

ADAPTATIONS OF FEMALE LIONS TO INFANTICIDE
BY INCOMING MALES

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There is increasing evidence that infanticide is widespread among animals (see reviews by Hrdy 1979; Sherman 1981). The killing of young by immigrating males is a common context of infanticide and it appears to occur regularly in several primate species (Hrdy 1979), lions (Bertram 1975), and captive rodents (e.g., Mallory and Brooks 1978). In these species males kill infants of unfamiliar females when they first encounter them, but subsequently are unlikely to kill their own offspring. Infanticide by immigrating males has been viewed as a male reproductive strategy whereby males stop females from investing in the offspring of other males and speed up the return of the females to sexual receptivity (Hrdy 1974; Bertram 1975; Chapman and Hausfater 1979; but see Curtin and Dolhinow 1978; Boggess 1979).

Although infanticide may be advantageous to the infanticidal male, it is clearly disadvantageous to the females in these species, and there is growing interest in mechanisms whereby females may reduce their losses to infanticide. These fall into two major categories. The first consists of behavior of females that prevents males from killing their young. Female lemmings sometimes succeed in aggressively defending their young against unfamiliar males introduced into their cages (Mallory and Brooks 1978). In Hanuman langurs, some females with young successfully avoid the new male by leaving their group in the company of the ousted male (Hrdy 1977). Finally, pregnant female langurs show pseudoestrus and mate with the new male. Subsequently, the new male does not kill the female's offspring even though the infant is not his (Hrdy 1974). Hrdy suggests that by mating with the new male, the pregnant female confuses paternity and thus ensures the survival of her infant.

The second category consists of responses by which the female minimizes her losses when the death of her offspring is inevitable. Several species of rodents show the "Bruce effect" (Bruce 1960), whereby pregnancy is terminated by exposure to new males or their scent. Females may thereby minimize the time and energy invested in offspring that would be killed after birth regardless of the behavior of the female (Labov 1981; Sherman 1981). Female langurs sometimes abandon infants that have been wounded by a new male (Sugiyama 1967).

Although there is considerable interest in this topic, at present most data are either anecdotal or come from laboratory studies. Here we provide further evidence of infanticide by incoming males and increased cub mortality at male takeovers in natural populations of lions (*Panthera leo*). We describe the responses of females to new males and to infanticide according to the categories described above. We also describe two further responses of female lions to male takeovers. Females show a period of infertility and heightened sexual activity in the first few months after a takeover. We show how these responses may reduce the frequency with which females lose offspring to infanticidal males, thus increasing their own lifetime reproductive success.

METHODS AND BACKGROUND

Between July 1978 and May 1981, we studied 15 prides of lions, including the population in the Serengeti National Park, Tanzania, first described by Schaller (1972), and all of 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 and Bygott 1979). Each day we recorded the incidence of wounds and the reproductive condition and mating activity of the females of as many prides as possible. In addition, we collected over 500 h of behavioral data on mating pairs during 2-h watches at dawn and dusk.

Although females usually keep their cubs hidden for the first 4–8 wk, it is obvious when a female has given birth because she exhibits dark rings around her nipples caused by the suckling of her cubs. Furthermore, in late pregnancy, females have enlarged nipples and a conspicuously swollen udder. Therefore, date of parturition can be ascertained even for females whose cubs die in the first few weeks of life. Pregnancy was either inferred retrospectively from date of parturition, or from the appearance of the female.

Lions range over large areas and often conceal themselves in river courses or thick vegetation. In consequence, gaps between observations of any one individual can sometimes be as long as several weeks or months. Thus demographic events such as births and estrous periods could have gone undetected. Therefore, in our analysis of intervals between such events, we excluded those intervals during which there were gaps in observation of sufficient duration to have missed such an event.

Lion Social Organization and Female Reproductive Parameters

Lions in northern Tanzania live in stable social groups ("prides") composed of 2–18 adult females, their dependent offspring, and a coalition of 1–7 adult males (Schaller 1972; Hanby and Bygott 1979; Packer and Pusey 1982). There is competition between male coalitions for groups of females and the successful coalition controls the pride for several months or years before either leaving it spontaneously or being ousted by another coalition. A coalition of males may control several female prides simultaneously, and larger coalitions have longer tenure

than small coalitions (Bygott et al. 1979). Replacement of one male coalition by another is referred to as a "male takeover."

