

MALE TAKEOVERS AND FEMALE REPRODUCTIVE PARAMETERS: A SIMULATION OF OESTROUS SYNCHRONY IN LIONS (*PANTHERA LEO*)

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Abstract. The takeover of a pride of lions by a new coalition of adult males synchronizes the reproductive states of the females because the females' dependent offspring either die or are evicted at the takeover. Using data on the consequences of male takeovers on female reproductive parameters in wild lions, but without allowing for any interaction between females, we simulated the reproductive histories of 100 female lions for the first 2 years after a male takeover and then cast them into simulated prides of varying sizes. The simulations produced levels of oestrous synchrony similar to those observed in prides of wild lions.

Lions do not breed seasonally, but females living in the same pride often come into oestrus synchronously (Schaller 1972; Bertram 1975). Bertram showed that synchrony of oestrus was greater within the same pride than between adjacent prides, and therefore suggested that females might come into oestrus in response to within-pride mechanisms such as the oestrus of their pridemates. Such an interaction between oestrous females is well documented in laboratory rats and hamsters, and appears to be pheromonally based (McClintock 1978; Handelman et al. 1980). However, the existence of interactions of this kind in wild lions has yet to be proved. In this paper we provide evidence that male takeovers induce oestrous synchrony by synchronizing the reproductive state of females in the same pride.

At a takeover, incoming males either attack and kill or otherwise cause the deaths of small cubs and evict larger cubs (Schaller 1972; Bertram 1975; Packer & Pusey in press; also see below) and this has a strong effect on the incidence of oestrus within a pride. Females with dependent offspring do not usually resume sexual activity until their cubs reach 1.5-2 years of age (Schaller 1972; Bertram 1975). However, females quickly resume mating activity once they have lost their dependent offspring, with the result that the synchronous loss of cubs at a takeover is followed by a synchronous resumption of mating activity.

In this paper we examine the effects of male takeovers on the reproduction of individual females, describe female reproductive cycles, and present a simulation in which a male takeover acts separately on each female yet produces a

level of oestrous synchrony among females equal to that observed in the wild.

Methods

Between July 1978 and May 1981 we studied 15 prides of lions including the population in the Serengeti National Park first described by Schaller (1972) and all the lions resident on the floor of the Ngorongoro Crater. Two of these prides have been studied continuously since 1966 and the rest since 1974 (Bertram 1975; Hanby & Bygott 1979). Each day we censused all the individuals in as many prides as possible and recorded the reproductive condition and mating activity of each female.

Since lions of the same pride are often widely dispersed and individuals are often difficult to locate, no one female was ever observed for more than ten consecutive days and there were often gaps in observations of up to several months. Therefore we restricted our analyses to the most complete data for each parameter of female reproduction.

Results

A. Female Reproductive Parameters

The reproductive patterns of females were examined in order to test for the effects of male takeovers on oestrous synchrony.

1. Cub mortality at male takeovers. Bertram (1975) found a significant increase in mortality of cubs less than 24 months old in the first 4 months after a male takeover. In our study, there were 11 male takeovers and in 10 of these we knew their immediate consequences on cub survival (Packer & Pusey 1983). In one of these 10 takeovers the 'new' males were returning to

their natal pride. Two females (one of which was a full sibling of all three males) were pregnant at the time of the takeover, subsequently gave birth, and kept their cubs. This was the only case in which small cubs survived a takeover.

In the remaining nine cases a total of nine females were pregnant at the time of the takeover. Seven were known to give birth to live young, all of which disappeared within 58 days; the other two females were not seen at the time of parturition but had lost their cubs by 32 days after giving birth. Ten females had cubs of 4 months old or less at the time of the takeover and all these cubs disappeared within 26 days of the takeover. Seven females had cubs aged 13–20 months and these cubs were all evicted. As a consequence five of the seven mothers were separated from their cubs a median of 30 days (range 16–102) after the takeover. Each of the other two mothers accompanied their evicted cubs to a new area and returned to the pride after 265 days (range 260–270 days).

