were seen to copulate on days 21, 28 and 36 following removal. Two cubbed five months later and the remaining one appeared to lose her cubs (having suckled) but definitely cubbed again in the following March.

Two of the 18 control lionesses were 'lost' at the start of the study period and a further two only became sexually mature in the last months of 1984. The remaining 14 lionesses gave birth to 13 litters. Eight adult, untreated lionesses were observed for three years and produced 18 cubs from eight litters giving a birth rate of 0·77 cubs/lioness/year.

The number of lionesses that could conceive each year varied considerably when corrected for age, mortality, emigration and contraceptive effects. Table VI shows the number of litters born to control lionesses.

TABLE VI

Birth rates of control lionesses

	1982	1983	1984
Fertile lionesses	9	12	15
Litters born	0	3	10
Cubbing percentage	0	25	66

TABLE VII

Total number of months during which adult lionesses could either have conceived or were receiving contraception, and litters born in that period

Category	*n*	Fertile or treated months	Number of litters	Actual number cubs	Predicted number cubs
Untreated controls	14	420	13	28	28
MGA implants	10	197	0	0	13
After treatment	6	103	6	11	7
Total			19	39	48

Contraception

To assess the effect of the contraceptive it was important to record the period over which the lionesses were treated, and for how many months the controls were sexually mature. Cubbing incidences were then compared on a lioness/month basis.

The youngest lioness that cubbed was four years old and this age was taken as the onset of fecundity. The age of lionesses at the start of the study period (or when they became fecund), the duration of contraceptive treatment, and the subsequent fate of each lioness was recorded.

The total number of months for which control lionesses could have cubbed, or that contraceptives were functioning in treated lionesses, were calculated (Table VII). Totals were reduced because some lionesses were non-fecund at the onset of the trial and others died or emigrated; 57% of lionesses received contraceptive treatment in 1982, 34% in 1983 and 32% in 1984. Since the estimated cubbing rate for control lionesses was known, it was possible to predict the number of cubs that would have been born (Table VII) had there been no contraceptive treatment.

Treated lionesses did not cub during the study but the control lionesses produced 39 cubs in the same period. The inference is that the MGA implants prevented the conception of 13 cubs. Return to fecundity following the cessation of contraception is demonstrated by the results. The MGA implant is an effective contraceptive in free-ranging lionesses.

TABLE VIII

The fate of branded male lions to December 1984

Category	*n*	Alive	Missing	Dead
Cubs	3	2	1	0
Sub-adults	3	2	0	1
Nomads	9	3	3	3
Pride males	7	4	0	3

TABLE IX

The fate of branded lionesses and uncaptured controls to December 1984

Category	*n*	Alive	Missing	Dead
Cubs	2	1	1	0
Sub-adults	13	12	1	0
Pride lionesses	14	9	2	3
Uncaptured controls	3	3	0	0

Mortality

Fifty four lions comprised the five study prides in January 1982 and their composition was monitored during 1982-1984. Of the 54 known lions in January 1982, 18 died or left the area, representing an annual loss of 11%.

The fate of the 22 male lions is reflected in Table VIII. The loss from the 22 marked male lions was 11 (50%) with a known mortality of seven (32%) giving an annual emigration/mortality of 17%. Of the seven male lions marked initially, four had tenure over prides more than four years later while three died in their prides, aged 9, 11 and 14 years. The prides received three pride males during the study period; a nomad from outside the study area and two sub-adults that became mature and remained in the natal pride. No pride take-overs by male coalitions occurred in the five prides over a six-year period.

Twenty nine lionesses were marked between May 1981 and September 1984 and a further three animals had natural identifying markings; only one lioness was classified as nomadic. The fate of these lionesses to December 1984 was recorded (Table IX).

