

# **Infanticide & Parental Care**

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## CHAPTER 12

# INFANTICIDE IN LIONS: CONSEQUENCES AND COUNTERSTRATEGIES

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### INTRODUCTION

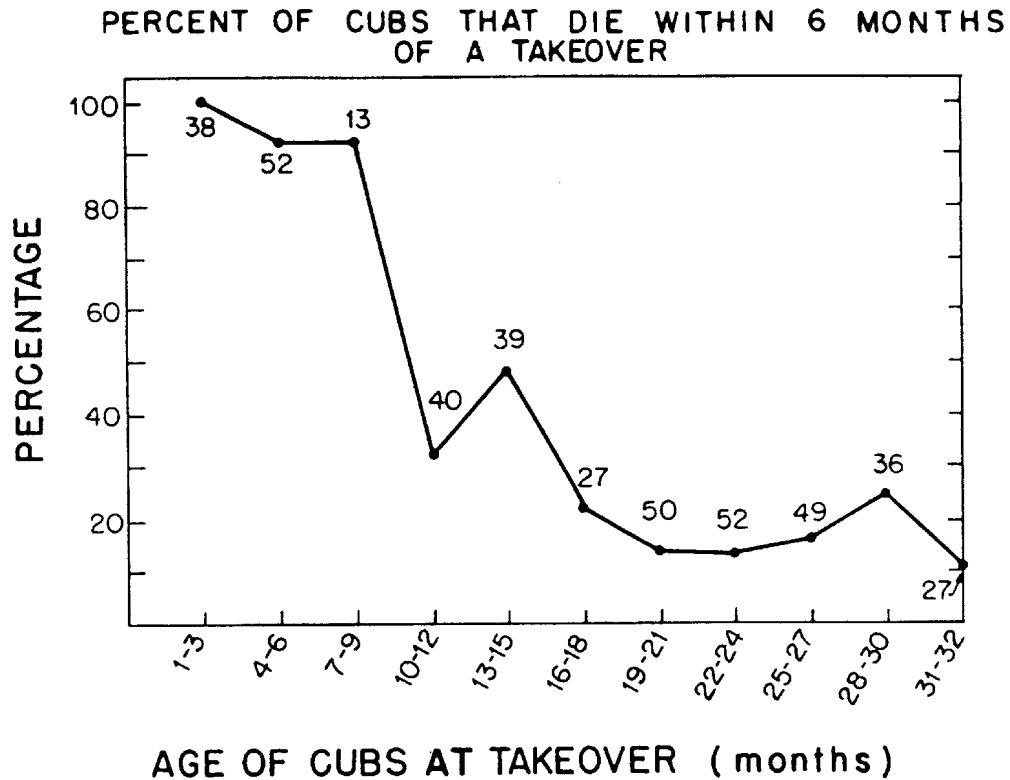
The regular occurrence of infanticide by males that have just entered a new social group or area has now been described in a wide variety of mammals (*e.g.* primates, Hiraiwa Hasegawa, this volume, Sommer, this volume; carnivores, Packer and Pusey, 1984; rodents, Parmigiani, this volume). It has become widely accepted that this behavior gives the males a reproductive advantage because they thereby speed up the females' reproduction and sire their own infants more quickly (see Hrdy, 1974, 1979). However, rigorous evidence in support of this theory (see Boggess, 1984) has only been obtained in a subset of these species (*e.g.* Crockett and Sekulic, 1984; Packer and Pusey, 1984; Sommer, this volume). Perhaps the most extensive data from a single species come from the 24 year study of lions in the Serengeti ecosystem (Schaller, 1972; Bertram, 1975; Packer and Pusey, 1984; Pusey and Packer 1987a, Packer *et al.*, 1988). In this chapter we review data on the incidence of male infanticide in lions, and the advantages that males gain from infanticide. We discuss the counterstrategies that females and males show to infanticide, and show how the threat of male infanticide has had far reaching effects on lion social structure and behavior.

## **STUDY POPULATION AND METHODS**

The study areas consist of a 2000 km<sup>2</sup> area of the Serengeti National Park, and the floor of the Ngorongoro crater, Tanzania. The Serengeti ecosystem covers about 25,000 km<sup>2</sup> and contains a population of 2000–3000 lions. Our Serengeti study area contains about 200 individuals at any one time. The Ngorongoro crater is an extinct volcanic caldera that contains a closed population of about 100 lions. All individuals can be recognized by natural markings (see Pennycuik and Rudnai, 1970). Demographic records of individually identified lions have been maintained continuously on all the lions in the two study areas since 1974 or 1975 (Hanby and Bygott, 1979, Packer *et al.*, 1988), and the descendants of two social groups (“prides”) in the Serengeti have been continuously studied since 1966 (Schaller, 1972; Bertram, 1975). Since 1984 we and our associates have used radio telemetry to locate study prides in the Serengeti. Each resident lion is located about once every two months and its location, group composition and reproductive state are recorded.

## **LION SOCIAL STRUCTURE**

Lions live in permanent social groups, prides, that occupy stable territories (Schaller, 1972, Packer *et al.*, 1988). Prides typically consist of 2–9 adult females (range: 1–18) and their offspring, and a coalition of 2–6 adult males (range: 1–9). All the females in a pride were born in the same natal pride, while all resident males are immigrants (Pusey and Packer, 1987a). DNA-fingerprinting of 78 cubs and their parents has shown that all cubs are fathered by males of the resident coalition (Gilbert *et al.*, 1991). Females start breeding at about 3 years of age and males at about 4 years of age (Packer *et al.*, 1988). Cohorts of cubs are often born to several females in the pride at about the same time. Most subadult females are recruited into the pride but some leave with companions and form a new pride nearby. All subadult males leave their natal pride with other males of their cohort before breeding and most remain together as a coalition (Pusey and Packer, 1987a). Male coalitions compete to take over prides. When a new male coalition takes over a pride, the males evict all the previous resident males, all the subadult males, and the subadult females that are too young to mate (Hanby and Bygott, 1987; Pusey and Packer, 1987a).



**Figure 1** Age-specific cub mortality at takeovers. The percentage of cubs of each age that died within six months of a male takeover (excluding the two cases where males took over their natal pride, see text). Numbers give sample sizes for each age. (Reprinted from Pusey and Packer 1987a).