Gestation in lions is about 110 days and mean litter size is 2.3 (Schaller 1972). Females cease lactation when their cubs are 5–8 mo old (Schaller 1972), but do not resume sexual activity until their cubs are about 18 mo old (Bertram 1975; Packer and Pusey 1983). However, females that lose their dependent cubs generally resume sexual activity within days or weeks of the loss (Schaller 1972; Bertram 1975; Packer and Pusey 1983). Lions do not breed seasonally (Schaller 1972; Bertram 1975).

RESULTS AND DISCUSSION

Evidence of Infanticide at Male Takeovers

Infanticide by incoming males has been observed six times in these populations (Packer and Pusey, in press). In addition to these direct observations of incoming males killing cubs, cub mortality has been found to be much higher during male takeovers than at other times. Bertram (1975) showed a significant increase in mortality of cubs less than 2 yr old during the first 3 mo after each of seven male takeovers. Bertram's definition of mortality included the disappearance of cubs too small to have survived on their own.

In our study there were 11 male takeovers and in 10 of these we knew their immediate consequences on cub survival. At these takeovers, a total of nine females were pregnant and subsequently gave birth to live young, and 10 females had cubs less than 4 mo old. Except for the cubs of two females that were closely related to the incoming males, none of these cubs survived to 6 mo of age (Packer and Pusey 1983). In contrast, at least one cub from each of 58 of the 98 litters born more than 6 mo before the end of the tenure of the cubs' fathers survived to the age of 6 mo. The greater chance that all the cubs of a litter less than 6 mo old will die at a male takeover is highly significant ($\chi^2 = 13.20$, $P < .001$). Not included in our calculations are three cases in which a total of four females lost cubs less than 4 mo old during temporary intrusions by alien males into their prides.

At the 10 takeovers, seven females had cubs aged 13 to 20 mo, and all these cubs were evicted. Two of these females accompanied their cubs to new areas (see below).

The only case in our study in which small cubs survived a takeover was also the only case in which the incoming males were close relatives of the cubs. In all other cases the small cubs died and the older cubs were evicted. Because females keep small cubs hidden, it is usually impossible to determine the immediate causes of cub mortality (Packer and Pusey, in press). The only dead cubs that have been found at takeovers have all been killed by the incoming males. Regardless of whether most cubs are killed by males or not, the consequence of a male replacement in the pride is a sharp increase in cub mortality. Male takeovers therefore have a detrimental effect on the fitness of females.

Immediate Responses of Mothers to Incoming Males

1. *Defense of cubs.*—In the case of infanticide that we observed, the mother of the cubs and another adult female vigorously attacked the infanticidal male and

during the fight one of the three cubs was able to escape (Packer and Pusey, in press). We also observed a group of three lactating females successfully defend their cubs against a group of alien males by attacking the males. During this fight all three females were wounded. In two other attempted takeovers, three of five females were wounded and the other two disappeared, leaving surviving cubs with the remaining females. In one, two 4-mo-old cubs also disappeared. The missing females, therefore, are assumed to have died as a result of defending their cubs.

These observations suggest that groups of mothers are sometimes successful in defending their young against intruding males and that they undertake such defensive actions despite considerable risk to themselves. Therefore cooperative defense may be an important aspect of the communal rearing of cubs shown by female lions (Packer and Pusey, in prep.).

2. *Avoidance of new males.*—Older cubs (1.5–2 yr old) are usually evicted by the new males (J. D. Bygott and J. P. Hanby, in prep.) and we observed two cases in which mothers accompanied their older cubs to new areas, thus temporarily becoming nomads. We commonly saw nomadic subadults accompanied by adult females that were old enough to be their mothers, and it is likely that many of these had recently been evicted at male takeovers. In two different prides, mothers of cubs over 12 mo old split off from the rest of their pride and stayed with their cubs in a small part of their former range. This resulted in only part of each pride being taken over and in the prides effectively splitting.

Takeovers rarely occurred in prides in which the majority of cubs were 6–17 mo of age. This may have been because cubs of this age could remain with their mothers while avoiding alien males, thereby forestalling a takeover. Smaller cubs are far less mobile than cubs of these ages, and mothers of older cubs are nearing the end of postpartum amenorrhea (and hence near the end of exclusive investment in these cubs).

3. *Pseudo-estrus.*—Female lions sometimes show estrous behavior and mate during pregnancy (Schaller 1972); this is similar to the “pseudo-estrus” described in langurs by Hrdy (1974). However, estrus during pregnancy is rare in lions (Packer and Pusey 1983) and we only observed two cases in which a pregnant female mated with the new males at a takeover. In one of these, the female subsequently lost her cubs and in the other the female kept them. In the latter case, however, the new males were returning to their natal pride and the female was a full sibling of the males. Usually, cubs born to females that were pregnant at the takeover did not survive.