2. Oestrus and inter-oestrus interval. We define days of oestrus as days with mating. Figure 1A shows the cumulative distribution of the durations of 43 oestrous periods for which we had the most complete data. The median duration of oestrus was 4 days (range 2–6 days), which agrees well with results from previous field studies (Schaller 1972; Rudnai 1973; Bertram 1975).

After seven of 39 oestrous periods for which the end of oestrus was observed, the females resumed mating for a brief period (≤ 1 day) after a gap of 1–4 days. We refer to these episodes as 'secondary oestrus'. These are distinguished from 'primary oestrus' periods because of their predictably short duration and because the mating partner often showed little or no possessive behaviour (in contrast to the behaviour of a partner during primary oestrus) (Packer & Pusey 1983). The cumulative distribution of gap lengths between primary and secondary oestrus is given in Figure 1B.

Data on inter-oestrus intervals (gaps between midpoints of primary oestrous periods) are more difficult to collect since gaps between sightings of any one female can be long enough for whole oestrous periods to be missed. We estimate that the median inter-oestrus interval was 16 days ($N = 32$, range 10–31 days) (see Fig. 1B). In making this estimate we excluded all intervals that were more than double the average interval when these included gaps in observation long enough to have included an entire oestrus period.

3. Pregnancy. We have no reliable data on gestation length in wild populations. Cooper (1942) reported an average of 109.7 days ($N = 51$, range 100–114 days) in captive lions.

4. Interval from loss of cubs to next birth. Once a female lost her cubs, she resumed sexual activity within a few days or weeks (also see Schaller 1972), then cycled regularly until she

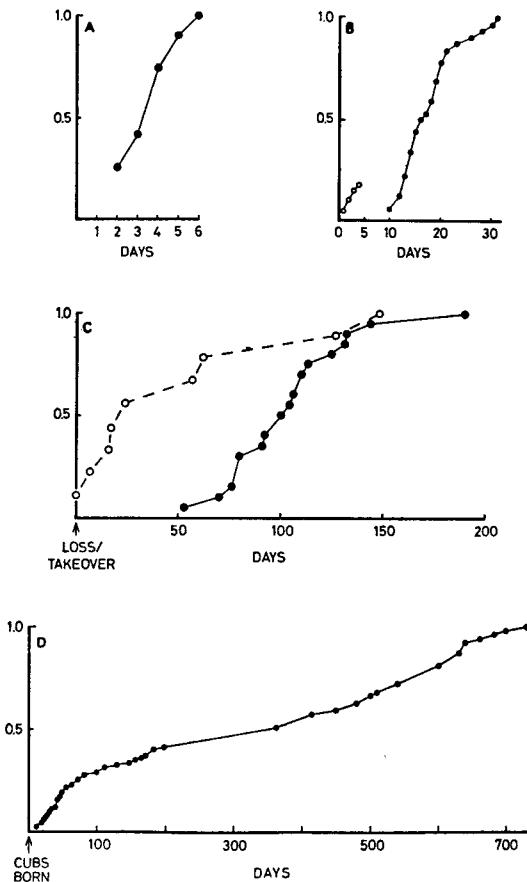


Fig. 1. The cumulative distributions for (A) the duration of oestrus, (B) the interval between the midpoints of successive primary oestrous periods (closed circles) and the gap length from the end of primary oestrus to the beginning of secondary oestrus (open circles) (plotted as the probability of a 1-day secondary oestrus occurring after the respective gap lengths), (C) the proportion of females to have conceived by respective intervals after takeover (closed circles) or loss of unweaned cubs at other times (open circles), and (D) the proportion of females that had lost all the cubs of their litter or whose cubs had become independent by the respective intervals after parturition, excluding females whose cubs were lost at a male takeover.

conceived. However, the period from loss of cubs to next conception depended on whether the female's previous cubs died at a takeover or under other circumstances (Packer & Pusey 1983). Females that lost their unweaned cubs at a takeover took a median of 134 days to conceive ($N = 5$, range 100–164 days) whereas females that lost their unweaned cubs under other circumstances took a median of only 24 days ($N = 9$, range 0–144 days). Therefore, females that had lost their cubs at a takeover took an estimated 6–9 cycles to conceive, whereas females that lost their cubs at other times took only 1–2 cycles.

