



Eric Nishe

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The African lion

The lion *Panthera leo* was one of the most fearsome beasts which roamed the African and Asian plains with the early pastoralists. Although the lion has been the dominant large carnivore in Africa and south-western Asia for millennia, this may not always have been so. Paintings by Cro-Magnon man, for example, show both the lion and another large felid without a mane or a tufted tail. Along with skeletal remains, this felid has been identified as the cave lion *Panthera spelaeus* which inhabited Europe between 340 BC and 100 AD. In the fossil evidence from Africa there also are sabre-toothed cats, another large cat *Panthera crassidens*, and a lion-sized cat with a jaw like a tiger. The rise of the African lion as the dominant carnivore of Africa is therefore relatively recent, and may well have coincided with the rise of man.

The lion is Africa's largest cat, but food intake and genetics play a major role in determining the actual size of a lion, and therefore it varies in size from region to region. Big males in Etosha can weigh up to 260 kg, and females 165 kg. In southern Africa lions usually weigh in the region of 200 kg and 140 kg respectively. The lions from East Africa are smaller than those from southern Africa, and males usually weigh about 180 kg and females 120 kg, although the maximum known weight for an East African male lion is 238 kg and 182 kg for a female. The African lion has a fair degree of genetic variation as opposed to the small population of Asiatic lions which has little such variation. The African lion was first described scientifically as *Felis leo* by Linnaeus in 1758, from a specimen collected at Constantine on the Barbary coast of

THE AFRICAN LION

In terms of size the African lion has been the dominant large mammal carnivore in Africa in recent times.
Photo: J. du P. Bothma.



Algeria. It was renamed *Panthera leo* by R.I. Pocock in 1917. The generic name *Panthera* was first used by L. Oken in 1816, and Oken also created a genus *Leo* in 1816, which is no longer in use. However, it was Pocock who separated the Felidae into three subfamilies: the large or roaring cats of the subfamily Pantherinae, the cheetah of the subfamily Acinonychinae, and the small cats of the subfamily Felinae. This division of the subfamilies is based on the structure of the hyoid bones which are fully ossified in the Felinae and Acinonychinae, but imperfectly in the Pantherinae.

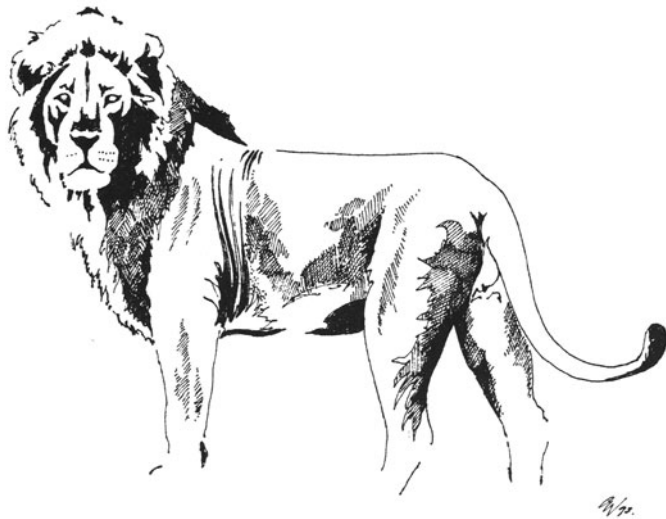
A lion's eyes seem to have always held a great fascination for man, and were, for example, carefully rendered in Assyrian and Ancient Egyptian sculpture. In many parts of Africa the successful initiation of young hunters also depends on a test which requires the initiate to face a lion's fierce and awesome stare directly. In ancient Egypt, the city of Leontopolis was named after a lion cult which flourished there. Moreover, the annual flooding of the Nile River which was the most important event in the Egyptian calendar was depicted hieroglyphically by a lion's head. Ramses II kept lions, as did most of the royalty of those times. Ramses II was also said to have trained a lion called *Autom-nekht* to run beside his chariot horses and knock down anyone approaching the chariot. The great menageries in Alexandria, which were built up by the Ptolemies, the successors to the pharaohs of ancient Egypt, were ultimately destroyed by the emperor Theodosius who banned all animal cults in the year 384 AD.



The lion's piercing eyes have long fascinated man.
Photo: C.H. Walker.