4. *Spontaneous abortion.*—Because of the low frequency of births that Bertram (1975) recorded in the first few months after a male takeover, he suggested that pregnant females may abort at the takeover. However, his data included one female that did not abort and we knew of nine females that were pregnant at takeovers and gave birth to live young 1–2 mo afterwards. Two additional females were in late pregnancy at the time of the takeover but there were gaps in our observations of them at the estimated time of parturition and they were never observed lactating. Thus we have no evidence that female lions in the second half of pregnancy aborted at a takeover, and we suspect that Bertram may have missed the births of some of these litters because of the very short life expectancy of cubs born in the first few months after a takeover. Because of the difficulties of

detecting pregnancy in its early stages, however, it is impossible to determine whether newly pregnant females abort at takeovers.

5. *Abandonment*.—Because relatively few deaths of cubs are directly observed, Bertram (1975) mentioned the possibility that females neglect their cubs as a result of stress induced by the presence of new males. Neither he nor we have good evidence that this occurred at takeovers. Females, however, have been observed to abandon their cubs in other circumstances (Rudnai 1973; Packer and Pusey, in press).

Effects of Male Takeovers on Female Reproduction and Reproductive Activity

1. *Reduced fertility*.—Most females with dependent offspring lose their cubs within a month of a takeover and females that are pregnant at the takeover lose their cubs shortly after giving birth. Although most females quickly resume sexual activity after the loss of cubs at a takeover and have regular estrous cycles (Packer and Pusey 1983), fertility is lower than at other times. The loss in fertility at a takeover is most apparent when the time from loss of small cubs to next birth for females that were lactating at a takeover is compared with the time from loss of cubs to next birth for lactating females that lost their cubs under other circumstances. Lactating females that lost their cubs at a takeover and then mated with the incoming males gave birth a median of 110 days later than females that lost their unweaned cubs and then mated with the same males that fathered their previous litters (fig. 1). We estimate that females that lost their cubs at a takeover took 6–9 estrous cycles to become pregnant, whereas most females that lost their cubs under other circumstances conceived in the first or second estrous period (Packer and Pusey 1983).

This period of infertility is also apparent in the data of Bertram (1975) which show that no full-term pregnancies were initiated during the first 3.5 mo after a takeover. In our study, females were infertile for a median of 102 days after the takeover irrespective of their reproductive state at the time of the takeover ($n = 20$ females; Packer and Pusey 1983). The duration of this infertility was the same across different prides and once it ended, females became pregnant with a constant probability (Packer and Pusey 1983).

The fact that females in all reproductive states show a similar period of infertility following a takeover suggests that they are reacting in some way to the “newness” of the males and that as females become familiar with the males, they are more likely to become pregnant. Even females that had initially avoided new males would become more familiar with them through olfaction. Males frequently mark the ground and bushes with urine and glandular secretions (Schaller 1972). Females frequently investigate these markings (Rudnai 1979), and each lion's scent may be unique (Brahmachary and Dutta 1981). Table 1 shows that the period of infertility depends more on the time from the takeover than the time from the loss of cubs. Females that kept their previous cubs longest into the tenure of the new males became pregnant most quickly after the cubs were finally lost or left the pride. These findings suggest that the period of infertility is not a specific response to the loss of the cubs, but rather a general response to the “newness” of the males.