### **INCIDENCE OF INFANTICIDE BY MALES**

In addition to evicting adult males and subadults, new males cause the death of virtually all small cubs that were present in the pride at the time of the takeover. Bertram (1975) demonstrated that an increase in cub mortality was a regular feature of male replacements and suggested that infanticide accounted for about a quarter of all cub deaths. With more extensive data, we confirmed that virtually all small cubs die after takeovers (Packer and Pusey, 1983a,b, 1984; Pusey and Packer, 1987a) (Figure 1), and calculated that death following male takeovers accounts for 27% of

all cub deaths before the age of 12 months (Packer *et al.*, 1988). Figure 1 does not include two takeovers where males were returning to breed in their natal pride. In these cases the mothers of the cubs were close relatives of the males and the cubs survived (Pusey and Packer, 1987a).

Despite the high incidence of cub deaths following male takeovers in the study areas, the precise cause of death is usually unknown. Dead cubs are likely to be consumed quickly and completely by scavengers, so the chances of finding bodies are low. Because most behavioral observations are made in daylight and lions are primarily active at night, infanticide, when it occurs, is unlikely to be observed. Nevertheless, direct observations of infanticide by males have been made 10 times in the Serengeti (Schaller, 1972; Bertram, 1975; Packer and Pusey, 1984; Packer *et al.*, 1988; Caro and Borgerhoff Mulder, 1989; Matthews and Purdy, pers. comm.) and once in the Masai Mara National Reserve, Kenya, at the northern edge of the Serengeti ecosystem (Jackman and Scott, 1982). Most of these cases involved incidental observations of extra-pride males with wounded or dead cubs (Schaller, 1972; Packer and Pusey, 1984; Caro and Borgerhoff Mulder, 1989).

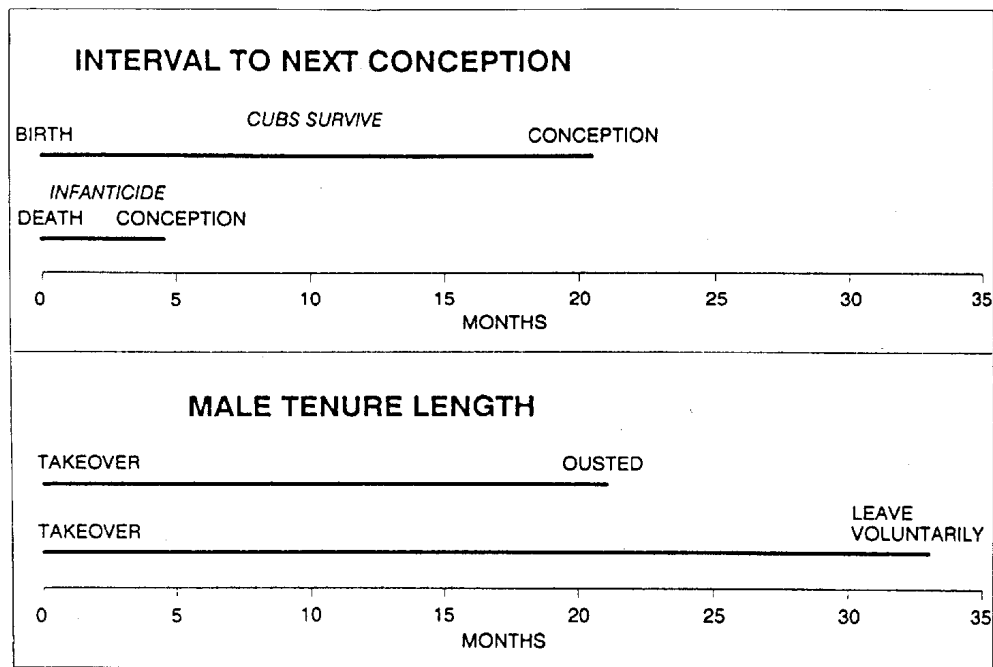
The most complete observation was made by a film team who had set out specifically to film infanticide. After several weeks of monitoring females that we knew were vulnerable to a male takeover, they observed a mother with three cubs aged 3 months being chased by another pride of females. The cubs remained alone in the initial location. A single resident male from the invading pride followed behind the females and stopped in the vicinity of the cubs. After an hour or so, the male noticed the cubs and immediately ran to them, bit the first in the head, dropped it, and then successively picked up and bit each of the remaining two in the abdomen. He then carried one cub to the shade and ate some of it. The killing was over in less than two minutes. During the attacks, each cub screeched, and one rolled on its back with teeth bared and claws extended. The male growled aggressively in a manner that is completely unlike lions' behavior while killing their prey (Matthews and Purdy, pers. comm. see also the film, *Queen of the Beasts, Survival, Anglia*).

Besides losing their cubs by infanticide, it is also possible that females sometimes abandon their cubs at a takeover, or are kept from them by the new males until the cubs die of starvation (Bertram, 1975), but we have no evidence of this (Packer and Pusey, 1984). From our observations of attempted takeovers, females appear more likely to defend their cubs than abandon them (see below).

## ADVANTAGES OF INFANTICIDE TO MALES

How do new males benefit from infanticide? The average tenure of male coalitions in prides is only 24 months before they are ousted or move on voluntarily to new prides (Pusey and Packer, 1987a) (Figure 2). Because cubs are vulnerable to death following takeovers until they are at least 9 months old (Figure 1), males only have a good chance of fathering surviving cubs if they inseminate females soon after they have taken over a pride. After females have given birth to surviving cubs, they do not come into estrus again until their cubs are at least 18 months old; the average interbirth interval between surviving cubs is 24 months (Pusey and Packer, 1987a) (Figure 2). However, if they lose their cubs, females resume mating activity within days or weeks, regardless of season (Schaller, 1972; Bertram, 1975; Packer and Pusey, 1983a,b), and they mate with whichever males are resident in the pride. Females that lose small cubs (less than 4 months of age) at a takeover conceive again about 4.4 months after the loss (Packer and Pusey, 1983b). In calculating the precise gains males make by killing small cubs rather than waiting for females to come into estrus, it is necessary to consider both females whose dependent cubs died in other circumstances than at a takeover and those whose cubs survived, because cub mortality is high even in the absence of takeovers (Packer *et al.*, 1988). Considering all these females, median postpartum amenorrhea in the absence of a takeover is 11.3 months, and conception occurs about one month later (Packer and Pusey, 1983b). Thus, by killing small cubs when they first take over a pride, males sire cubs about 8 months sooner, on average, than they would if they spared the cubs of the previous males (Packer and Pusey, 1984). Besides speeding up the females' reproduction, another possible advantage of infanticide to males is that the cubs will not provide feeding competition for younger cubs fathered by the males. Bertram (1975) provided evidence that the presence of older cubs depressed the survival of younger cubs within the same cohort, but we have not been able to confirm this between successive cohorts (Pusey and Packer, 1987a).