The classical Phrygian goddess Cybele also became the object of a widespread lion cult called the Galli. This Asian goddess personified the earth in its primitive and savage state, and held dominion over all wild beasts. She was symbolically represented being drawn in a chariot by two lions. Some of the priests of the Corybantes, as the followers of this cult were called, travelled far and wide and were often accompa-

nied by a bear or a lion which was used in the exorcism of evil spirits. The Romans in turn used lions as sacrificial beasts, and Julius Caesar had 400 lions killed to consecrate his Roman Forum. When Germanicus was nominated as consul, a further 200 lions were sacrificed. In Africa there are also numerous tales of wizards with magical powers who associated with lions. Even more powerful were the secret societies that killed people at night in the guise of spirit lions or lionmen. Even outside Africa lion trophies have long been held to have powerful medicinal and magical effects. For example, in 1563 the Swiss physician Konrad Gesner described how the dried and powdered blood of a lion could be used to treat carbuncles, other growths and swollen glands. He also wrote that this powder would make blemishes and spots on the face disappear when mixed with other ointments; that eating a lion's heart could alleviate a cold, and that drinking the liquid of a pickled lion liver would relieve liver ailments.



The Shona people of Zimbabwe believe that there are three types of lion. These are the normal lion which can be hunted, and two other types that must not be harmed. One of the latter is the benign spirit of a former chieftain who comes to visit his family at times. He is a maned lion and will not harm them. The other is the embodiment of an evil person whose craving for raw flesh has caused him to transform himself into a maneless lion which must be avoided at all costs. It is interesting to note that the possession of a mane is part of lion folklore, much as it is also part of a current controversy over the relationship and

existence of maned lions. In African lions, manes have developed in varying degrees. The extinct Barbary and Cape lions lived in worlds many thousands of kilometres apart, yet they both had well-developed manes which came fairly far down the body, as did other lions elsewhere. However, the Horn of Africa, of which Somalia forms a major portion, has a peculiar fauna, and the main characteristic of its lions, which were still relatively abundant there as late as 1984, is the absence of a mane, even in fully grown males.

Our hunting ancestors knew the lion well, and it appears in a lot of African folklore. Many parts of a lion's body are used in superstitious practices and in traditional medicines. The lion's stature among men is projected by many honorary titles and garments relating to lions. The head of the ancient dynasty of Ethiopia assumed the title The Lion of Judah. The warriors of many African tribes also use headdresses which imitate a lion's mane. This mane seems to have a special significance for them because the maneless lioness is never imitated. It has been suggested that the male lion's proud bearing, his thunderous roar, and perhaps even the resemblance between manes and beards, have all led to the adoption of the lion as a martial symbol for many people.

Lions can be identified individually from the pattern of their whiskers. These whiskers occur between the upper lip and the nose, and there are distinctive spots where they emerge from the skin. These spots form four to five rows above and roughly parallel to the upper lip. The shape and number of these spots, and the distribution of the rows



The male lion's proud bearing and his impressive mane may have contributed to its adoption as a martial symbol by many people in Africa. Photo: C.H. Walker.

varies with individual lions. Some South African lions in and around the Kruger National Park also show a coat colour anomaly in that they have an inherited recessive white coat. They are not albinos, however, because the eyes of a white lion have the normal yellow pigment and are not pink-red as in an albino. The presence of leopard-like spots on the cubs and on some adults is a vestigial characteristic retained from an ancestral cat which probably lived mainly in forests.

Social behaviour

With lions, the lioness and her young are the focus of the pride and there is no consistent leader. The pride usually occupies a limited area, but there are also nomads of both sexes who wander widely. Nomadism and pride membership are not mutually exclusive, and a nomad may become a resident, and vice versa, but each category implies a vastly different way of life. A pride usually occupies a defended area of limited size, which is sometimes called a territory, while a nomad occupies an undefended range. The size of the pride's range is related to the size of the pride, and the ranges of various prides may overlap. The lion's pride size varies from area to area according to the availability of prey. In Serengeti the modal pride size in one study was 2 (mean: 2,8) and the maximum pride size 13. Elsewhere in East Africa prides may be much larger. In the prey-rich Ngorongoro Crater the largest lion pride studied had 30 members (mean: 8). In the Kruger National Park prides of up to 39 individuals may be found. In Etosha pride size ranges from 5 to 16 members, although prides of up to 30 (mean: 7,2) have been recorded there. In the southern Kalahari savanna the largest pride recorded by F.C. Eloff had 14 members (mean: 4,2).

Because lion pride size varies from area to area, so will lion density. One lion requires at least 100 prey animals over a full year to remain alive. In Etosha however, there seems to be more lions per unit of prey than in most known conservation areas. Where prey is more abundant, as in the more mesic savannas, lion density should therefore also be higher. This is indeed so. In Serengeti, for example, the available prey density varies markedly between a mean of 20 000 kg/km² in the wet season when the migratory prey is present, and 1000 kg/km² in the dry season. There the mean annual density of lions is one lion per 10 km² (10 lions per 100 km²). By contrast, in the Ngorongoro Crater the prey biomass is much more stable, varying from a mean of 11 693 kg/km² in the wet season, to 12 000 kg/km² in the dry season. The mean lion den-