Figure 1C compares the cumulative distribution of conceptions in females during the first 200 days after a takeover (regardless of their reproductive state at the takeover) ($N = 21$, range 53–190 days), with the distribution of conceptions in females that lost unweaned cubs at other times. Females of all reproductive states are included because the delay in conceiving after a takeover was independent of the female's reproductive state at the time of the takeover: females that were without cubs at the takeover took as long to conceive after a takeover as females with dependent cubs and pregnant females (Mann–Whitney U test, $P > 0.10$).

Only one female conceived in the first 70 days after a takeover, but after 70 days females began to conceive at random (i.e. the distribution of conceptions over the period of 70–200 days after a takeover does not deviate from a truncated negative exponential distribution (Kolmogorov–Smirnov test, $P > 0.10$)). Synchrony of pregnancy after a takeover was no greater within the same pride than it was between different prides (Kruskal–Wallis test for heterogeneity between prides, $P > 0.10$).

5. Postpartum amenorrhoea. Females with dependent offspring almost never showed oestrous periods: out of 147 oestrous periods observed, only three involved pregnant females, two involved lactating females, and one involved a female that had recently stopped lactating but otherwise remained anoestrous for another 1.5 years. After giving birth, females usually did not resume sexual activity until their cubs either died or were evicted, or until the cubs reached about 2 years of age. Lactation ceases at about 5–9 months (Schaller 1972; Packer & Pusey, unpublished data), so postpartum amenorrhoea is not contingent on lactation as it is in primates (Knodel 1977; Altmann et al. 1978).

Cub mortality is very high in lions and more than 50% of cubs die before reaching 1 year of age (Schaller 1972; Hanby & Bygott 1979). Consequently, the distribution of the duration of postpartum amenorrhoea across females (Fig. 1D) reflects cub mortality for about the first 200 days after birth and reflects the approximate age of independence thereafter. Data from all births were included in these calculations except where amenorrhoea was terminated by a male takeover (median = 345 days, $N = 83$, range 12–710 days).

B. Simulation of Oestrous Synchrony

Using the findings from the preceding analyses, we simulated reproductive histories for 100 artificial female lions over the first 2 years after a male takeover in which cubs are killed or evicted by the incoming males. Two years is the average male tenure length (Bygott et al. 1979). In the simulations the history of each artificial female followed a sequence determined by a different series of random numbers (n_i, n_{i+1}, n_{i+2} , etc.) given by a 0–1 random number generator.

The initial reproductive state of each female was assigned according to the duration typical for each state. These states were (a) oestrus (4 days), (b) inter-oestrus (16 days), (c) pregnant (110 days), and (d) postpartum amenorrhoea (345 days). Therefore a female would begin in oestrus if the generator produced a number (n_i) that was less than 0.0084 (which is $4/(4+16+110+345)$); in inter-oestrus if $0.0084 \leq n_i < 0.0421 = (4+16)/475$; pregnant if $0.0421 \leq n_i < 0.2737 = (4+16+110)/475$; and in postpartum amenorrhoea if $0.2737 \leq n_i < 1.0000$.

Females were then made to respond to the takeover according to the changes observed in the wild. Thus a pregnant female would be made to give birth after (n_{i+1}) (110) days, then lose her cubs in (n_{i+2}) (58) days, and then take (n_{i+3}) (31) days to come into oestrus; a female with cubs less than 1 year old would be made to lose her cubs in (n_{i+1}) (26) days; and so on.

Transitions between subsequent states followed the pattern observed in wild lions and durations of each state were assigned according to the cumulative distributions shown in Fig. 1. For example, if a female was in oestrus, she would remain in oestrus for 2 days if $n_{i+j} < 0.26$, for 3 days if $0.26 \leq n_{i+j} < 0.42$, etc. Thus a female would be in oestrus for 2–6 consecutive days, and conceive with a probability appropriate for the time that had elapsed since the takeover