The overall loss for the 32 lionesses was seven (22%), the known mortality was three (9%) and the annual emigration/mortality was two. The annual loss of lionesses (7%) was less than for males (17%); more than half the male losses were among nomads, of which 67% died or disappeared. The annual loss for the 10 pride males, despite their greater age, was 10%. The pride system thus appeared to increase survival of male pride lions beyond that of male nomads, to a rate which is similar to that of pride lionesses. Thirty nine cubs were born during the study of which 16 (41%) died, giving a cub mortality rate of 20%/year. Cub mortality per pride varied considerably, which suggested an inverse relationship between number of births and cub survival. Table X shows the annual loss of known animals.

TABLE X

Deaths and losses from the study prides in relation to sex and treatment

Category	*n*	1st year	2nd year	3rd year	4th year	% mortality	% annual mortality
Adult males	10	—	1	2	—	30	10
Untreated females	15	2	—	—	—	13	3
MGA implant females	10	2	1	—	—	30	8
Uncaptured controls	3	—	—	—	—	0	0

The highest mortality among females was in the treated animals but no evidence was found to support a causal relationship. It is unlikely that MGA caused mortality in lionesses since no pyometria was found. In summary, 18 adult lions were lost, while 23 cubs survived during the three-year study period; representing a recruitment of five.

Population trend

The study period of three years was short to consider population trend. However, during the study, 54 known lions and lionesses were present, 34 were lost from the prides and 39 cubs were born. The net gain of five animals was not regarded as a significant increase in the number of lions inhabiting the study area.

Along the southern and eastern borders of Etosha, a minimum of 79 lions were shot in 1982, 39 in 1983 and 23 in 1984. The number of lions shot declined by 70% in three years, which suggests a decline in emigration of lions from Etosha.

The ground-census estimate for lions in Etosha was 500 in 1981, 250 in 1984 and 200 in 1987 (Berry, unpubl. data) which likely represents a clear indication of population trend.

It is unlikely that the contraceptive trial was a major factor in the general decline in lion numbers, as contraceptives were used in only four of Etosha's 21 known lion prides. The decline can probably be attributed to natural mechanisms of population control.

Model

Starfield, Furniss & Smuts (1981) suggested that reduced fertility in a lion population would result in a sustained decline. The control lionesses produced 28 cubs from 420 potentially fertile months, while the MGA-implanted lionesses produced no offspring from 197 months of treatment (Table VII).

A simple arithmetical calculation of $197 \times 28/420$ suggests that a further 13 cubs could have been born in the study period if contraceptives had not been administered, furthermore only five (40%) of these cubs were likely to survive two years.

Knowing that contraceptives reduce fertility in lions, by varying the numbers of lionesses treated and using demographic data obtained in Etosha, a simple theoretical model was created to predict the effect of contraception on population dynamics. This purposely simplified model was based on 35 known untreated lionesses of various ages. When corrected for onset of fertility, emigration and mortality, these lionesses would not have been able to conceive for the full three years, i.e. 35 (individuals) $\times$ 12 (months) $\times$ 3 (years) = 1,260 potentially fertile months, but for 780

TABLE XI

Predictive model for 35 lionesses intended to provide a management guide for future control of lion numbers with contraception

No. treated	Fertile months	Cubs	Total loss	Net 3-year gain/loss
0	780	52	26+18	+8
10	557	37	19+18	Even
15	446	30	15+18	−3
20	334	22	11+18	−7
25	222	15	8+18	−11

effective fertile months in the three-year period. Based on field observations, a cub mortality of 50% was assumed (approximately midway between the 41% for the study period and the two-year survival rate of 61%), plus a fixed mortality of 18 sub-adult and adult lions over the three years.

If none of the lionesses had been treated, they would likely have produced 52 cubs (39 actual births + 13 expected from treated lionesses) from 780 fertile months. Adult mortality was assumed to approximate 6/year. Half the cubs (26) were expected to die, giving a cub recruitment of 26/year. If 10 animals were treated, the remainder would have been fertile for ($25 \times 780/35 =$) 557 months and in this period ($557 \times 52/780 =$) 37 cubs would likely have been born, and so on for various numbers of lionesses treated over the three-year study period as shown in Table XI.