sity of one lion per 2,5 km² (40 lions per 100 km²) in the Ngorongoro Crater, is four times that of Serengeti. At Lake Manyara National Park conditions are probably close to a maximum sustained density of lions. There the prey biomass is 7200 kg per km² at most times, and the lion density there is around one lion per 2,6 km² (38,4 lions per 100 km²). This density is sustained over time. The Selous Game Reserve carries one lion per 12,5 km² (8 lions per 100 km²). The lion density in Etosha was estimated by some authors at one lion per 4,5 to 6,3 km² (15 to 22 lions per 100 km²), but others believe that it is as low as one lion per 35 km² (2,8 lions per 100 km²). However, it also varies according to local prey abundance, the highest being in western Etosha where prey densities are greater because of the presence of a number of artificial water points. In the Savuti Marsh prey biomass ranges from 2000 kg/km² in the dry season to 27 000 kg/km² in the wet season. The mean lion density there is one lion per 5 km² (20 lions per 100 km²). The Kruger National Park is essentially an arid savanna. Yet it has a relatively high lion density of one lion per 7,7 km² (13 lions per 100 km²) and there are 110 prey animals present for every lion. The southern Kalahari is an open, arid savanna. Consequently it has a relatively low density of one lion per 68,5 km² (1,5 lions per 100 km²). The arid Masai Steppe is known to have the lowest natural lion density in Africa at one lion per 306 km² (0,3 lions per 100 km²).

In a lion pride, the adult males are usually interrelated, as are the females, but the males are not related to the females. Female cubs born to pride lionesses usually remain in their natal pride for the life of that pride. In contrast, the male cubs are usually evicted at puberty. Any male cubs which do survive till puberty, leave the pride together, and may stay together, to become breeding adult males in a new pride. In the process of taking over a new pride, serious injuries are rare, but the conflict may be fierce and noisy. Occasionally a defending pride male may be fatally wounded or he may be disabled which will lead to a lingering death. However, an adult male is not a pride prerequisite, especially where prey is abundant and prides can easily kill food. For example, in the prey-rich Savuti 44% of all the lion prides found feeding at a kill, had no adult male lion in attendance. Large lion prides also typically dominate smaller ones in a given area.

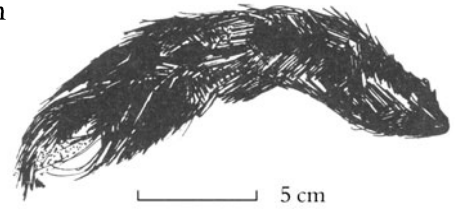
It is often believed that lion prides are prime examples of sociability in predators. However, this is not altogether true. Although most lion prides show a fair degree of social order among the females, the Etosha lions, for example, live in prides with no social hierarchy among the lionesses. Nevertheless, sisterhood does have its advantages, because

pride-mates will jointly defend their cubs against invading males, and will share in raising the young. An angry group of females can ward off the attack of a lone male which is nearly twice as large as a female, and will also frequently attack and kill less powerful, trespassing females. Although some females are also nomadic, it is mainly the males who become nomadic after puberty. They then wander widely and eventually evict the resident adult male(s) from a pride. After doing so, they often also kill all the cubs present (infanticide). The pride females may respond to the death of the cubs by all coming into oestrus simultaneously and ultimately producing new young in unison. Nomadic lions travel widely. In Serengeti one nomad used an area of at least 4700 km². The range size of these nomads is at least 10 times that of prides in the same region. Nomadic lions are markedly tolerant of one another, and these lions, which have no land of their own to defend, usually accept strangers easily.

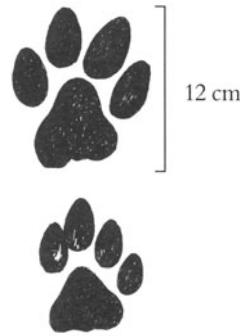
Lions have a well-developed communication system which incorporates many facets. Vocalisation, facial expressions, scents, body postures and much more, all play a role in the functioning of lion sociability. Roaring and scent-marking are usually long-range signals, while other vocalisations, facial expressions and body postures are used more for short-range communication. The acute senses of hearing, sight and smell are particularly powerful tools in such communication. Although lions also purr at times, this purr is unlike that of the domestic cat, being produced during exhalation only and not as a continuous action while breathing in and out. Purring does seem to signal contentment, but compared with cats of the *Felis* group, it appears to be unimportant in the social life of a lion.

