

Photographs by Craig Packer

Male companions usually stay together for life, together gaining and losing control over one or more prides. While some groups are composed of relatives, others, such as this threesome, are made up of lions from different natal prides.



Once and Future Kings

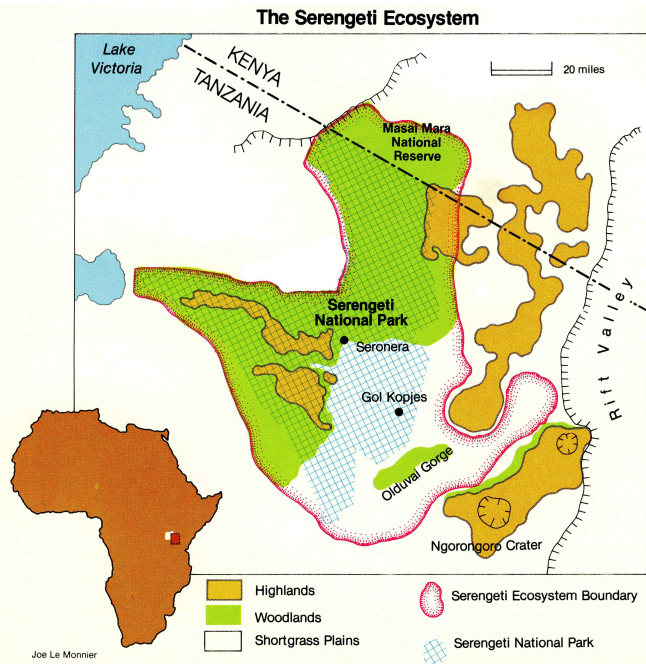
Groups of male lions compete for the chance to rule a pride and mate with its females. Their tenure is never secure

by Anne Pusey and Craig Packer

On April 11, 1980, we had one more area to check in our census of the Gol pride lions. We had already found most of the females and their resident males at the Gol kopjes, a series of granitic, rocky outcrops lying in the middle of the Serengeti plains of Tanzania. Six miles to the southeast lay another cluster of kopjes, also within the Gol pride's range, that we had not visited that day. As we rounded the largest kopje in the cluster we spotted two male lions asleep on their sides. We moved closer, driving very slowly because males in this part of the Serengeti are often shy and will run away from a vehicle. When we came to within ten feet of them, the nearest male opened one eye, regarded us briefly, rolled over on his back with all four feet in the air, and shut his eyes again. These were no ordinary Serengeti males. With mounting excitement we consulted our identification cards of males born in 1976, about sixty in all. In only one part of our study area were lions as blasé about cars: the Ngorongoro Crater, a huge caldera in the volcanic highlands more than forty miles to the southeast.

The Ngorongoro Crater's large resident ungulate population supports one of the densest populations of lions in the world: more than a hundred lions in an area of about a hundred square miles. Because many tourist vehicles visit the Crater every day and there is little cover in which lions can hide, they quickly become used to cars stopping beside them and ignore all but the noisiest of tourists. If these males were from the Crater, it would be the first recorded movement of Ngorongoro males into the Serengeti. Using binoculars, we carefully examined the pattern of vibrissae spots on each side of the males' faces and checked them against our identification cards. Judith Rudnai, who had studied lions in Kenya's Nairobi National Park, was the first to realize that these whisker-spot patterns are distinct and different in each lion and can be used as permanent identification since they remain the same from birth to death. Eventually we matched cards to the lions. They were Lebu and Lafua, born in 1976 in the Lake pride of the Crater and last seen by us there on February 4, 1980. Within the last two months they had traveled forty miles through country inhabited by the Masai—a hazardous journey because the Masai cattle herds are no friends to lions. Although only three and a half years old, the males were almost fully grown and their manes were already luxuriant, a testimony to the abundant and constant food supply in the Crater. Males of the same age in the Serengeti generally have not yet reached full size and their manes are not fully developed until they are at least five.

The Serengeti ecosystem, an area of about ten thousand square miles, is defined by the range of the annual migration of vast herds of wildebeest, zebra, eland, and gazelle. Each year the herds congregate on the shortgrass plains in the wet season (November-May), then travel west and north to the woodlands in the dry season (June-October). The woodlands of the Serengeti also support resident populations of buffalo, giraffe, hartebeest, topi, impala, reedbuck, waterbuck, and warthog. In contrast, the shortgrass plains have few resident ungulates. Thus the lions of the Serengeti plains lead a life of feast or famine as the herds move through their ranges, and even the lions of the woodland and woodland edge have a less constant food supply than in the Crater. As a result, cub mortality is high in much of the Serengeti, and cubs that survive grow more slowly than Crater cubs.