The predictive model suggests that, if no lionesses were treated, an increase of eight lions would result every three years. If, however, 20 out of the 35 lionesses received implants, a net loss of seven lions would occur every three years. A wet cycle or compensatory increase in cub survival could easily render the model invalid. Nevertheless, the major advantage of an implant is that it can be removed in harmony with variable changes in a park's lion population.

Activity and behaviour studies

The study quantified the activities of treated lionesses and compared them with those of the controls. A total of 2,545 resightings of known lions were made which indicated that contraceptive treatment of lionesses in the five prides did not alter pride (social) or individual behaviour. The five prides did not disperse during the study period but were regularly seen around favoured water holes. Pride cohesion, harmony between pride members, and minimal aggression (except when feeding) were a feature in all five prides.

Instantaneous groups scans

Lionesses in prides were scanned routinely between 1982 and 1984, except during the wet season. The day-time scans differentiated between control lionesses (1,694 observations) and MGA-treated lionesses (1,695 observations). The percentage activity derived from pride scans for seven mutually-exclusive activities is shown in Table XII. The preliminary results suggested that there was a significant decrease in walking and hunting by MGA-treated lionesses. The results of Bonferroni analysis (Table XIII), however, demonstrated that hormone treatment does not affect the behaviour of lionesses. The observed frequencies of walking and hunting in MGA-treated lions

TABLE XII

Chi-square tests on the frequency of behaviours (day-time scans) of MGA-treated and control adult lionesses

Behaviour	Frequency		Chi-squares	P
	Controls	MGA-treated		
Resting	1472	1512	1·09	N.S.
Walking	86	59	8·48	$P<0·01$
Drinking	20	13	2·45	N.S.
Hunting	12	5	4·08	$P<0·05$
Feeding	78	88	1·28	N.S.
Socializing	16	16	0·0	N.S.
Threatening	5	2	1·28	N.S.

TABLE XIII

Simultaneous confidence intervals using the Bonferroni approach for comparison of frequency of behaviour (day-time scans) of MGA-treated and control adult lionesses

Behaviour	Proportions of behaviours		Bonferroni intervals for Pi
	Controls	MGA-treated	
Resting	0·872	0·892	$0·872<P<0·912$
Walking	0·051	0·035	$0·023<P<0·047$
Drinking	0·012	0·008	$0·002<P<0·014$
Hunting	0·005	0·003	$0·000<P<0·007$
Feeding	0·046	0·052	$0·037<P<0·067$
Socializing	0·009	0·009	$0·003<P<0·015$
Threatening	0·003	0·001	$0·000<P<0·003$

fell well within the expected frequencies predicted by the Bonferroni confidence intervals. It is suggested, however, that future studies investigate the locomotor activity and hunting practices of treated lions relative to controls as this may have marked effects on the hunting success of prides.

Focal animal studies

Focal animal data were collected randomly in daylight hours (07:00 h-19:00 h) between 1982 and 1984. Control lionesses were observed for 275,880 seconds (77 hours) and MGA-treated lionesses for 164,700 seconds (46 hours). MGA implants were removed from three lionesses after 22 months and their behaviour was observed for 34,200 seconds (10 hours). The percentage occurrence of 13 mutually-exclusive activities are shown in Table XIV.

Sexual activity following removal of MGA implants was significantly higher ($P<0·01$) than that of either control or MGA-treated lioness groups, which was likely caused by the return to natural hormonal secretion. No other significant differences were found.

TABLE XIV

Percentage activity of adult lionesses as indicated by focal animal studies

Activity	Control	MGA-treated	Implant removed
Resting	84·9	89·5	83·1
Self-grooming	0·5	1·5	1·2
Walking	8·2	5·0	5·8
Running	0·0	0·3	0·0
Drinking	1·0	0·9	1·8
Vocalizing	0·3	0·0	0·3
Hunting	2·5	1·8	0·3
Feeding	2·2	0·6	4·0
Urination and defecation	0·1	0·1	0·6
Social encounters	0·1	0·2	0·0
Threat	0·1	0·0	0·0
Fighting	0·0	0·0	0·0
Sexual	0·1	0·0	2·3