Roaring is a characteristic of the *Panthera* group of cats to which the lion also belongs. Lions do not roar regularly, but both sexes may do so at intervals throughout the night. They often roar most at sunset and just before dawn. Roaring and scent-marking by lions in Serengeti and the Ngorongoro Crater are most frequent when prey is most abundant, a time when intruder pressure from nomadic lions is also the greatest. Lions can clearly scent-track other lions, or even their prey. As a lion moves about, it leaves tracks, urine and faeces in the environment. These may all convey messages to other lions which may pass by later, although in lions the faeces do not appear to be used for specific messages as in other carnivores. Although all cats advertise and mark their territorial boundaries, none do it on quite the same grand scale as the African lion. In combination with urine, all cats possess highly developed and usually sebaceous (fat) glands above the tail, as well as anal,

praegenital, circumoral, submandibular, and interdigital glands between the footpads. In common with some other cats, lions also scrape or wipe with their hind feet before marking with urine. This leaves an olfactory and visual signal to other lions, and such behaviour complements rather than supplements the other. When scraping, a lion rakes the ground from 2 to 30 times with the claws of the hind feet, undoubtedly leaving a concentration of scent. Both males and females scrape, but lions do not defecate on their scrapes as tigers do. The frequency and intensity of scraping varies with the type of habitat. Scraping by one lion in a pride also frequently stimulates others to do so.



Urine is used widely by lions in communication. Male, nomadic or resident lions especially, squirt urine against objects in their range. In doing so, a musk-smelling secretion from two anal glands near the base of the tail mixes with the urine. Lions often rub their faces on vegetation before spraying it with urine and scent. As the same objects may be used repeatedly for scent-marking in this way, it is possible that they receive certain chemical messages during such rubbing. The subsequent spraying may then be a reaction to this kind of message. When spraying the fluid is squirted upward at an angle of 30 to 40° for a distance of 3 to 4 m. The musky odour can be detected from as far away as 5 m. Male lions prefer bushes or tree trunks at least 1 m high against which to spray-urinate. Small squirts of urine are also used by lions to scent-mark. In doing so, the animal often wets its hindlegs. This fluid has little or no scent from the anal glands, and its flow is usually steady but weak. Lions of all ages also rake the trunks of trees with their forepaws. Although this could serve to sharpen and groom the claws, it also serves as a signpost, because some of these trees are clawed repeatedly. Lions also roll on the faeces of other animals, but the reason for this is unknown.



Reproduction and young

Lions reproduce at rates which are in balance with the abundance of their resources, particularly food. They have no clear mating season in some areas, but in the Nairobi National Park their births show a distinct peak in December and January although they do mate throughout the year. In Serengeti lion reproductive rates are the highest in those years with relatively wet dry seasons, or with relatively dry rainy seasons. At such times, the migrating prey herds remain in the same area

of the park for a greater length of time, creating more ideal conditions for cub survival. Pride size also influences reproductive success, because the females in the larger prides often breed synchronously and help to raise each other's cubs, resulting in increased cub survival.

Lions use chemical signals to display their readiness to mate as domestic cats do. Both the urine and the cheek gland secretions of a female cat appear to contain pheromones which inform the males about her hormonal phase. Males react to such messages by showing flehmen, which is a grimace following a whole array of stimuli, including a female's urine, and helps to determine the receptiveness of such a female. The age of sexual maturity in lions varies. Female lions in the Nairobi National Park first conceive when they are about 30 months old, but this could take place at a younger age. In Serengeti it is from 40 to 54 months. In the Kruger National Park female lions first conceive at the age of 43 to 66 months (median age: 48 months), and by the age of 5,5 years all females have been pregnant at least once. Pride males, and consequently reproducing males, are usually between 5 and 9 years old. Although males may be sexually mature from an age of 30 months, they are prevented from mating at that stage by social behaviour.

Pride females in the Kruger National Park tend to come into oestrus and give birth simultaneously. Oestrus in lions usually lasts a week, and recurs at 3-week intervals. Mating lions stay together for 2 to 3 days, copulating two to three times every hour. It is also possible that a lioness may produce cubs fathered by different males, in the same litter,

A male lion in the southern Kalahari savanna sniffing the urine of a receptive female to determine her reproductive status.

Photo: J. du P. Bothma.

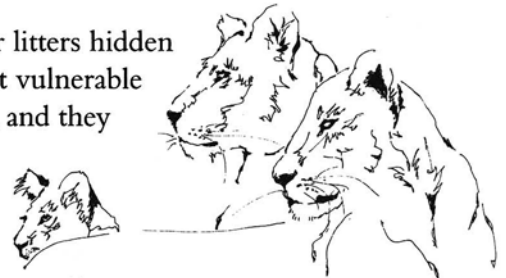




A male lion showing flehmen in response to the pheromones in a female's urine in the southern Kalahari savanna. Photo: J. du P. Bothma.

because multiple-mate copulations do occur occasionally, although this is rare. Competing males may also fight fiercely over a receptive female. In Kenya, for example, a case is known where two males fought a raging battle for 10 hours in the presence of a receptive female, ending in the death of both combatants. Mating lions seldom attempt to hunt. Gestation lasts about 110 days, but relatively few copulations actually lead to conception. In Serengeti, for example, conception occurs in only 20% of all matings. In one study of lions in the Kruger National Park, 20% of all the parous females were pregnant, 21,7% were lactating and consequently had cubs younger than 9 months old, and 6,7% were sterile. The rest were in an interlitter phase. Females usually have a reproductive life of some 11 to 13 years.