Above: On the Serengeti plains, a herd of wildebeest stands alert as a young nomadic male lion ambles by. Right: A rival withdraws as a male consorts with an estrous female. The normally affectionate relations among male companions become tense when an estrous female is around, but as long as one male is in clear possession of the female, fighting is unlikely.



On this day, Lebu and Lafua seemed to have found a lion's paradise. Thousands of wildebeest, zebra, and gazelle spread in all directions across the rolling green plains. The air vibrated with the grunts of wildebeest and the periodic high-pitched brays of zebra stallions. At night, the female lions of the nearby Gol pride roared enticingly. But this was not to last. In a few weeks the rains would stop and the dry southeasterly winds would start to blow incessantly, turning the plains to a near desert. The herds would leave and the resident lions would have to scatter to survive on the few remaining gazelle. What had caused these two males to leave the Crater? What would they do next? And more generally, how would their lives compare with those of other males in this vast area? These are some of the questions we have tried to answer in the last five years.

We started our study in 1978 and were joined in 1982 by Sara Cairns. We are the most recent in a series of scientists who have been studying the lions of the Serengeti for the last seventeen years. George Schaller began his famous study of the Serengeti lions in 1966. He was succeeded in 1969 by Brian Bertram, who was followed, in turn, by David Bygott and Jeannette Hanby in 1974. Although each scientist has concentrated on different aspects of lion ecology and behavior, between us we have managed to monitor two prides near Seronera, the Seronera and Masai, continually since 1966, and an additional fifteen prides living in the Serengeti woodland edge, the plains, and the Ngorongoro Crater, since 1974. From these observations we are beginning to get a good picture of the life history of lions, both male and female.

The lions' basic social unit is the pride—a permanent social group consisting of two to eighteen adult females and their offspring and one to seven resident adult males. Prides occupy the same area for generations. The Masai pride still occupies the area it did when Schaller first observed it in 1966, although all of the lions born during his study have died of old age. The Seronera pride has split into two groups, each occupying half of the original pride range.

The core of a pride is formed by the adult females, most of which are born, live, breed, and die in the same pride with their mothers, aunts, sisters, and cousins. A few may leave with female peers and form new prides or become nomadic, but none join other, preexisting prides. In contrast to females, all male lions, like the males of most other mammalian species, eventually leave the pride of their birth and breed elsewhere. Groups of adult males compete with other groups to monopolize the pride and mate with the females. In the last decade, Bygott, Bertram, and Hanby

found that the average tenure of male groups with prides was only two years before they left of their own accord or were ousted by other groups of males. In the last seventeen years, the Masai pride has had nine sets of resident adult males. However, Bygott, Bertram, and Hanby also found that tenure length varied enormously—from a few months to as much as six years—and that the largest male groups achieved the longest tenure. Our particular interests have been how these male groups form and how the males in each group cooperate and compete with each other in their quest for females.

Females frequently give birth at about the same time, then pool their cubs and rear them communally. Thus, from the age of about six weeks, males are in the constant company of their brothers, sisters, cousins, and a variety of more distantly related peers. Cubs are weaned at about seven months, but their mothers continue to hunt for them until they are about two years old. In their second year cubs start to participate in hunts, but it takes time for them to become proficient hunters. Females give birth to new litters when their previous cubs are about two years old, but they often allow the older cubs to stay with the pride.

Although all males leave their natal pride eventually, the age at which they leave depends to some extent on the fate of their fathers. If their fathers remain in their natal pride, subadult males sometimes stay until they are three or four years old and almost fully grown. We observed the only surviving male from a litter remain with his pride until he was four years old, at which point his two elderly "fathers" were evicted by a new set of males. The young male then joined forces with his fathers, and the threesome succeeded in taking over a neighboring pride for a few months. However, cases of sons joining their fathers are uncommon and may only occur when their fathers' coalition is very small. Most males leave their prides with their male peers if they have any and stay with them for life.



Lebu and Lafua remained in their natal pride until they were three and a half, although they had become somewhat peripheral. Their fathers were a group of six large, black-maned males that has resided simultaneously in three of the five prides in the Crater for seven years. In the last few months before they left the Crater for the first time, Lebu and Lafua had bite wounds that had been inflicted by other lions. We do not know which lions were the aggressors, but we have observed the six resident males chasing some of their other subadult sons away from their natal prides.