TABLE XV

Comparison of the activity patterns in adult lionesses, using daytime scans and focal animal studies

	Control		MGA-treated		
Activity	Scan	Focal	Scan	Focal	Mean
Resting	86·9	84·9	89·2	89·5	87·6
Self-grooming	—	0·5	—	1·5	—
Walking	5·1	8·2	3·5	5·0	5·4
Running	—	0·0	—	0·3	—
Drinking	1·2	1·0	0·8	0·9	1·0
Vocalizing	0·3	0·3	0·0	0·0	—
Hunting	0·7	2·5	0·3	1·8	1·3
Feeding	4·6	2·2	5·2	0·6	3·1
Urination and defecation	—	0·1	—	0·1	—
Social encounters	0·9	0·1	0·9	0·2	—
Threat	0·3	0·1	0·1	0·0	—
Fighting	—	0·0	—	0·0	—
Sexual	0·0	0·1	0·0	0·0	—

TABLE XVI

Comparison of percentage activity in free-ranging lionesses from different areas of Africa

Activity	Schaller (1972)	Rudnai (1979)	Present study
Feeding	3	2·09	2·25
Grooming	—	1·22	0·5
Walking	8·3	2·95	8·23
Hunting	—	1·39	2·45
Playing	—	0·12	—
Other	2·7	0·52	1·77
Resting	87·0	91·71	84·9

The methods employed in focal animal studies and group scans were independent, and therefore their reliability can be inferred by direct comparison. The scans and focal studies measured different numbers and categories of activities but no obvious differences occurred between equivalent categories (Table XV).

No statistical analysis was applied to the data reported in Table XVI. No obvious gross differences were present, except that the group scan animals appeared to hunt less and feed more than focal animals. The difference was probably due to chance and was likely counterbalanced, since the behaviours are equivalent. Otherwise, the activity patterns for the lionesses during daytime were equivalent whether determined by the focal animal method or by the group scans. The treated lionesses appeared to function as integrated members of their prides.

Discussion

The use of progesterone contraceptives in free-ranging lions is described for the first time. The method is known to be a safe and efficient form of contraception in caged lions (Seal *et al.*, 1978). The essence of the trial at Etosha was to compare the effect of contraceptive treatment in a group of wild, free-ranging lionesses with a like group of controls. The major objective was to show that if the method was practical for free-ranging lions, it would provide for an effective alternative to culling lions in national parks.

Age and body mass

The mortality of pride lions/lionesses in Etosha was 8% annually; but the longevity of males was greater than that of females. The oldest lion had an estimated age of 14 years while the oldest lioness was aged 9 years. In the Kruger National Park, maximum ecological longevity is estimated at 14 years for lionesses, nine years for male pride lions and 16 years for nomadic males (Smuts, Hanks & Whyte, 1978*b*).

At Kruger, all pride lions were expelled from their pride by the age of nine years, but this did not occur at Etosha, where lions died of old age in their own prides. The mean age of pride males at death was 12 years. The security of the pride likely contributed to the increased lifespan of the male lions in Etosha.

Behaviour and social organization

Two lion prides in Serengeti have been studied continuously for 16 years (Schaller, 1972; Bertram, 1975; Bygott, Bertram & Hanby, 1979; Packer & Pusey, 1982). The composition of pride females was influenced by deaths and the emigration/retention of sub-adult lionesses in the pride, but all sub-adult males left the pride to become nomadic (Schaller, 1972). Young nomadic lions often formed coalitions of genetically related individuals and sometimes prides with a group of lionesses; the larger the male coalition the longer they were likely to hold tenure over a pride (Bygott *et al.*, 1979). Packer & Pusey (1982) observed male coalitions taking over prides on 11 occasions; older cubs were driven out of the pride, younger cubs were killed, and pregnant lionesses lost their cubs soon after cubbing. The females returned to oestrus and mated with the immigrant males, which caused synchronous oestrus (Schaller, 1972; Smuts *et al.*, 1978*b*). This pattern has not been observed at Etosha. Male tenure of a pride in the Kruger National Park

seldom lasts more than two years and expelled lions become nomadic, with poor prospects of survival (Smuts *et al.*, 1978*b*).