(i.e. virtually zero until about 70 days after the takeover and increasing continuously thereafter (Fig. 1C)). If she did not conceive she would have an 18% chance of a 'secondary oestrus' after a 1-4 day gap, then have an 8-31 day interval from the midpoint of her previous primary oestrus to the midpoint of her next primary oestrus. She would then be in oestrus again, and continue cycling until she conceived. After conception she would be pregnant for 110 days (gestation length was considered to be invariant), and then be in postpartum amenorrhoea for 12-710 days. The female would not come into oestrus during pregnancy or postpartum amenorrhoea. If she lost her cubs before the 2 years had elapsed, she would come into oestrus in 1-31 days if she had been lactating at the time of their loss (within 200 days of birth) or would come into oestrus immediately if she was no longer lactating (since the end of amenorrhoea for non-lactating females was defined as the first oestrus after the

previous birth). She would then conceive with a probability appropriate for the number of days after the loss of these cubs (which is different from the probability of conception after a takeover (Fig. 1C)).

Note that for each female we assumed that (a) the duration of one state is independent of the duration of the previous state, so that, for example, a female with a very long oestrus could have an inter-oestrus interval of any allowable duration, (b) there are no consistent individual differences in durations of each state, and (c) the probability of conceiving changes with the number of days after a takeover, or loss of cubs at other times, not with the number of oestrous periods. The few available data did not show significant individual differences (assumption b) but there were insufficient data to test the validity of either of the other two assumptions (a and c).

Ninety nine of the 100 females were randomly cast into nine 'prides' of 11 females each (Fig. 2)

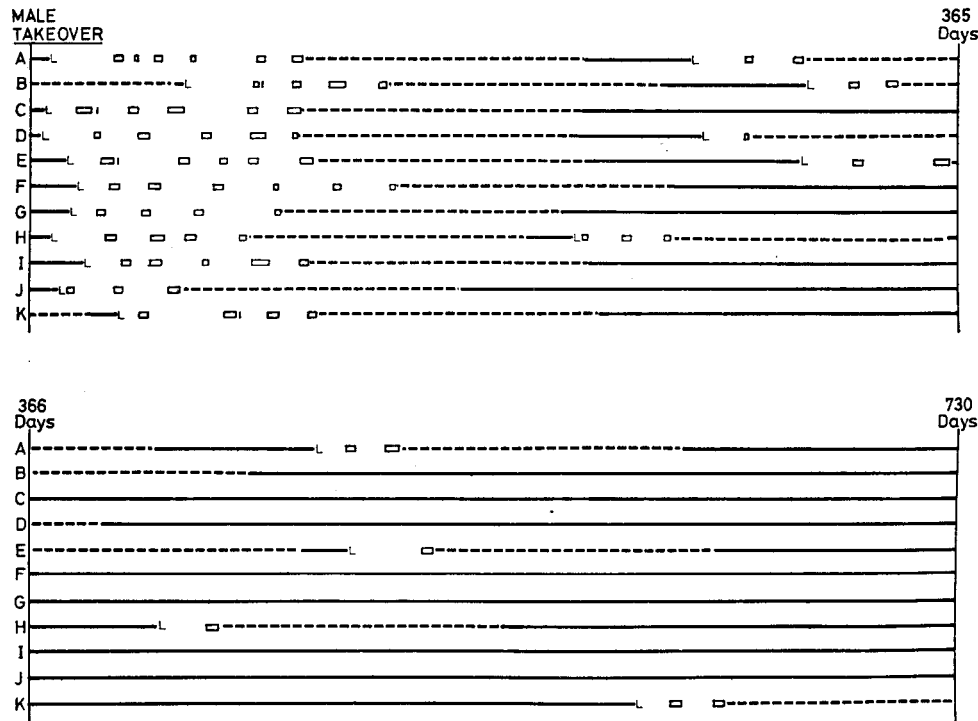


Fig. 2. The reproductive pattern for the first 2 years after a male takeover of a simulated pride comprising 11 simulated females (A through K). Boxes and vertical lines represent primary and secondary oestrous periods, solid lines denote postpartum amenorrhoea, and dotted lines denote pregnancy. 'L's mark the loss of a female's previous litter.

and then recast into 11 prides of nine females each. Each pride was sampled over a 2-day period every 10 days to find the number of females in oestrus during each period. In Table I the results of these censuses are compared with those from the two real lion prides studied by Bertram (1975). Bertram used a similar sampling method, but considered all females seen in oestrus over a 4-day period to be synchronous. It is rarely possible to locate all the females of a wild pride within a 4-day period, and we estimate on the average Bertram found about half of the females during each period. We therefore sampled all females over a shorter period in the simulated prides to compensate for the higher 'visibility' of the simulated females.