FEMALES MATE WITH SAME MALES x—x OR NEW MALES o—o

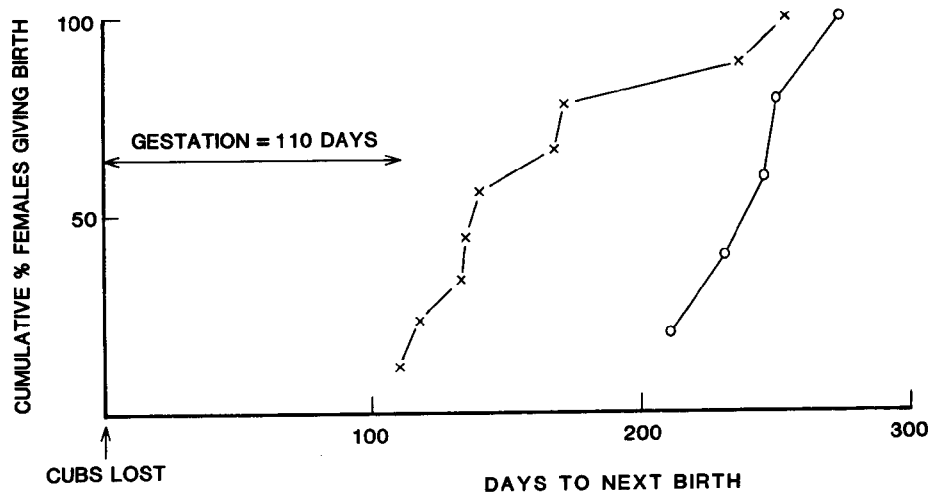


FIG. 1.—Interval from loss of unweaned cubs to next birth when females mated with males that fathered the previous cubs (median interval = 134 days), and when females mated with incoming males (median = 244 days). The difference is statistically significant ($n_1 = 9$, $n_2 = 5$, $U = 6$, $P < .05$, two-tailed Mann-Whitney U test). The intervals from loss of cubs to next conception can be estimated by subtracting gestation length from day of birth. There was no significant difference between the two groups of females in the age at which their cubs died ($U = 21.5$, $P > .50$).

2. *Heightened sexual activity.*—Although the fertility of females was reduced in the first months after a takeover, they showed heightened sexual activity when mating with the new males. First, although the copulation frequency of females with new males was the same as with males that had fathered their previous cubs, females initiated more copulations when mating with the new males (fig. 2).

Second, females sought more partners when mating with new males. During a typical estrous period, one or more males consort with the female. The first male that encounters a potentially estrous female may guard her for several days before she finally comes into estrus. They then mate for an average of three days. Throughout the consortship the male periodically sniffs the female and her urine, and presumably detects changes in the female's hormone levels indicative of ovulation or the waning of estrus (Schmidt et al. 1979). Toward the end of the consortship they cease to mate but the male may continue to guard the female for one more day. After leaving her, he does not mate with that female again for at least 10 days. Because such males can resume mating with another female directly after leaving the previous female, and because males show significantly higher copulation rates when consorting simultaneously with two females than when consorting with only one female (3.48 copulations per h per female vs. 2.16 per h; $T = 0$, $n = 6$ males sampled with both 1 and 2 females, $P < .05$, two-tailed

TABLE 1

EFFECTS OF A MALE TAKEOVER ON FEMALE REPRODUCTION (Each line represents a different female)

| Reproductive State of Each Female at Takeover | (A) No. of Days from Takeover to Loss of Cubs | (B) No. of Days from Loss of Cubs to Next Pregnancy | (C) No. of Days from Takeover to Next Pregnancy |
|---|--|--|--|
| Lactating | 0 | 144 | 144 |
| Lactating | 0 | 125 | 125 |
| Lactating | 0 | 92 | 92 |
| Lactating | 0 | 91 | 91 |
| Not lactating, has cubs | 0 | 76 | 76 |
| Not lactating, has cubs | 0 | 53 | 53 |
| Pregnant | 23 | 56 | 79 |
| Lactating | 26 | 164 | 190 |
| Not lactating, has cubs | 28 | 42 | 70 |
| Not lactating, has cubs | 29 | 50 | 79 |
| Pregnant | 62 | 38 | 100 |
| Not lactating, has cubs | 102 | 30 | 132 |
| Pregnant | 103 | 7 | 110 |
| No cubs, not pregnant | ... | ... | 113 |
| No cubs, not pregnant | ... | ... | 106 |
| No cubs, not pregnant | ... | ... | 100 |
| No cubs, not pregnant | ... | ... | 79 |

NOTE.—The interval from loss of cubs to the beginning of a full-term pregnancy (B) decreased significantly as the length of time females kept their previous cubs after a takeover (A) increased ($r_s = -0.763$, $n = 13$, $P < .01$). Females without cubs at the takeover took as long to become pregnant after a takeover as did females that lost their cubs at a takeover (C) ($n_1 = 4$, $n_2 = 13$, $U = 23.5$, $P > .50$).

Wilcoxon test), it is unlikely that the male abandons a female because he is exhausted.