Schaller (1972) found that pride home ranges in the Serengeti varied between 30 to 400 km^2, which is comparable with the pride areas in Etosha of 81 to 207 km^2, although some individually-known lions were resighted over an area of 662 km^2 during the study. The location of lion pride territories in Etosha are determined by the availability of permanent water; if water is not available, the pride disperses to a new area (Orford, 1987).

Pride composition

The mean number of adults recorded in each pride was 1·5 male lions and 4·8 lionesses. Schaller (1972) reported that pride male numbers vary from two to four ($\bar{x} = 2{\cdot}1$, $n = 14$) and lioness numbers from two to eleven ($\bar{x} = 5{\cdot}8$, $n = 14$) which approximates pride size of Etosha.

The total number of adult lions in the study area remained remarkably constant during the study period. Seven male pride lions were marked and none of these was displaced from its pride; three died, however, and were succeeded by three other lions. Three pride lionesses died and three disappeared but nine of ten sub-adult females branded became pride lionesses.

The sex ratio of lions is usually equal at birth but the number of males subsequently declines in free-ranging animals due to intra-sexual competition for pride tenure and mating rights. The sex ratio of all adults captured was 1·0♂:1·5♀. Two large random samples of adult animals from the Serengeti and the Kruger National Park were found to have a ratio of approximately 1♂:2♀. The difference is probably explained by the emigration of marked male lions (Brand, 1963; Schaller, 1972; Smuts *et al.*, 1978*b*).

At Etosha, the number of adult (nomadic and pride) lions and lionesses remained constant each year. The sex ratio of the pride animals was 1♂:3♀ but the ratio of local nomadic males (which were seen regularly in the study area) plus pride males was 1♂:7♀.

The proportion of nomadic males (20%) in the Etosha population was very similar to that found in the Serengeti (Schaller, 1972). Eight nomadic males were marked initially, of which six died or disappeared, but in the same period six out of eight marked young males became nomadic. Schaller (1972) has seen lionesses mate with males from outside their own pride and it is possible that the nomads at Etosha were involved in reproduction.

Smuts *et al.* (1978*b*) stated that the average tenure of male lions in a pride is two years, but of ten pride lions immobilized here, three died in their prides while five were still in their prides at the end of the study, four having been pride lions for a minimum of four years. Schaller (1972) believes all sub-adult male lions leave the pride of their birth to form nomadic male coalitions. Environmental and demographic parameters influencing social structure appear to operate differently at Etosha than at Serengeti and the Kruger National Park (Packer & Pusey, 1983; Smuts *et al.*, 1978*b*). The low lion density at Etosha may lead to longer pride tenure. The lion density in Etosha approximated one per 45 km^2-90 km^2, which is considerably less than at Serengeti (1 per 8-12 km^2) where most pride take-overs by male coalitions have been observed (Packer & Pusey, 1983).

Contraception

The use of progesterone contraceptives in feral cats and caged lions effectively reduced birth rates, suggesting that similar results could be anticipated in free-ranging lions (MacDonald, 1980; Seal *et al.*, 1975).

No free-ranging lionesses treated with MGA implants became pregnant. Theron (1984) pointed out that the advantages of an implant are fixed sustained hormone release and a rapid return to fertility on removal. In this study, implants prevented pregnancy in lionesses without clinically important changes in mass, condition or steroid hormone levels occurring (Orford, 1987). The effect of progesterone on breast carcinoma in beagle dogs (Briggs, 1980) and the incidence of pyometria in cats (Dow, 1962) is probably overemphasized and certainly no evidence of such pathology occurred in the small sample of lions treated here. Moreover, these complications do not occur in humans on long-acting progesterone contraceptives (Beck, Cowsar & Pope, 1980).