Discussion

The simulations produced a level of oestrous synchrony remarkably similar to that observed in the real pride of 11 females (Table Ia), but a generally higher level than that in the real pride of nine (Table Ib). Levels of oestrous synchrony that we observed during our own field study were no greater than those found in simulated prides of comparable size.

Because the simulation began with each female in a reproductive state that was independent of the states of the other females in her 'pride' and because the duration of each oestrus and inter-oestrous interval was determined at random without any reference to the oestrus of the other females in that pride, the number of

Table I. Comparisons of Oestrous Synchrony in Simulated Prides and Wild Prides

Table Ia										
No. of females in oestrus at once	Nine simulated prides of 11 females:									Masai pride
	1	2	3	4	5	6	7	8	9	
0	60	50	50	52	51	55	53	57	53	43
1	7	13	16	14	14	9	10	7	13	5
2	3	8	3	2	7	5	7	6	4	8
3	3	1	3	4	0	2	2	2	2	3
4	0	1	1	1	0	1	0	1	1	1
5	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	1	1	1	0	0	0
Mean	0.30	0.49	0.48	0.47	0.47	0.48	0.49	0.40	0.42	0.57
Variance	0.54	0.72	0.74	0.80	0.85	1.13	1.02	0.73	0.68	1.03
Var/mean	1.79	1.45	1.55	1.71	1.83	2.35	2.06	1.85	1.63	1.81

Table Ib												
No. of females in oestrus at once	Eleven simulated prides of nine females:											Seronera pride
	1	2	3	4	5	6	7	8	9	10	11	
0	54	60	58	58	51	61	55	56	53	56	57	54
1	11	10	8	8	16	7	12	9	15	10	8	17
2	6	1	3	4	5	3	4	6	3	6	5	5
3	1	1	3	2	1	2	1	1	2	0	3	1
4	0	1	1	1	0	0	1	1	0	0	0	0
5	1	0	0	0	0	0	0	0	0	1	0	0
Mean	0.43	0.26	0.37	0.36	0.40	0.26	0.37	0.38	0.37	0.37	0.37	0.39
Variance	0.76	0.47	0.73	0.67	0.46	0.44	0.59	0.65	0.48	0.67	0.62	0.45
Var/mean	1.78	1.79	1.96	1.85	1.15	1.69	1.59	1.70	1.30	1.81	1.67	1.15

Each part of Table I shows the number of sampling periods with 0-6 females in oestrus in that period. The first columns show the results of sampling the simulated prides over 730 days, and the far right column shows the data presented by Bertram (1975) for the two wild prides of 11 and nine females respectively. The variance/mean ratio gives an indication of the degree of clumping in the data, and hence of oestrous synchrony: the greater the ratio the greater the synchrony. In Table Ia the average variance/mean ratio for the simulations was 1.80 and 4 of the 9 simulated prides showed greater oestrous synchrony than was observed in the Masai Pride. In Table Ib the average ratio was 1.66 and all but one of the simulated prides showed greater oestrous synchrony than the Seronera Pride. Note that the variance/mean values for Bertram's data are not the same as he originally reported because his variance values were erroneously high.

females in oestrus on the same day in each pride is dependent only on the number of cycling females in that pride on that day. Thus the number of females in oestrus is highest shortly after the synchronous loss of cubs at a takeover (Fig. 3). Thereafter, most females are pregnant at once, and then because of high cub mortality in the first few months of life a few females may cycle at the same time (Fig. 3). Similar to the simulations, our field data showed that most synchronous oestrous periods occurred in the first 3 months after a takeover.