Males of the same coalition sometimes fight over access to individual estrous females (Packer and Pusey 1982) and fights occasionally result in a change of mating partners. However, a more common context of change in partner is when the female resumes mating with another male a few minutes, hours, or days after the initial consortship has ceased. The subsequent male is usually from the same male coalition as the first male but is occasionally from a different coalition. Subsequent males differed from first males in their consorting behavior. Subsequent males never guarded prior to mating ($n = 9$) whereas first males guarded in 67% of consortships ($n_2 = 6$, $U = 9$, $P < .05$, two-tailed), and subsequent males only mated for one day ($n_1 = 9$, $n_2 = 9$, $U = 0$, $P < .001$). The indifference of the first male to the female at the end of their consortship, and the characteristically short durations of consortships with subsequent males, suggest that subsequent consortships served more of a social function than a reproductive one. However, biochemical data are required to determine if this behavior resulted in mixed paternity of a litter (Hanken and Sherman 1981).

Females were significantly more likely to move to subsequent males in the first few months after a takeover (17 of 17 estrous periods in which the end of the first male's consortship was observed) than when mating with males that had fathered their previous litters (3 of 6, $P < .03$, two-tailed Fisher test).

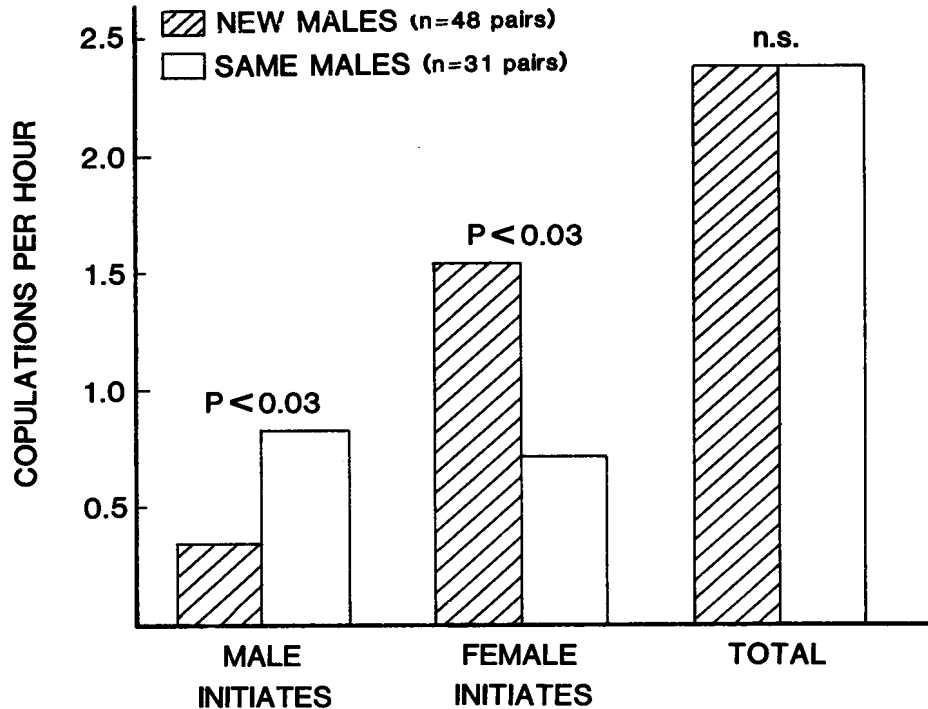


FIG. 2.—The number of copulations with ejaculation per h when females mated with new males or with males that fathered their previous cubs. Females initiated mating by “walking sinuously past” the male (Schaller 1972) or by presenting to him. Males initiated by licking or sniffing the female, pushing her down, or mounting her before she made any movement toward him. As well as copulations clearly initiated by the female or the male, total copulation rates include cases in which mating was initiated in a more ambiguous manner and cases in which initiation was not clearly observed. Ejaculation could be inferred from a vocalization by the male (Schaller 1972) which only occurred with intromission and rhythmic spasms of the male’s genitals and tail.

Adaptive Significance of Heightened Sexual Activity and Temporary Infertility

The high levels of sexual activity and low fertility of female lions have been the source of considerable speculation (Schaller 1972; Bertram 1975, 1976; Eaton 1978). Our results show that this “mating inefficiency” is virtually restricted to the first few months after a male takeover, since females that resume sexual activity at other times conceive very rapidly. Our results also indicate that “mating inefficiency” may depend more on the duration of exposure of females to new males than on the loss of cubs that occurs after the takeover. There is evidence from post-mortem examinations of female lions that most infertile cycles are anovulatory (Smuts et al. 1978), but females can ovulate even in the absence of males (Schmidt et al. 1979). Therefore the phenomenon of temporary infertility is likely to be regulated by the female.