Such aggression by fathers is not so severe as that by new males that have just taken over a pride. Because average tenure is only two years, the fathers of most young males are evicted while their sons are still large cubs or subadults. Then the large cubs are evicted too. During our study we found several nomadic groups of cubs as young as one and a half years old that had already been evicted. Many more were between two and three years old.

Once evicted, these cubs and subadults lead a nomadic life for several years until they are old enough to take over a pride and become resident. For the first time in their lives they must feed themselves by scavenging or hunting and avoid aggression from resident lions. It is a hazardous time. The wet season in the Serengeti is not so bad, and young male lions from miles around follow the herds to the plains. With plentiful prey and low densities of resident lions there is little strife. But in the dry season, nomads must return to the woodlands, where they risk attack from residents or starvation in marginal areas. Mortality is high; cohorts of relatives returning to the plains after the dry season are usually reduced in numbers each year. Even the survivors frequently have scars from bite wounds, and several times we have found the corpses of young males that have been bitten to death by other lions.



Females of the Gol pride surround and attack a lone young male that had been trying to associate with them. Females do not tolerate the presence of nomadic males.

Once they have reached full size, the goal of all males is to take over a pride. Since females usually mate only with the resident males of their pride, and only the cubs of females living in prides have much chance of surviving, males must become resident in prides in order to father surviving offspring. Groups of nomadic males are always on the lookout for prides they can take over. As they wander, they have various means of determining which prides might be available. Resident males actively patrol the pride range, mark the ground and bushes with urine, and roar at night. In open areas, we were able to hear roars up to five miles away and lions can probably hear them farther than this. Females also mark their range and roar. Thus, nomadic males are probably able to discover a great deal about the relative numbers of males and females in an area even without seeing them.

When resident males abandon prides of their own accord to take over a neighboring pride, there is often an easy opportunity for nomadic males to move in and mate with the females. However, females with cubs sometimes successfully repel new male groups. If the resident males are still present in the pride, the outcome depends on the number, age, and vigor of males in each group. If the invading group is much larger, the residents are likely to leave without a struggle. In the last five years a group of seven males, the largest so far observed in the Serengeti, has taken over, then abandoned six prides on the plains and at the woodland edge. The takeovers were rapid with no sign of fights between the invaders and the resident males. Probably the roars of seven vigorous males were enough to convince the residents that their tenure was over.

For smaller groups of males it is more difficult. In their first wet season on the plains, Lebu and Lafua hovered at the edge of the Gol pride, but were kept away from the females by the four resident males. The following dry season they returned to the Crater. By the next year the resident males of the Gol pride had moved on and Lebu and Lafua took over the pride for several months. Then a group of three males started penetrating the Gol pride range, roaring at night and marking. Eventually Lebu and Lafua retired to a small portion of the pride range with one subgroup of females and their cubs, while the threesome continued to expand their range and mated with the rest of the females. By the end of 1981, Lebu and Lafua had been completely evicted and Lafua was seen, severely wounded, near Seronera, thirty-five miles to the north. After Lafua recovered, he and Lebu were back in the Crater again in the dry season of 1982. Other males have died from wounds inflicted during takeovers.

Since large groups of males do so much better than small groups, what becomes of single males that are either unfortunate enough to be the only males in their litters or that lose their male companions during their nomadic phase? Over the years, many single nomadic males have been seen periodically for months or years before disappearing for good. While some may move to new areas, many must die. However, we have found that single subadult males are often gregarious. They try to join bands of subadults or in some cases to join prides with large cubs. On a few occasions we have seen young males following resident females to scavenge food, but they invariably meet with aggression. Resident females do not tolerate the presence of strange subadults at their kills although their sons are often tolerant of strangers.

The plains in the wet season provide a neutral meeting ground for nomadic males. They often meet at kills, in this way probably becoming familiar with a large number of other males. Like Schaller, Bygott, and Hanby, we have observed males forming permanent companionships with males from different prides. Males may associate with several different companions before settling down with one, and if their companion dies, they may seek another. Chosen companions are usually the same age and size. Whether a pair of males accept another male into their group depends on whether they are nomadic or resident in a pride. Males that have managed to gain a pride are intolerant of other males. However, we observed two different pairs of males that had been evicted from a pride accept a third companion and together each trio took over another pride. In early 1982, before they returned to the Crater, Lebu and Lafua joined up with a male that we had seen alone in the Serengeti during the previous two years. He did not accompany them to the Crater, however, and it remains to be seen whether they will reunite.