A final advantage that invading males may gain by killing cubs is that they thereby weaken the alliance between females and their resident males, as has also been suggested in red howlers (Crockett and Sekulic, 1984). Mothers of small cubs appear to cooperate with their resident males to keep out new males. Once they have lost their cubs their current maternal investment is terminated and this may terminate their interest in maintaining the status quo.



**Figure 2** The advantages males gain from infanticide. Females do not conceive until a median of 20.3 months after the birth of surviving cubs (Pusey and Packer, 1987a), but they conceive a median of 4.4 months after their cubs die at takeovers (Packer and Pusey, 1983b). Median tenure length is 21 months for male coalitions that are eventually ousted by other coalitions, and 33 months for coalitions that leave voluntarily (Pusey and Packer, 1987a).

## COUNTER-STRATEGIES BY FEMALES

Because infanticide by males is highly detrimental to female reproductive success, females are likely to have evolved counterstrategies that reduce the occurrence or impact of infanticide (reviewed by Hrdy, 1979). Do females behave in ways that reduce the incidence of infanticide? We divide their behavior into immediate responses to alien males, and behavior that may serve to forestall future takeovers.

### 1. Immediate Responses To Alien Males

#### *a. Responses to roars of alien males*

Because they are active at night, the responses of females to extra-pride males are rarely observed. However, in a series of experiments, recorded

male roars were played back to females from loudspeakers placed in their territories. It was thus possible to simulate the presence of various classes of males in the close vicinity of a pride and monitor the responses of females that had cubs (McComb *et al.*, 1993).

Lions of both sexes roar regularly, and males roar more than females (Schaller, 1972). Roaring is mostly nocturnal, and roars can be heard from up to 5 km away; thus roaring lions are usually out of sight from other lions. Male roars were played to females with cubs at times when the resident males of their pride were not present. Roars of two classes of males were played: those of males that were resident in the pride and therefore the fathers of the cubs, and roars of males from elsewhere in the study areas that had not been observed in the vicinity of the females. Females showed a striking difference in response to their own resident males and to alien males (McComb *et al.*, 1993). On hearing the roars of resident males they would usually look up, but remain relaxed, and generally did not move from their initial location. In contrast, when they heard the roars of alien males, all the mothers became highly agitated. They always stood or sat up, usually grimaced or snarled, and stared in the direction of the roars. Sometimes they took a few steps in the direction of the roars in a threatening posture. If several females were present, they usually bunched together. Most females then turned and ran or walked with their cubs in the opposite direction from the roars. Females are thus clearly able to distinguish the roars of resident and alien males, and appear to be aware of the dangers of alien males.

*b. Response to direct encounters with alien males*

Whereas the playback experiments show that females with cubs will often run away from the roars of alien males that are out of sight, what happens when females come face to face with alien males? Over the study period, we have evidence of the outcome of 11 face-to-face encounters between alien males and females with cubs that were unaccompanied by resident males (Packer *et al.*, 1990). In several cases we actually saw females threatening or attacking the males, who fought back; in other cases we found females to be wounded or even dead (two cases) directly after the encounter (Packer and Pusey, 1984). In these encounters, there was a significant effect of female group size on the mortality of cubs (Table I). The cubs of solitary females were significantly more likely to be killed than the cubs of groups of two or more females. Therefore, grouping by females is an effective defensive strategy.



**Table I** Aggressive encounters between females and extra-pride males.

Number of defending females:	some cubs survive	all cubs die
≥ two:	5	0
one:	1	5

p < 0.05, Fisher test

Data collected between 1978 and 1988. Note that no defending males were present in any of these encounters. (Reprinted from Packer *et al.*, 1990).

### *c. Avoidance of alien males*

Although virtually all cubs up to the age of 9 months at the time of a takeover subsequently die, cubs over 10 months old have a better chance of surviving (Figure 1). The mothers of these older cubs sometimes stay with them, and together they successfully avoid the new males by going to new areas or by avoiding the rest of the pride and occupying a peripheral portion of their former range (Packer and Pusey, 1984). Sometimes the females return to the rest of the pride after their cubs have become independent, but sometimes this behavior leads to a permanent pride split (Pusey and Packer, 1987a). Takeovers rarely occur in prides in which the majority of cubs are 6–17 months of age (Packer and Pusey 1983a). This may be because cubs of this age can successfully avoid alien males with their mothers, thereby preventing a takeover. Smaller cubs are much less mobile, and thus more vulnerable to infanticide, while cubs of 18 months or older are better able to survive on their own (Pusey and Packer, 1987a), and their mothers are less likely to accompany them.

## **2. Behavior That Minimizes The Chances Of Future Takeovers and Infanticide**

### *a. Grouping by females*

Because females are better able to defend their cubs from alien males when they are in groups (see above), it might be expected that females would group together when they have cubs. Grouping can occur at two levels: the formation of subgroups within the pride, and the formation of prides of a particular size.