Any factor that reduces fertility or increases interbirth interval must have some selective advantage since, all else being equal, females with greater fertility would

be expected to have more descendants than females of lower reproductive output. Hrdy (1979) suggested that females could "penalize" infanticidal males by delaying reproduction after the loss of their offspring, thus reducing the advantage of infanticide to the male. She also pointed out that although this may have advantages to the species in potentially eradicating infanticide, it would not be advantageous to individual females.

However, the pattern of high sexual activity and temporary infertility after a male takeover could be advantageous to individual females in several ways. These include increasing "paternity uncertainty" (Hrdy 1979) or ensuring birth synchrony (Bertram 1975). Here we consider a third possibility. We suggest that increased sexual activity, combined with temporary infertility after a takeover, may be an adaptation by which females incite competition between different male coalitions (see Cox and Le Boeuf 1977). The result of the increased competition is that the coalition that becomes resident is also one that can protect the females from a subsequent takeover at least long enough for them to rear their next set of cubs.

The duration of male tenure is of extreme importance to the reproductive success of females. A young lion is almost completely dependent on its mother for acquisition of food until it is 1.5–2 yr old (Schaller 1972). Adding the gestation length of 3.5 mo and the infertile period of 3.5 mo, a female needs to be protected from male harassment of her cubs for at least 25 mo if she is ever to raise any offspring.

The tenure length of different male coalitions varies dramatically, and the most important variable in determining the duration of tenure is the size of the male coalition. Bygott et al. (1979) showed that most coalitions of one or two males have tenure for less than 25 mo, almost all coalitions of three or more males have tenure for more than 25 mo, and groups of four to six often have tenure for over 46.5 mo with the result that females in their prides could rear two successive sets of cubs. Therefore, females would be more likely to rear cubs to adulthood if their pride were defended by as large a male coalition as was available.

After a takeover, most females show regular estrous periods for several months and there are more estrous females present in a pride at this time than at any other time (Packer and Pusey 1983). There is evidence that the heightened sexual activity of females after a takeover attracted males to their pride range, and that their pride was consequently taken over by a larger coalition. During the period of infertility, females often mated with males of several different coalitions. We observed five cases in which males of more than one coalition mated with the pride in the first 100 days after the departure of the previous male coalition. In all five, the larger coalition (each comprising at least 3 males) eventually became resident.

Some male takeovers resulted from the forcible eviction of the resident coalition by a new coalition. Other takeovers occurred after the resident coalition had abandoned their pride. In the latter case it would be especially likely that the first males that encountered the pride would be members of small coalitions. Coalitions of nomadic adult males were regularly seen passing through pride ranges and 92.5% of these groups were singletons or pairs ($n = 40$). In either case, by

attracting a number of coalitions but having a period of infertility, females would increase the chances that the largest coalition in the area would find them before they became pregnant.

The costs and possible benefits to a female of temporary infertility are presented below based on the following simplified assumptions. Over a female's lifetime, her pride is controlled by a number of small coalitions (1 or 2 males) and a number of large coalitions (3 or more males). If a coalition stays with her until her offspring reach the minimum age of independence (18 mo), the cubs survive; otherwise no cubs survive. Cub mortality only occurs at a takeover. A female whose cubs survive to 18 mo mates, thereafter, with males from a new coalition. If the cubs do not survive, she mates with a new coalition immediately after the departure of the previous males. A female follows one of two strategies. She can either become pregnant as soon as she mates with the new males, or she is infertile for 3.5 mo.

Under these assumptions, the proportion of litters reared successfully (L) by a female that immediately becomes pregnant will be equal to the probability ($c_{\geq 3}$) of a large male coalition remaining with her pride for the required period ($i = 18 \text{ mo} + 3.5 \text{ mo}$ gestation), multiplied by the proportion of coalitions that reside in her pride that are large coalitions (p); plus the probability ($c_{\leq 2}$) of a small coalition remaining until i , multiplied by the proportion of resident coalitions that are small coalitions ($1-p$). Thus,

$$L = c_{\geq 3} p + c_{\leq 2} (1-p).$$

For a female that is infertile for d mo, the proportion of litters reared successfully (L^*) is as above, except that fewer coalitions can remain for $i + d$ mo (hence, $c_{\geq 3}^* \leq c_{\geq 3}$, and $c_{\leq 2}^* \leq c_{\leq 2}$). However, by being infertile, a female has a different probability of gaining a large coalition in her pride (p^*). Thus,

$$L^* = c_{\geq 3}^* p^* + c_{\leq 2}^* (1-p^*).$$

The number of litters a female has in her lifetime is the female's reproductive life expectancy (e) divided by the average duration of her reproductive sequences. Reproductive sequences are either the intervals from a takeover until the cubs reach independence (i or $i + d$) or until the cubs die at the next takeover. The latter interval is equal to the average tenure length of coalitions that fail to remain in the pride long enough for the cubs to reach 18 mo (f or f^*). The average duration of female's reproductive sequences will be somewhere between i and f or $i + d$ and f^* , depending on the proportion of intervals that are successful (L or L^*).