Lionesses give birth in isolation, and keep their litters hidden for the first 6 to 7 weeks when the cubs are most vulnerable to predation. A lion cub's eyes are closed at birth, and they only really join the pride when they are 10 weeks old. In the Kruger National Park the mean litter size is 3,08 at birth dropping to 3,02 when the cubs are a year old or less, and to 2,71 when they are between 1 and 2 years old, but litters of



Young lion cubs in the southern Kalahari savanna are often left alone for extended periods, a time when they are vulnerable to various forms of mortality.
Photo: J. du P. Bothma.



up to 6 are possible. This is much the same as that found in lions in the Nairobi National Park, or in the southern Kalahari savanna. Litter size therefore does not seem to be influenced by food abundance, but litter survival definitely is.

Infanticide is a common and normal reproductive strategy in lions, although it has long been considered an aberrant form of behaviour. It usually follows the takeover of a pride by a new male or a cohort of males. In the process all the cubs already present in the pride are killed by the new males. The females then often come into oestrus synchronously and mate with the new males. This is a reproductive strategy which prevents females from investing more energy into raising progeny from males which have been displaced, and also speeds up the return of sexual receptivity in the females. However, it is clearly disadvantageous to the females who have already invested in cubs and who then adapt to it in various ways to try and minimise the loss of their existing cubs. One way in which they try to counter such a loss is to physically prevent the males from killing some or all of their cubs. A second way is to accept the inevitable and imminent loss of their cubs rapidly and without further aggression. Sometimes older cubs may not be killed by the new males. However, they will be evicted from the pride and may then be accompanied by some females resulting in only a partial pride takeover. Despite all these countermeasures, cub losses from infanticide may be considerable.

The interval between successive litters from the same female is usually 2 years, except for litters born synchronously, which can be about 43 months apart. There is some evidence suggesting that females may refuse to raise single cubs, or cubs that have become sole survivors of larger litters, when such a cub is less than 3 months old. In Etosha pregnancy control in lions was carried out successfully when there appeared to be too many lions in the area. This was done by implanting a small capsule into the neck muscles of a lioness. The capsule released a constant but minute flow of hormones into the lioness's system, simulating pregnancy and preventing ovulation for up to 5 years.

The sex ratio is usually equal in even-sized litters. However, the ratio of cubs born within the first 300 days after a male takeover of a pride favours male offspring, and it differs significantly from that of cubs born later. In large litters sex ratios also favour male cubs significantly. Lactation in lions continues for 8 to 9 months after the birth of the cubs. All female lions help to raise the young, and the young cubs are usually gathered in a crèche. Females returning from a distant hunt often drop off to sleep as soon as they return, when any cub will suckle from any lactating female. However, if a female stays awake, she will usually nurse only her own cubs, possibly allowing other cubs to suckle when she has a surplus of milk. Such generosity among female lions is therefore more a matter of indifference than one of active choice. Males are rarely affectionate to their cubs, but they do provide effective protection for them. Nomads may also breed successfully, but their cubs seldom survive the first few weeks because of poor care.

Lion cubs grow rapidly when food is abundant, but those born synchronously survive better. Cubs also eat more, relative to their size, than adult lions. When the mother returns to the den after hunting, she makes a short, deep, humming sound to call her cubs to suckle. At their den lion cubs are highly vulnerable, being attacked and killed by other predators like spotted hyaenas *Crocuta crocuta*, leopards *Panthera pardus* and black-backed jackals *Canis mesomelas*, and even in some areas by safari ants. They can also be trampled to death by big game such as buffalo *Syncerus caffer* and elephant *Loxodonta africana*. As many as 80% of all lion cubs never reach adulthood. Although well-fed cubs can survive long periods between successive sucklings because lion milk is rich and nutritious, and although cub survival is high where food is abundant, many still die of starvation and malnutrition. This happens especially in relatively prey-poor areas where the mother may be absent from her cubs for as many as 2 to 3 days at a time. In all lions, male cubs suffer higher mortality rates than females. In Serengeti and the Ngorongoro

Crater, the survival of male cubs to 1 year also depends upon the number of male cubs present in the litter, and is significantly higher when there are three or more male cubs in the litter. However, the survival of all cubs to 3 years old is more than twice as high in the Ngorongoro Crater with its more stable year-round prey base than in Serengeti with its seasonally migrating prey.