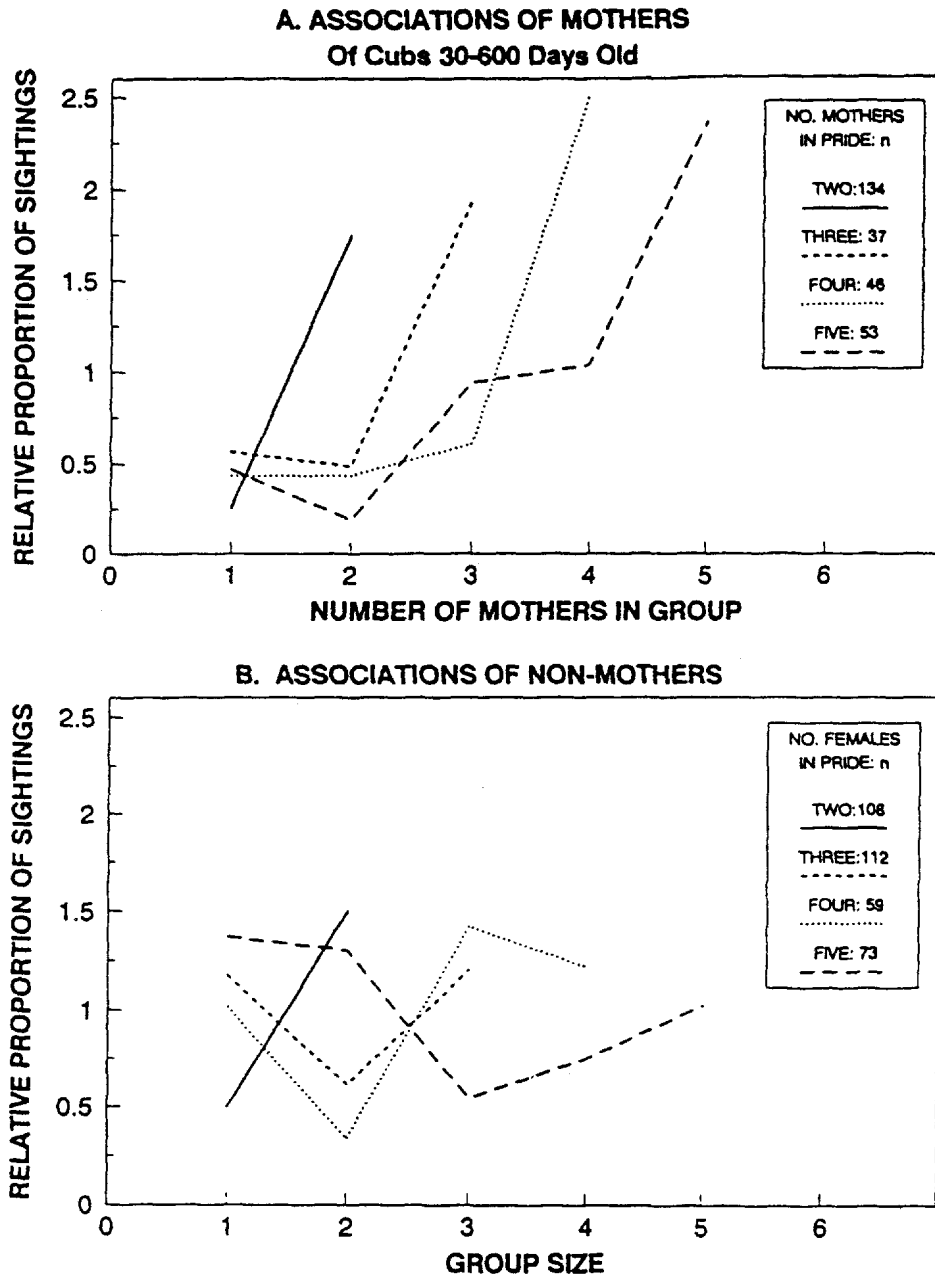
*i. sub-grouping within the pride*

Although prides are permanent social units consisting of several individuals that associate peacefully together, they are fission-fusion units. Individuals within prides spend considerable periods alone and the rest of the time in temporary sub-groups of varying combinations of individuals (Schaller, 1972; Packer, 1986). However, when females have cubs they pool their cubs in a creche with the cubs of other females in the pride, and the mothers associate together almost constantly. Figure 3 shows that when females have cubs they are much more likely to be found together in a group consisting of all the mothers than when they do not have cubs.

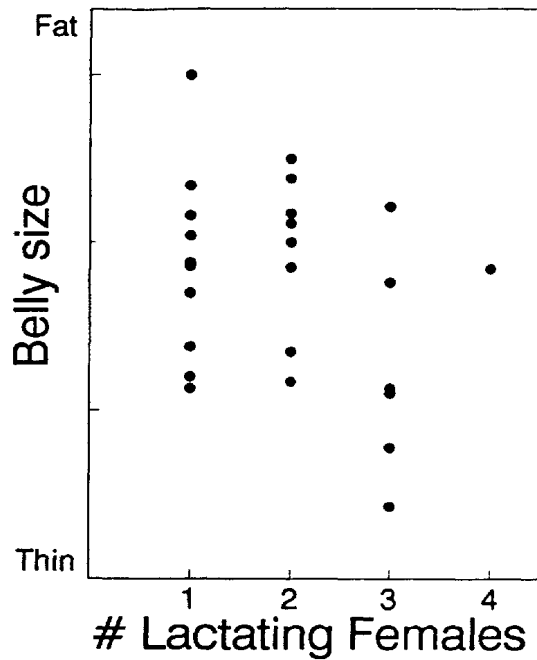
This grouping of females when they have cubs is consistent with female defence of cubs, but other advantages of such grouping must also be considered. It has often been suggested that females group to obtain nutritional advantages from cooperative capture of large prey (reviewed in Packer *et al.*, 1990), but recent data show that solitary females gain as much food as females in any sized group, and that females in moderate sized groups of 2-4 actually suffer nutritionally during periods of food scarcity (Packer *et al.*, 1990). In addition, in an earlier analysis, mothers in groups of three and four were found to have thinner bellies indicative of lower levels of recent food intake than mothers in groups of two or single mothers (Packer, 1986) (Figure 4). We conclude, therefore, that females suffer nutritionally from constant association with other mothers, and that group defence is the best explanation for creche formation by mothers.

*ii. optimal Pride Size*

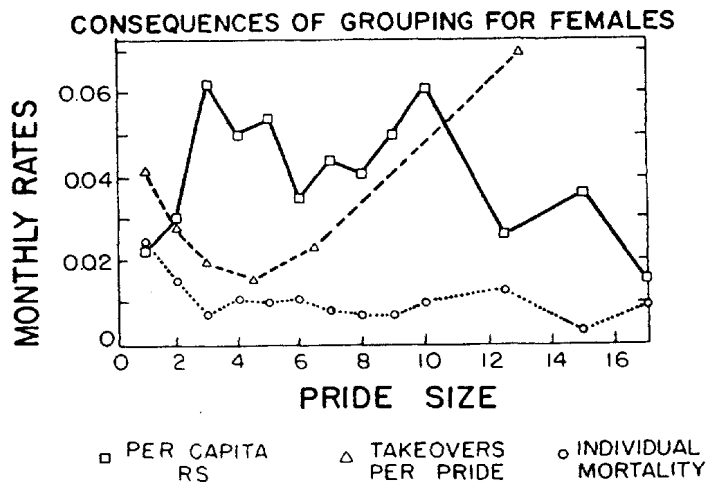
Pride sizes vary from 1–18 adult females, and females living in prides of 3–10 have significantly higher reproductive success than females living in smaller or larger prides (Packer *et al.*, 1988). Two important correlates of these differences are female mortality and the rate of male takeovers (Figure 5). Females in prides of one or two suffer higher mortality than those in larger prides, and takeover rates are significantly lower for prides of 2–7 than smaller or larger prides. The higher mortality rates of females in small prides are probably at least partly due to aggressive encounters with infanticidal males, although aggression from female neighbors may also be important (Packer *et al.*, 1990). Small prides are probably more vulnerable to male takeovers both because solitary or pairs of females are less able to repel males, and because they are less likely to have resident males that are always present to protect them (Packer *et al.*, 1988). The reasons for the high takeover rates of large prides are unknown, but it may be that large prides present a particularly attractive target for males