Thus, the lifetime reproductive success of a female that becomes pregnant as soon as she mates with new males will be:

$$nL \frac{e}{iL + f(1 - L)},$$

whereas the lifetime reproductive success of a female that is temporarily infertile after a takeover will be:

$$nL^* \frac{e}{(i + d)L^* + f^*(1 - L^*)}.$$

Each variable and its estimated value (as taken from Schaller 1972; Bertram 1975; Bygott et al. 1979) are summarized below:

- n = 2.3 = average litter size;
- e = 144 mo = reproductive life expectancy;
- i = 21.5 mo = interval from takeover until cubs reach independence in the absence of a delay (18 mo + 3.5 mo gestation);
- d = 3.5 mo = average period of infertility after a takeover;
- f = 16 mo = average length of tenure if less than i ;
- f^* = 17.5 mo = average length of tenure if less than $i + d$;
- $c_{\leq 2}$ = 0.333 = proportion of coalitions of ≤ 2 males that hold tenure for periods greater than i ;
- $c_{\geq 3}$ = 0.923 = proportion of coalitions of ≥ 3 males that hold tenure for periods greater than i ;
- $c_{\leq 2}^*$ = 0.083 = proportion of coalitions of ≤ 2 males that hold tenure for periods greater than $i + d$;
- $c_{\geq 3}^*$ = 0.923 = proportion of coalitions of ≥ 3 males that hold tenure for periods greater than $i + d$;
- p = probability that the new coalition contains ≥ 3 males if the female became pregnant immediately;
- p^* = probability that the new coalition contains ≥ 3 males if the female is infertile for d mo.

We can estimate p^* from our own data on the proportion of female groups that were held by coalitions of different sizes (see Packer and Pusey 1982). In the 15 prides, the pride was held by a large coalition in 23 of 28 cases, thus because all females had an infertile period $p^* = 23/28 = .821$. However, we cannot estimate p . We lack good data on the appearance of male coalitions of different sizes at the time that females are first subject to a takeover. A lower limit of p would be .075 since this is the proportion of nomadic male coalitions of three or more males. However, large coalitions are better able than small ones to evict resident coalitions and are more likely to be resident in several prides at once. Thus p is probably considerably greater than .075, but because not all takeovers result from evictions, p is also probably well below .821.

With the above values, a female that shows temporary infertility will have a higher lifetime reproductive success than a female that does not if $p < .542$. Thus, temporary infertility after a takeover will be advantageous if it increases a female's chances of gaining a large coalition by 30%.

This model greatly underestimates the advantages to a female of being controlled by a large coalition. Large coalitions often keep tenure with the same set of females for periods over 46.5 mo and thus females might rear two litters per coalition (and females become pregnant immediately if mating with the same males that fathered their previous litter [fig. 1]). Also, much cub mortality occurs under circumstances other than a male takeover, so that if a female was with a small coalition and lost her cubs in the middle of their tenure, she would be even less likely to rear a subsequent set than if she was with a large coalition. Further-

more, females are sometimes wounded in encounters with new males, so that females subjected to higher rates of male turnover may not have as long a reproductive life expectancy.

Finally, the dichotomy between two and three males is an oversimplification since it does not allow for the greater tenure lengths of coalitions of four or more males than those of trios. Further, this dichotomy is only relevant to the current conditions in the Serengeti and Ngorongoro Crater (see Hanby and Bygott 1979). In earlier years, few coalitions of three or more males were found in the Serengeti and Schaller (1972) emphasized the difference in success between single males and pairs. Therefore, a female should try to gain as large a coalition as is available, not one of a particular size.

SUMMARY

Female lions with cubs show various direct responses to immigrating males, including defense of their cubs or avoidance of the new males. Despite these responses, male replacement in the females' pride results in considerable cub mortality. Those females that remain in the pride and mate with the new males show low fertility in the first few months after a takeover of their pride. At the same time, however, females show heightened sexual activity, being more active in initiating copulations and seeking a greater number of mating partners. These two factors appear to elicit competition between male coalitions for control of the pride, with the result that larger coalitions eventually become resident. We suggest that this is adaptive because a female needs protection from male harassment of her cubs for over 2 yr in order to rear her cubs successfully, and only large male coalitions are likely to remain in a pride for more than 2 yr. We present a simple model that specifies one set of conditions under which a female will improve her lifetime reproductive success by showing temporary periods of infertility, but attracting a larger coalition.