From the age of 5 months lion cubs start showing an interest in other animals, but they only start to hunt actively when about 11 months old, although they do eat meat from an earlier age. A lioness may fetch her older cubs to feed on a kill if it is close enough to them. Weaning extends over a long period, from the age of 6 to 12 months. Young lions learn to hunt by watching the adults in a pride, and leave their natal pride from the age of 24 to 42 months. However, most subadult females will remain with their natal pride. In most areas male lions which disperse become nomadic, but in the Kruger National Park such males may remain in the vicinity of their natal pride for up to 4 years. In all lions more subadults disperse when food is abundant than when it is scarce.

Range use

The general pattern of range use in lions is that a pride occupies a defended range or territory, whereas a nomad has an undefended range. Pride territories are, however, not entirely exclusive, and may show some overlapping. The territorial system in lions is dynamic because it fluctuates in response to numerous environmental factors. Pride lions patrol their territories regularly and thoroughly, often to the exclusion of almost all else and at the expense of large amounts of energy. Although neighbouring prides may occasionally meet and fight, they more often merely approach each other, and then withdraw. When a strange lion enters a pride's territory, it keeps its distance, well away from any pride members. Many prides remain resident in the same area for years.

In the Kruger National Park, females dominate the territorial segment of the lion population, and all territorial (pride) males have a high turnover rate. The territory tenure of a male lion usually only starts when he is at least 5 years old, and does not last beyond the age of 10 years. As in other cats, range use by a female lion may decrease considerably when she has small cubs to care for. In Serengeti, prides travel further and wider, and have a lower food intake than those in the more prey-rich Ngorongoro Crater. This is so because of a migrating prey





Lions in the Serengeti-Mara ecosystem often follow the migrating prey. Consequently they travel further and more widely than the lions living in areas with more sedentary prey.
Photo: J. du P. Bothma.

base in Serengeti. Consequently a lion pride in Ngorongoro Crater has a range in the order of 45 km² compared with one of 200 km² in Serengeti. The larger ranges of Serengeti lions place an additional burden on the young cubs who may become weak, and are then abandoned to die when they cannot keep up with the moving pride. In times of extreme hardship, the territorial system of Serengeti lions may even break up altogether.

In the more arid, open savannas, lions must occupy huge ranges to meet all their life requirements. These ranges are usually much larger than those recorded in the more mesic savannas. Moreover, they may expand considerably in times of drought, as happened in the central Kalahari savanna where a specific pride's range increased from 702 km² to 3900 km² in response to prey dispersion during a drought. In one study in Etosha, the territories of 14 prides varied from 150 to 1075 km². The larger the pride, the larger its territory. In the more arid, tall, deciduous woodland savanna of the Kaudam area of Namibia, two prides had ranges of 1055 and 1178 km² respectively, and one in the Tsumkwe area had a range of 1745 km². These ranges are considerably larger than what has been reported for lions before, probably in response to a prey resource that is poor in abundance and availability, but which most likely also does not reflect a natural system. In the southern Kalahari savanna with its prey-poor resources, at least three different prides of females shared the same area with a single roving male on one occasion. Six months later, seven prides shared the same

area, although not always at the same time. Sharing the same area could have been the only way to survive a period of prey stress in a generally inhospitable environment.

Activity and movement

Lions rest for most of the day and much of the night, but they are capable of extensive movement. In Serengeti, 88% of all lion kills are made at night. In Etosha, 98% of all the hunts occur at night, more often between 21:30 and 22:30 than at any other time. Even when hunting, lions will often stop to rest or to indulge in other activities. There is some evidence that lions will increase their hunting activity levels during storms, when the noise, wind and vegetation movement make it difficult for prey to detect them.

Lion movements can be seasonal or diurnal in nature. In Serengeti lions follow the migratory herds of large herbivores seasonally. The same phenomenon, but on a smaller scale, occurs in the Kruger National Park where lions will follow migrating blue wildebeest over distances of up to 50 km. In Etosha lions move a mean distance of 13,2 km in 24 hours. In a study in the southern Kalahari savanna, the distances moved by five prides in 24 hours varied from 11,3 to 26,3 km. Another southern Kalahari pride once moved a maximum recorded distance of 33,8 km in 24 hours, but the mean distance moved in 24 hours by all prides in the area was 15,2 km. This is close to that found in

Although lions rest for most of the day in some suitable shade, they are ever-watchful for an opportunity to kill unsuspecting prey. Photo: J. du P. Bothma.