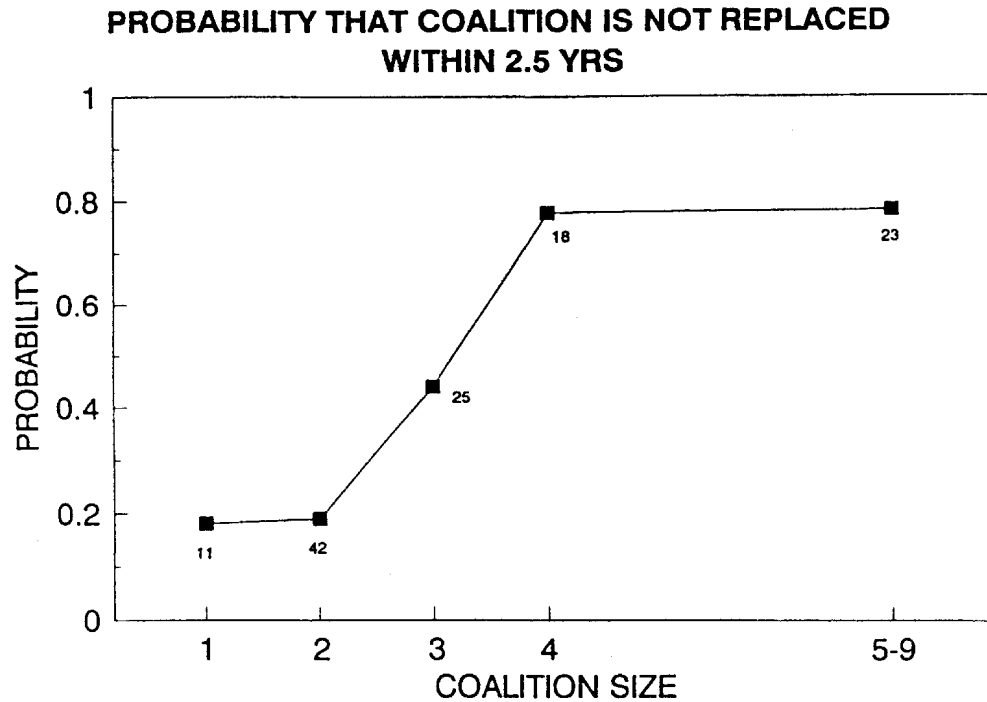
**Figure 3** Relative proportion of sightings in which (A) mothers, and (B) non-mothers, were found in groups of each size. The relative proportion is the observed number of sightings of each group size multiplied by  $x/n$ , where  $x$  is the number of mothers (or non-mothers) in the pride (the number of possible group sizes for mothers in that pride) and  $n$  is the total number of sightings of that sized group. Thus, females found equally often in each group size would have a relative proportion of 1.0 for each, regardless of numbers of mothers in the pride. (Redrawn from Packer, *et al.*, 1990).



**Figure 4** Average belly size of lactating females rearing their cubs alone or communally. Each point is the mean across females of a set when all were lactating simultaneously (minimum of three measurements per female, range = 3–16). Age of cub does not have a significant effect on mother’s average belly size. Singletons and pairs had significantly larger belly sizes than sets of three and four. (Reprinted from Packer, 1986).



**Figure 5** Pride-size-specific reproductive rates, mortality, and frequency of male takeovers. Females in prides of 3–10 have significantly higher reproductive rates than those in smaller prides; mortality rates of solitaries and pairs of females are also significantly higher than those of females in larger prides, and takeover rates are significantly higher for solitary females and females in large prides. (Reprinted from Packer *et al.*, 1988).



**Figure 6** Relationship between male tenure length in prides and male coalition size. For each coalition that gained residence between 1966–1988, the duration of its tenure in each pride was measured. Where the same coalition was resident in more than pride, its tenure in each pride was measured separately. We then calculated the proportion of these tenure lengths for each coalition size that were greater than 2.5 yrs (numbers refer to the number of tenure lengths).

seeking prides to take over. Females can regulate pride size by dispersal of subadult females from the pride, and most females live in prides within the optimal size range (Pusey and Packer, 1987a). We therefore conclude that the risk of infanticide by males is an important factor in the determination of pride size.

*b. Behavior that attracts a large male coalition*

The length of tenure of male coalitions in prides increases with coalition size (Bygott *et al.*, 1979, Packer *et al.*, 1988) (Figure 6). Because their cubs remain vulnerable to infanticide for many months, females will benefit from having a large male coalition resident in their pride so that their cubs can be protected until they are past the vulnerable stage. Certain aspects

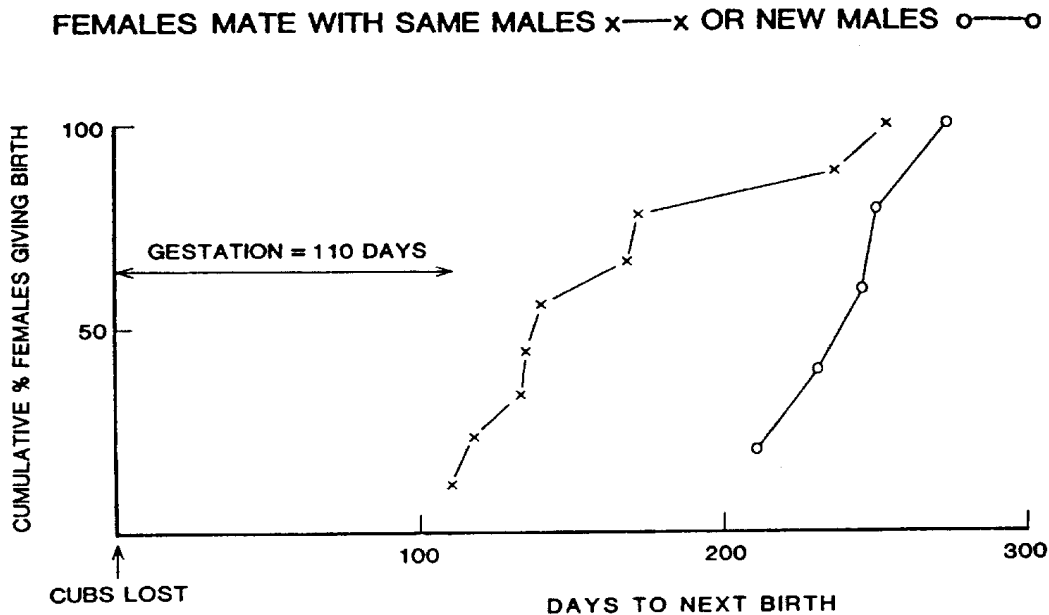
of female reproductive behavior appear to result in the attraction of large male coalitions. Females show a period of heightened sexual activity but reduced fecundity following a takeover.