Scientists have assumed that all males within a group are relatives and that the cooperative behavior they show during competition against other groups for prides has evolved through kin selection. During our study we found that 44 percent of sixteen coalitions of males resident in prides contained males from different prides. The unrelated males appeared to be as affectionate and cooperative toward

their partners as the related males. How can cooperative behavior between non relatives evolve? Bygott, Bertram, and Hanby showed that groups of three or more males were not only much more likely to become resident in prides in the first place but they also had longer tenure, more females per male, and left larger numbers of cubs per male than smaller groups of males. Therefore, as long as all the males in a coalition can mate and leave some offspring, single males and pairs will each leave more offspring if they join up with other males, regardless of whether they are relatives or not. There are two reasons why males in the same group are likely to have reasonably equal mating success. First, females are often in estrus simultaneously, and second, although males compete for females, they are usually fairly evenly matched in competitive ability and respect each other's temporary ownership of estrous females.

When a male group succeeds in ousting the resident males from a pride, it evicts the large cubs and there is a simultaneous increase in the mortality of all small cubs in the pride. Since 1966, scientists in the Serengeti studies have observed infanticide by incoming males six times, and given the small likelihood of an observer being present, we suspect that most of the small cubs that disappear after takeovers are killed by the males. Females attempt to resist the new males until their cubs are lost, and we have circumstantial evidence of two females dying in defense of their cubs. The result of the death of small cubs and the eviction of large cubs is that the females that would not otherwise become sexually active for from six to eighteen months come into estrus and mate with the males within days or weeks of the loss of their cubs. Bertram was the first to suggest that cub killing in lions was a male reproductive strategy whereby males brought the females into sexual receptivity more quickly, thus increasing their chances of fathering cubs before they themselves were ousted from the pride. Given that average male tenure in prides is only two years, and that cubs must be protected from other males for two years if they are to survive, infanticidal males are likely to leave more offspring than noninfanticidal males and the behavior will be favored by natural selection. Infanticide by new males has also been observed in a variety of species of primates and rodents, apparently with similar advantages for the males.

One result of the simultaneous loss of cubs by females at takeovers is that the females return to receptivity at the same time and are often in estrus synchronously. Estrus, the period in which females mate, lasts an average of four days and occurs every two or three weeks until the female conceives. During our study two or more females of the same pride were in estrus synchronously for more than 40 percent of all estrous periods. The resident males are always on the lookout for potentially estrous females. If two males are together when they encounter an estrous female, they race to be the first to reach her. We have seen one male knock his partner over in such a race. Once with her, the male becomes temporarily dominant to his partners and threatens all other males that come too close to the female. We found that the first male to reach an estrous female usually stayed with her and mated with her for at least three days. Toward the end of this period, they cease to mate and the male continually sniffs the female's urine until he seems to decide that she is no longer interesting. Then he either allows her to walk away or leaves her. At this stage she may mate briefly with other males, but they are not so possessive of her as the first male was.

Serious fights between males over females are rare and usually occur only when the ownership of the female is unclear, as when the female is equidistant from two rival males. In the majority of male coalitions, males are the same age and size, and each male in the coalition respects the ownership of his partners, not because they do not compete, but more likely because the costs of fighting (the possibility of blinding or the loss of a partner) are so high. The result is that each male achieves fairly equal mating success. In some coalitions (seven out of twenty in our study), there is a discrepancy in size or age of the males. In these cases, the larger or more vigorous male is likely to get first access to estrous females. But even in these coalitions, subordinate males are likely to be able to mate whenever there is more than one female in estrus at the same time and the more vigorous males are already occupied.



A male and two females, part of a pride on the Serengeti plains

Once they have successfully taken over a pride, resident males may appear indolent to the casual observer. Most of the time they rely on the females to hunt then eat what they want from the carcass before allowing the other pride members to feed. But to protect their cubs they must constantly patrol the pride range and evict intruding males. While the maximum life span of females in the Serengeti is about sixteen years, males do very well if they survive to eleven years. By this age they bear the scars of many battles; some have broken teeth, missing eyes or tails, and withered hindquarters.

Several questions remain. How do changes in lion density and cub survival affect male group size and tenure length in prides? Why do some nomads remain solitary while others find companions? What makes groups of males voluntarily abandon a pride and move on to a neighboring pride? By continuing our observations on males such as Lebu and Lafua, we hope to increase our understanding of the king of beasts.