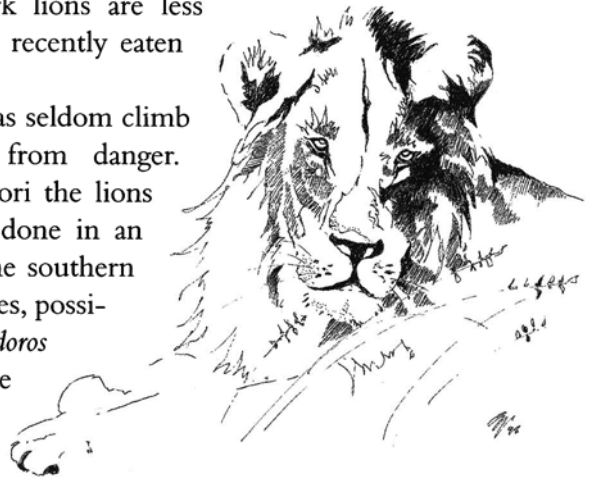


In contrast to most other areas, the lions of the Lake Manyara National Park often rest in trees, possibly to avoid the irritation of being bitten by flies.

Photo: J. du P. Bothma.

Etosha. However, although lions may cover vast distances in a single night, they rarely seem to hurry in doing so. In Serengeti, lions may also move long distances of as much as 21,5 km in 24 hours but, probably because of greater prey abundance, the distances covered over such a period are usually less (4,5 to 6,5 km) for its various prides than elsewhere. In the Ruwenzori National Park lions are less inclined to move about when they have recently eaten than when they are hungry.

When moving about, lions in most areas seldom climb trees, except occasionally, to escape from danger. However, at Lake Manyara and Ruwenzori the lions climb trees quite often, which may be done in an attempt to escape biting flies. Lions of the southern Kalahari savanna also sometimes climb trees, possibly to escape the sand tampsans *Ornithodoros savignyi* which congregate in any available shade in that hot environment.



Feeding ecology

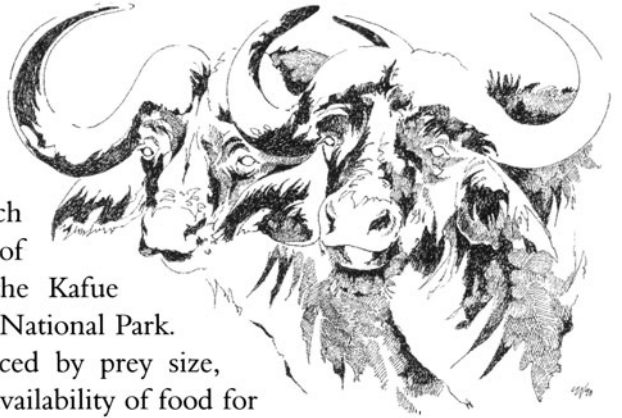
Lions hunt mainly at night. Food is important not only for daily survival, but because reproductive success and cub survival to adulthood in cats also depend upon the quality and quantity of available food. Lions eat any suitable food that is abundant and accessible, and their diet is

more varied throughout their geographic range than that of any other large cat. In areas of low food availability, environmental stress and/or a high density of lions, cannibalism may occur as a normal predatory activity on isolated occasions. Although such cannibalism has long been thought of as aberrant behaviour, it is a natural phenomenon, but one which is more often directed at juveniles by adult males as a result of infanticide, rather than as a sincere effort to procure food. Although the lion is a highly efficient hunter, it will also scavenge for food. Those lions living in the *Acacia* savanna of Serengeti, however, are hunters rather than scavengers, killing 83% of all their food while, by contrast, lions in the open plains of Serengeti scavenge 53% of their food.



Although lions eat a wide spectrum of food, they more often eat prey ranging from 20 kg in size to a buffalo of 800 kg or more. However, large lion prides may occasionally attack larger prey such as a black rhinoceros *Diceros bicornis*, hippopotamus *Hippopotamus amphibius* or even

the occasional young elephant and, in the Masai-Mara National Reserve buffalo account for a large proportion of the lion's food. In some areas, small prey make up a substantial portion of a lion's diet, but in other areas such small prey is usually taken only to tide a pride over difficult times, especially in areas where the larger prey migrate seasonally. In the relatively prey-rich Serengeti, lions use only 18 types of prey in comparison with 19 in the Kafue National Park and 38 in the Kruger National Park. This variation in choice is influenced by prey size, availability and abundance, and the availability of food for scavenging. Because lions are opportunistic feeders, they will utilise whatever food is easiest to find, and they consequently scavenge readily in some areas, but rarely so in others. Other carnivores are not generally used by lions as food, even when they are hungry.



THE AFRICAN LION

Lions eat a wide spectrum of prey varying in size from about 20 kg to a buffalo of 800 kg or more.

Photo: J. du P. Bothma.