Females without cubs show regular estrus periods of about 4 days every 16 days (Packer and Pusey, 1983b). Usually a single male forms a consortship with a potentially estrous female during which he stays close to her and guards her from other males. He sniffs her urine frequently throughout the consortship. Males usually guard females for one or two days before they start mating. They then mate about every 20 minutes for two to six days and the male continues to guard the female for a day or more after mating has ceased until he finally loses interest in her. After the first male has stopped guarding her, the female sometimes has a brief consortship with a second male during which mating starts immediately and ceases after one day (Packer and Pusey, 1983a).

Once a new coalition of males has taken over a pride, the females soon start to mate with the males. Their sexual behavior with new males differs from that with familiar males (who fathered their previous cubs) in several ways (Packer and Pusey, 1983a). Although copulation rates are the same with new males and familiar males, females initiate a higher proportion of copulations with new males. They are also more likely to mate with a succession of males during a single estrus in the first few months after a takeover than when mating with males that had fathered their previous litter. These subsequent males are usually from the same coalition as the first male, but occasionally they are from different coalitions.

Despite their active sexual behavior, females show reduced fecundity in the first three months after a takeover (Packer and Pusey, 1983a). This is most obvious when the time from loss of small cubs to next birth for females that were lactating at the time of the 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 lose their cubs at a takeover and then mate with the incoming males give birth a median of 110 days later than females that lose their unweaned cubs then mate with the same males that fathered their previous litters (Figure 7). We estimate that females that lose their cubs at takeovers take 6–9 estrus cycles to become pregnant, whereas most females that lose their cubs under other circumstances conceive in the first or second estrus period (Packer and Pusey, 1983b). This delay in becoming pregnant for the first three months following a takeover is also shown by females that have older, weaned cubs or no cubs at the takeover (Packer and Pusey, 1983a).

The result of this period of reduced fecundity but heightened sexual behavior is that following a takeover there are more estrous females present



**Figure 7** 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 (Packer and Pusey 1983a). The intervals from loss of cubs to next conception can be estimated by subtracting gestation length from day of birth. (Reprinted from Packer and Pusey, 1983a).

in the pride and more sexual behavior taking place than at any other time (Packer and Pusey, 1983b). Frequently, males from more than one coalition are attracted to the pride and mate with the females during this period. The coalitions then compete and the largest coalition eventually becomes resident in the pride (Packer and Pusey, 1983a). Often, prides that have been abandoned by their resident males (Pusey and Packer, 1987a) are first taken over by nomadic coalitions of pairs or single males who have little chance of remaining resident for long (Figure 6). In these circumstances, females will do better not to conceive straight away and suffer another takeover, but rather to attract a larger coalition before conceiving. We therefore suggested that instead of decreasing the reproductive success of females as it appears to do at first sight the reduction in fecundity following a takeover is actually an adaptation which leads to the attraction of the largest coalition in the area. This increases the chances that the

pride is taken over by a coalition that can remain resident long enough to protect the females' subsequent cubs (Packer and Pusey, 1983a). We have calculated that as long as the delay in having cubs increases the chances of attracting a large coalition by 30% it will lead to higher lifetime reproductive success of the females (Packer and Pusey, 1983a).

### **3. Other Possible Female Counterstrategies To Infanticide**

Female langurs that are pregnant at the time of male takeovers sometimes solicit copulations with the new male, and Hrdy (1974) suggested that by doing so they might confuse paternity and persuade the male to spare their young once born, although Sommer (this volume) found no evidence that the infants of pregnant females that mated with the new male were any more likely to be spared than those of pregnant females that did not mate with him. Estrus behavior by pregnant females has only rarely been observed in lions (Schaller, 1972; Packer and Pusey, 1983b) and the cubs of females that are pregnant at takeovers do not usually survive (Packer and Pusey 1983a). So pseudoestrus does not seem to be a counterstrategy to infanticide in lions.

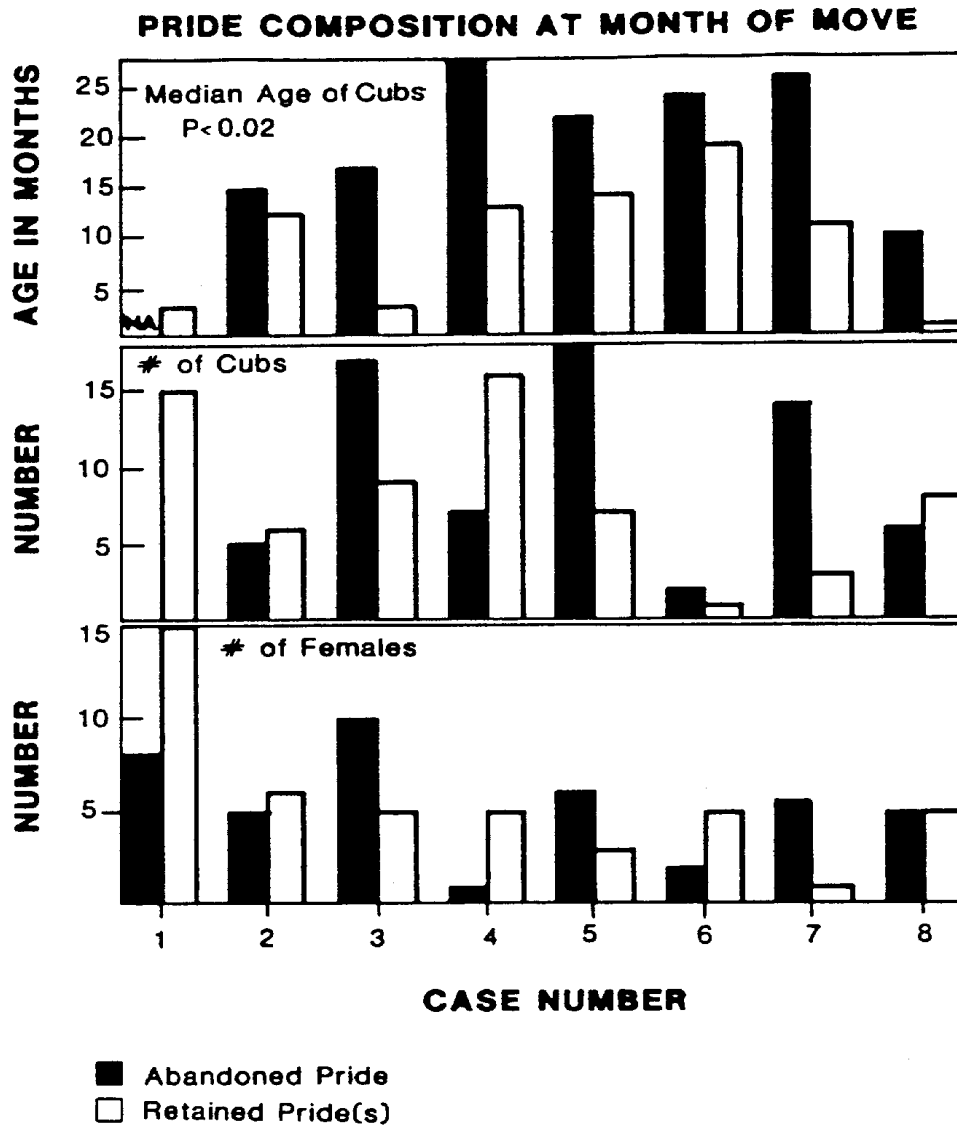
Abortion at takeovers has been described in several species (*e.g.* Bruce, 1960; Berger, 1983; Pereira, 1983; Mori and Dunbar, 1985; Sommer this volume), and in some cases may be a reproductive strategy of females in which they terminate investment in young that would later be killed (Hrdy, 1979; Schwagmeyer, 1979; Labov, 1981). In lions, however, there is no evidence of abortion following takeovers. Bertram (1975) speculated that abortion might take place in lions because he observed few births in the first few months after a takeover. However, we looked for direct evidence of abortion but found that females that were obviously pregnant at the time of the takeover all carried their young to term (Packer and Pusey, 1983a). Because of the difficulties of detecting early pregnancy in lions, we have no means of discovering whether abortion occurs at this stage (Packer and Pusey, 1983a).