The return to fertility of lionesses on implant removal was confirmed in all three lionesses in Etosha, as well as in more than 100 cages lionesses (Seal *et al.*, 1978), amply demonstrating the reversible nature of the contraceptive implant.

Activity and behaviour

MGA implants prevented pregnancy in free-ranging lionesses, but a most important consideration was the effect they may have had on the behaviour and social organization of lions.

The focal-animal and group-scan methods employed to quantify behaviour gave similar values for control and MGA-treated lionesses, thereby indicating that no deviations occurred in the behaviour of treated lionesses. Treated lionesses continued their various social activities within the prides, such as mutual grooming, hunting and the care of cubs in a harmonious manner.

Group scans showed no differences in behaviour between MGA-treated lionesses and controls. Similarly, focal-animal studies did not reveal any marked difference in activity between the control group, the treated group or following removal of the MGA implant. Sexual activity occurred in 0·1% of the controls, but was not recorded in MGA-treated lionesses. It may have occurred outside of the sample period for it has been observed in cages lions with MGA implants (Seal *et al.*, 1975).

Schaller (1972) measured the activity of free-ranging lions in the Serengeti, while Rudnai (1979) carried out a more detailed study of the activity rhythm of free-ranging lions in the Nairobi National Park. The results from those studies have been compared with those for focal animal activity studies at Etosha (Table XVI).

Treated and control lionesses had a similar pattern of activity to each other at Etosha and to lionesses elsewhere in Africa, except for those observed by Rudnai (1979) that walked for only 2·95% of the time they were observed. Quantified activity measurements are of value in determining the behavioural effects of a drug. Here, the testing of hormonal contraceptives was carried out under the exacting environmental pressures which are encountered by free-ranging lions. Less stringent conditions, e.g. when lions are restrained in safari parks/cages, remove a large source of the social interactions necessary for survival in wild lions.

Social matings

The majority of matings in free-ranging or caged lions do not result in pregnancy (Schaller, 1972; Seal *et al.*, 1975). The production of a litter of cubs requires 1,500 copulations and has been described as 'mating inefficiency' (Bertram, 1975). Reduced pressure on natural selection for successful matings likely occurred to facilitate pride cohesion and cooperative hunting.

Three lionesses mated just prior to capture and the vaginal smears of two of these were found to contain spermatozoa. A further four lionesses were not observed to copulate but sperms were

present in their vaginal smears. None of these lionesses became pregnant in the following two years. The presence of spermatozoa in the vaginae of lionesses without conception supports the hypothesis that lion matings are often unsuccessful.

Eaton (1978), speculating on why some felids copulate so much, proposed a model for the evolution of copulation frequency. He believes that high copulation frequency is adaptive in lions so females can evaluate male vigour. Frequent copulation deceives and gratifies males and is part of the system of related females sharing a male territory. It appears that sexual receptiveness out of oestrus in lions is a correlate of sociality in large sexually dimorphic carnivores.

Conclusions

The explosive increase in man's population has resulted in unrelenting destruction of the lion and its habitat. The proclamation of African national parks created a haven for the last free-ranging lions and in these areas their numbers have increased considerably.

The concept of using hormones to control numbers of free-ranging animals in national parks has only been considered for a few species. Contraception is perhaps aesthetically more attractive than culling, causes less disruption of biological processes, is reversible and prevents the loss of genetic reserves in a species. The behaviour and activity rhythm of control and treated Etosha lions was comparable to those observed elsewhere in Africa (Schaller, 1972; Rudnai, 1979; Smuts, 1982).

A danger of culling programmes stems from the difficulty of predicting population trend. Data are not yet available which allow precise conclusions to be drawn as to whether or when lion populations will fluctuate. If a culling programme had been initiated in 1980 at Etosha, the results might well have been disastrous for the predator-prey system and in particular to the lion population. The unexpected decline in the lion population illustrates the value of a reversible mechanism for controlling population density. The final and irrefutable argument in favour of contraceptives is that the treated lionesses which have had implants removed have produced cubs.

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