The fact that the simulations produced oestrous synchrony comparable to or greater than that observed in the wild prides suggests that the consequences of male takeovers alone can account for oestrous synchrony in wild lions without invoking any pheromonal interaction between oestrous females. However, the results of the simulation do not rule out the possibility that such an interaction might occur. For example, certain combinations of females within a pride may cycle synchronously, as has been found in closely associated humans (McClintock 1971); but such data are exceedingly difficult to collect in lions where sightings are so irregular. However, if there were a strong interaction of this sort in lions as well as synchrony induced by a male takeover, the levels of oestrous synchrony observed in the wild would be much higher than those produced by the simulations.

Bertram (1975) showed that there was synchrony of births as well as of oestrus within prides, and suggested that whereas the arrival of new males might contribute to birth synchrony (also see Starfield et al. 1981), other factors such as interaction between females must also be in-

involved. However, our data showing that birth synchrony is no greater within prides than between prides, when measured from the time of a takeover, suggest that the timing of births could depend solely on the effects of a takeover on cub survival and female fertility. The constancy across different prides of the delay in fertility after a takeover suggests that females respond to the 'newness' of the new males (Packer & Pusey 1983).

In the simulations we assumed that each of the females would have a reproductive history independent of the other females in her 'pride' except for the fact that they had all experienced a takeover simultaneously. This is probably an oversimplification for the following reasons. First, nutrition affects reproductive condition (Schaller 1972; Rudnai 1973), and because lions feed socially, females of the same pride may show improved or decreased condition at about the same time. Second, there may be residual synchrony from previous takeovers. Third, females with dependent cubs often resist incoming males. If many of the females in a pride have cubs at the same time resistance is sometimes successful (Packer & Pusey 1983). Thus takeovers are infrequent when most females in a pride have 5–12 month old cubs. Fourth, cub mortality may be affected by birth synchrony. Cubs have lower mortality when born synchronously (Bertram 1975), and mothers of single cubs are more likely to abandon them if they are born asynchronously than if they are born at the same time as other cubs in their pride (Rudnai 1973). The first three of these factors would act to synchronize reproductive states further and the fourth would reduce the small rise in numbers of oestrous females at 250–320 days after the takeover shown in Fig. 3.

Bertram (1975) suggested that oestrous synchrony is adaptive since it reduces male–male competition within the pride. By reducing competition among the males of their pride, females would lessen the chances that one of the males might be killed in a fight with his companions and thus prevent a reduction in the size of the coalition. This would be beneficial to the females since the period of time during which a male coalition retains control of a pride depends on the size of the coalition (Bygott et al. 1979), and replacement of one coalition by another results in the loss of the females' cubs.

However, direct observations of lions show that oestrous synchrony does not reduce the incidence of male–male competition. Serious

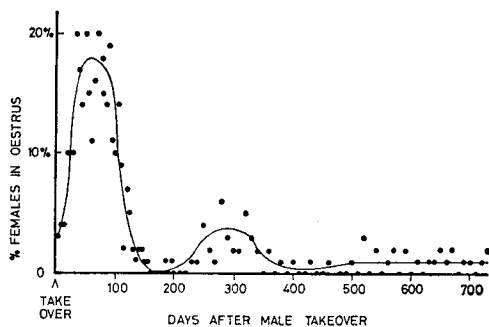


Fig. 3. The percentage of the 100 simulated females that were in oestrus at each elapsed time after a male takeover. The females were sampled on every fifth day for the first 200 days and every tenth day thereafter. Curve fitted by hand.

fight between two consorting males are as common as between a consorting male and a non-consorting male and aggression over oestrous females most commonly results from the efforts of a consorted female to move into close proximity to a second male (Packer & Pusey 1982). Thus oestrous females actually increased levels of male-male aggression within their pride.

Finally, although oestrous synchrony may not be an adaptation by females, a consequence of oestrous synchrony is that it results in a reduction in differential male mating success within a coalition (Trivers 1972; Emlen & Oring 1977) and this reduces the disadvantages to a subordinate male of being in a coalition with bigger or more vigorous companions. In our field study, more than one female was in oestrus at once in 43% of oestrous periods (Packer & Pusey 1982) and this was also true in 39% of fertile oestrous periods ($N = 18$). In a hypothetical coalition of two males where the subordinate could only gain access to a female when his dominant partner was already mating, the subordinate might father as many as $1/2$ (39%) = 20% of all cubs.

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