## **MALE COUNTERSTRATEGIES**

The increase in deaths due to infanticide at takeovers suggests that the presence of resident males deters infanticide by alien males. Resident males regularly patrol the pride range, roar, and keep out alien males (Schaller, 1972; Bygott *et al.*, 1979).

The voluntary movements of males between prides appear to be sensitive to the vulnerability of their cubs. Large coalitions often make





**Figure 8** The median age of cubs, number of cubs, and number of females in abandoned prides compared to prides that were retained by male coalitions. Coalitions showed a significant tendency to retain prides with younger cubs, but showed no tendency to retain prides with either more cubs or females (Pusey and Packer, 1987a). (Reprinted from Pusey and Packer, 1987a).

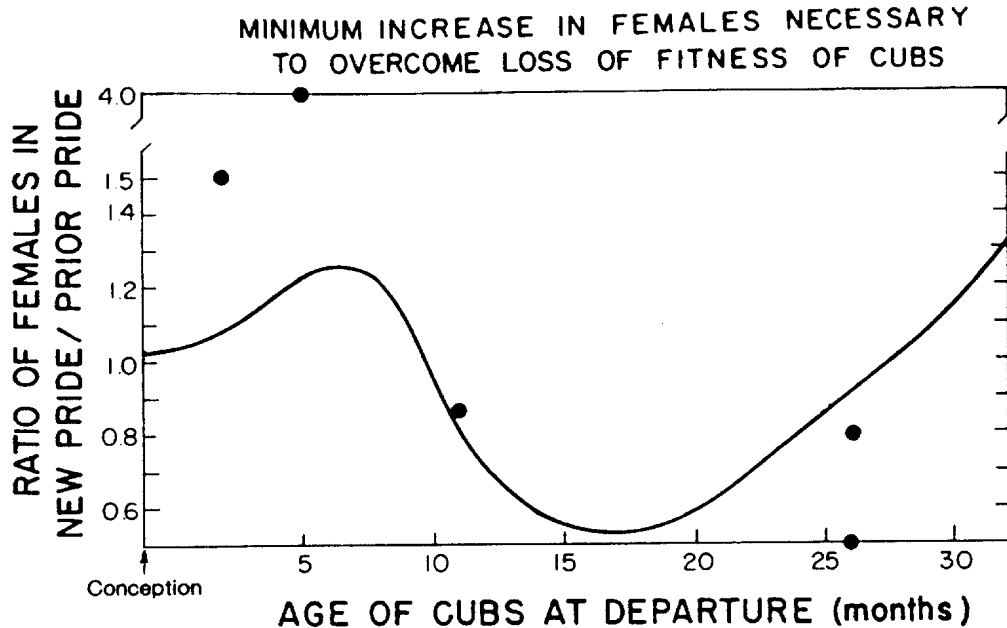
voluntary movements between prides that are not due to eviction (Pusey and Packer, 1987a). These are of three types: (1) a coalition may annex new prides without surrendering previous prides; (2) a coalition that has

been simultaneously resident in more than one pride and is nearing the end of its reproductive lifespan may relinquish one pride while maintaining residence in the other(s); (3) a coalition may completely abandon one pride and become resident in another. In the second case males always maintain residence in the pride that has the youngest and therefore most vulnerable cubs, rather than the pride that has the most females or most cubs (Figure 8). In the third case the movements of males seem to be sensitive both to the vulnerability of cubs, and the number of females in each pride.

We have modelled the conditions under which males should abandon one pride for another, as in (3) above, in order to maximize reproductive success. This model plots a curve of the minimum number of extra females the males should gain at each cub age in order for movement between prides to be profitable. It is based on the survivorship of cubs, their risk of mortality once they have been abandoned, and the interbirth interval of females with surviving cubs (Pusey and Packer, 1987a) (Figure 9). In the first few months after the birth of their cubs, the cubs are very vulnerable and males should only be willing to move on if they thereby gain access to a much greater number of females. When their cubs are 10–28 months, males should be willing to abandon that pride for a new one even if the new pride has fewer females. Cubs of 10–28 months have a good chance of surviving a subsequent takeover (Figure 1), but most of the mothers have not yet resumed mating. After 28 months, almost all the mothers will be breeding again and the males will do well to stay. We only had 5 cases of this type of movement between prides, but the male coalitions with young cubs conformed to the model and moved on to prides with much larger numbers of females. The two coalitions in which the cubs were older moved on to prides with smaller than expected numbers of females. Both these coalitions had maturing daughters in the pride, suggesting that inbreeding avoidance may also be a factor in their movements.