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LITERATURE CITED

- Bertram, B. C. R. 1975. Social factors influencing reproduction in lions. *J. Zool. Lond.* 177:463-482.
———. 1976. Kin selection in lions and evolution. Pages 281-301 in P. P. G. Bateson and R. A. Hinde, eds. *Growing points in ethology*. Cambridge University Press, Cambridge.
Boggess, J. 1979. Troop male membership changes and infant killing in langurs (*Presbytis entellus*). *Folia Primatol.* 32:65-107.

- Brahmachary, R. L., and J. Dutta. 1981. On the pheromones of tigers: experiments and theory. *Am. Nat.* 118:561–567.
- Bruce, H. M. 1960. A block to pregnancy in the mouse caused by the proximity of strange males. *J. Reprod. Fertil.* 1:96–103.
- Bygott, J. D., B. C. R. Bertram, and J. P. Hanby. 1979. Male lions in large coalitions gain reproductive advantages. *Nature* 282:839–841.
- Chapman, M., and G. Hausfater. 1979. The reproductive consequences of infanticide in langurs: a mathematical model. *Behav. Ecol. Sociobiol.* 5:227–240.
- Cox, C. R., and B. J. Le Boeuf. 1977. Female incitation of male competition: a mechanism of mate selection. *Am. Nat.* 111:317–335.
- Curtin, R., and P. Dolhinow. 1978. Primate social behavior in a changing world. *Am. Sci.* 66:468–475.
- Eaton, R. L. 1978. Why some felids copulate so much. A model for the evolution of copulation frequency. *Carnivore* 1:42–51.
- Hanby, J. P., and J. D. Bygott. 1979. Population changes in lions and other predators. Pages 249–262 in A. R. E. Sinclair and M. Norton-Griffiths, eds. *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago.
- Hanken, J., and P. W. Sherman. 1981. Multiple paternity in Belding's ground squirrel litters. *Science* 212:351–353.
- Hrdy, S. B. 1974. Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol.* 22:19–58.
- . 1977. Infanticide as a primate reproductive strategy. *Am. Sci.* 65:40–49.
- . 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.* 1:13–40.
- Labov, J. B. 1981. Pregnancy blocking in rodents: adaptive advantages for females. *Am. Nat.* 118:361–371.
- Mallory, F. F., and R. J. Brooks. 1978. Infanticide and other reproductive strategies in the collared lemming, *Dicrostonyx groenlandicus*. *Nature* 273:144–146.
- Packer, C., and A. E. Pusey. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* 296:740–742.
- . 1983. Male takeovers and female reproductive parameters: a simulation of oestrous synchrony in lions (*Panthera leo*). *Anim. Behav.* 31.
- . In press. Infanticide in carnivores. In G. Hausfater and S. B. Hrdy, eds. *Infanticide in animals and man*. Aldine, Hawthorne, New York.
- Rudnai, J. 1973. Reproductive biology of lions (*Panthera leo massaica* Neumann) in Nairobi National Park. *E. Afr. Wildl. J.* 11:241–253.
- . 1979. How lions communicate. *Swara* 2:8–13.
- Schaller, G. B. 1972. *The Serengeti lion*. University of Chicago Press, Chicago.
- Schmidt, A. M., L. A. Nadal, M. J. Schmidt, and N. B. Beamer. 1979. Serum concentrations of oestradiol and progesterone during the normal oestrous cycle and early pregnancy in the lion (*Panthera leo*). *J. Reprod. Fertil.* 57:267–272.
- Sherman, P. W. 1981. Reproductive competition and infanticide in Belding's ground squirrels and other animals. Pages 311–331 in R. D. Alexander and D. W. Tinkle, eds. *Natural selection and social behavior*. Chiron, New York.
- Smuts, G. L., J. Hanks, and I. J. Whyte. 1978. Reproduction and social organization of lions from the Kruger National Park. *Carnivore* 1:17–28.
- Sugiyama, Y. 1967. Social organization of Hanuman langurs. Pages 221–236 in S. A. Altmann, ed. *Social communication among primates*. University of Chicago Press, Chicago.