### **EFFECT OF INFANTICIDE ON THE SEX RATIO**

The regularity of male takeovers and subsequent infant death in lions creates a situation in which it may be advantageous for females to modify the sex ratio of their cubs (Packer and Pusey, 1987). Because the reproductive success of individual males depends critically on the number of males in their cohort, while the reproductive success of individual females does not depend on the number of females in their cohort, mothers will benefit by producing more sons than daughters when the chances of these males



**Figure 9** The relative increase in numbers of females necessary to overcome the loss of fitness of cubs at each age. The line represents the minimum ratio of females in a new pride compared to a prior pride that males would have to gain to achieve an overall increase in fitness if the cubs in the previous pride were consequently exposed to a takeover; observed values should all lie above that line (see Pusey and Packer, 1987a for details). The solid dots show the change in numbers of females that five male coalitions experienced when they abandoned one pride for another. (Reprinted from Pusey and Packer, 1987a).

having other male companions in the pride are high. Births are synchronized by male takeovers. Births are more synchronous in the first 300 days following a takeover than afterwards (Packer and Pusey, 1983b), and the sex ratio is indeed significantly biased towards males in the first 300 days after a takeover (Table II). This response by females increases the chances of their sons being able to invade new prides when they mature, thus helping to perpetuate the infanticidal trait.

## DISCUSSION AND CONCLUSIONS

Although infanticide by males has only been observed a few times in lions, it appears to be a deliberate and efficient act, and is probably the

**Table II** Sex of cubs and timing of male takeover

Days since most recent takeover			Proportion	
	Male	Female	Male	Deviation from 0.50
≤ 300	129	96	0.57	$\chi^2 = 4.84, p < 0.05$
> 300	268	281	0.48	$\chi^2 = 0.31, NS$
Two-by-two $\chi^2 = 4.63, p < 0.05$				

Note: Gestation takes 110 days, and the synchronous births associated with male takeovers occur in the first 300 days after the takeover (see Packer and Pusey, 1983a,b). Data are from 1974–1985 and exclude cubs for which we do not know the timing of birth relative to the preceding male takeover. Note that when all data are included, the overall sex ratio does not deviate significantly from equality: 50.9% male,  $N = 874, \chi^2 = 0.29$  (Reprinted from Packer and Pusey, 1987).

usual fate of cubs that die following takeovers. There is no doubt that male lions gain reproductive advantages from infanticide. Following a successful takeover, females mate with the infanticidal males, and DNA-fingerprinting shows that all cubs born in a pride are sired by the males resident in the pride (Gilbert *et al.*, 1991). By killing small cubs, males sire their own cubs an average of 8 months sooner than if they had spared them.

Whereas almost 100% of cubs aged up to 9 months die after takeovers, the percentage falls after this age. However, males evict all older cubs that have not been killed (Hanby and Bygott, 1987). Although some evicted cubs leave the pride with their mothers, the usual effect of eviction is to separate the cubs from their mothers and hence bring the mothers into estrus more quickly. As long as their cubs are present, females do not resume estrus behavior until their cubs are at least 18 months old.

In primates such as red howlers (Crockett and Sekulic, 1984) and langurs (Sommer, this volume) there is a similar relationship between infant age and the proportion that are killed by males after takeovers. In these species, however, more infants of all ages are spared than in lions. Possibly this difference reflects the greater gains male lions make in terms of speeding up the females' reproduction, or lower costs of the behavior. While male lions will speed up females' reproduction if they kill or evict cubs aged up to 18 months, the equivalent age is only 6 months in langurs and 9 months in red howlers. Because of their large size and weaponry, and the fact that lion cubs are sometimes left unprotected, male lions may also find it easier than male primates to kill young.

The behavior of female lions seems to be influenced by the threat of male infanticide in several ways. They are able to recognize the roars of alien males and retreat from them. They form more stable subgroups when they have cubs and these are almost certainly defensive in nature. It is possible, however, that these groups are not only necessary for defence of cubs against incoming males, but also against females from other prides. Females are also known to kill cubs in other prides (Schaller, 1972; Hanby, 1983; Packer and Pusey, 1984). Mothers with mobile cubs sometimes leave the rest of the pride to avoid new males, as has also been described in primates (reviewed in Pusey and Packer, 1987b). Female lions also show heightened sexual behavior but a delay in reproduction following takeovers that may serve to attract larger coalitions that can best protect their next batch of cubs. There is some evidence of a similar delay in conception following male changes in red howlers (Crockett and Sekulic, 1984), but langurs do not show such a delay (Sommer *et al.*, in prep.). This difference may be due to species differences in the likelihood that the first male to enter the group is able to remain there. Perhaps, in langurs, males that are able to enter a new group and start killing infants have a good chance of staying for a long time. In this case females would not benefit from delaying conception. Finally, females appear to respond to takeovers by synchronously producing male-biased litters. This increases the chances that their sons will have numerous coalition partners with whom they can eventually cooperate in taking over a pride elsewhere.

While females live in prides of the size in which takeover rates are lowest, the risk of infanticide is probably not the only factor causing lions to live in groups (Packer, 1986; Packer *et al.*, 1990). Other large cats such as tigers, leopards and cougars also show infanticide but are nevertheless solitary. One way that lions differ from these species is that they live at much higher densities (Packer, 1986). This may increase the costs of territoriality such that group defence of territories becomes advantageous (Brown, 1987; Davies and Houston, 1981). We have recently found that females in very small prides are unable to defend a permanent territory (Packer *et al.*, 1990).

When they encounter alien males, females with cubs sometimes fight with them. In two instances such encounters resulted in the deaths of females. This is in contrast to other species, such as langurs (Sommer, this volume), and rodents (Parmigiani, this volume), where males apparently never wound females that aggressively defend their infants. Clearly the killing of female lions by males is disadvantageous both to the female and the males involved, so why should it ever occur? Because of the rarity of observations of such encounters, we have no data on the factors that

influence a female's readiness to fight (cf. Parmigiani, this volume). It may be that whereas solitary females always run away without risking fighting, and females in very large groups are always able to overcome or drive off one or a few males, in cases of a more even match (e.g. between several females and one or two large males), the decision of the females and males to avoid combat is not clear cut. Once attacked, the males may have to fight for their lives and consequently risk wounding or killing a potential mate because of the lethal weaponry involved (see also Packer and Pusey, 1982). There is evidence that female lions can kill fully grown males (Packer and Pusey, unpublished data).

Resident male lions also behave in ways that protect their cubs. Males frequently remain with a pride for many months after all the females have cubs and there are no estrous females present. While resident, they regularly patrol the pride range, roar and keep out alien males. The voluntary movements of males between prides are also sensitive to the vulnerability of their cubs. If they have to abandon one pride out of several, they leave the pride where the cubs are least vulnerable, and they only abandon prides with small cubs if they thereby gain access to much larger numbers of females in another pride.

Although there is tremendous conflict between female lions and extra-pride males, there is a period when females have cubs during which they and their resident males share a common interest in protecting the cubs. The extent to which they cooperate in this endeavor is a topic of current research.

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