The prey size selected by a lion appears to increase with the number of lions present. There is an optimum pride size for the type of food resource of a given area, in which the combined energy provided is more efficient for the number of lions in the pride. When the pride is too large for the size of prey captured, it leads to intense competition at the carcass, to the detriment of the survival of the group. In Serengeti, for example, large lion prides may form when the migratory herds are present, but these prides will split into smaller groups which are energetically more efficient when the prey migrates out of the area. Opportunity and physical possibility will often determine whether a lion will kill a specific prey. Opportunity requires a lion to share the same habitat and activity cycle as its potential prey. For example, in Kafue, the puku *Kobus vardonii* and lechwe *Kobus leche* are abundant, but they are hunted with great difficulty by the lions who avoid the swampy habitat used by these prey. In comparison, the buffalo there are frequently killed by lions but more in the dry season (38,4% of all lion kills) when the vegetation density is reduced by bush fires, than in the wet season (18,1% of all lion kills) when the grass is tall and the cover dense. Lions in that region also often kill warthogs *Phacochoerus africanus*, which are easy to find.

In some areas lions definitely select specific prey. In Kafue they choose prey in their prime that are consequently in good condition. However, they also kill a higher proportion of prey in poor condition than the other predators present, and they definitely take fewer juvenile



Small herbivores such as the warthog are often killed by lions.

Photo: J. du P. Bothma.

animals than the other large carnivores. In other areas there seems to be little active selection of sick and disabled prey. However, some prey age groups may be more vulnerable than others, as happens in Savuti where lions kill significantly more buffalo cows than bulls, and where the buffalo bulls killed are mostly old individuals. Despite being effective hunters, lions may be infrequent feeders. In the Kruger National Park, for example, 47% of all lion stomachs examined were empty. Although these lions were found to feed at a mean rate of once every 4 days, some do so daily. The maximum interval between successive feeds there is 13 days.

The only known area where lions feed on a large proportion of small mammal prey consistently, is the southern Kalahari savanna with its poor prey resources. Some lions also eat large quantities of green grass, as do many other carnivores for reasons still unknown. In Etosha, lions rarely scavenge, but during the occasional anthrax epidemic, these lions do not have to hunt because they can live from scavenging the abundant carcasses, although some lions may continue to hunt. The lions there are not susceptible to anthrax and therefore do not suffer from the disease. Lions do not often eat other carnivores, yet they do kill carnivores such as black-backed jackals, spotted hyaenas, brown hyaenas *Parahyaena brunnea* and leopards, for no apparent reason.

Lion behaviour changes dramatically from day to night, transforming a shy and wary daytime animal into a bold and aggressive one at night. G.B. Schaller, who studied the lions of Serengeti for many years, states

that the movement of a cat is never more beautiful than when a lion purposefully snakes towards its prey. That fleeting moment of pause at the end of the stalk seconds before the final explosive rush, is one of almost unbearable tension to any observer. Lions hunt mainly at night when there is a greater chance of successful stalking. In their predation, however, they show extensive variation based upon the ecological constraints of each region, because the success or failure of a hunt depends as much upon the environment and the response of the prey as on the lion itself. In Ruwenzori lions hunting by moonlight are less successful than when there is no moon, possibly because the prey can detect the lions with more ease in the moonlight.

Lions must seek every possible advantage when hunting because of the fleet-footedness and keen senses of most of their prey. A lion normally starts hunting with a systematic search which is not directed at any particular prey animal. In searching, it sits or walks around slowly, scanning the environment. When potential prey is detected, a slow and deliberate stalk follows. Stalking can occur in bouts with the lion moving slowly and crouching low over the ground, often staring intently at its prey, and freezing when the intended victim becomes restive. Yet stalking can also take place as a slow but continuous movement with the lion making use of all available cover. Such cover would include all the main environmental features of an area such as weather, vegetation height and density, wind direction and even the time of day. Most of the hunting is done by the females and in Serengeti only 3% of more than a thousand observed lion stalks involved males. The lions there also usually hunt at night and do not seem to select for wind direction when hunting. In Etosha, by contrast, they hunt significantly more often and more successfully in downwind conditions. Lions may increase their hunting activities during rainstorms when the noise, wind and vegetation movement make it difficult for prey to detect the hunting lions.

A typical lion hunt involves a stalk of varying length during which the lions orientate themselves, mainly by sight. This is followed by a final rush which may reach speeds of up to 60 km/h for a short time, resulting in the kill if successful. The lion is not built for a prolonged chase. Its heart, for example, forms only about 0,5% of its body mass as opposed to 10% in a spotted hyaena, which can sustain chases over long distances. Lions will, however, adapt their hunting technique to the prevailing circumstances, sometimes surprising a prey animal at rest and killing it by simply pouncing on it without stalking or chasing, or by hunting from ambush. In Serengeti such opportunistic hunting attempts have the highest success rate. Female lions hunt proportion-

ately more often than the males, and ecological factors will lead to local adaptations in the hunting behaviour of male lions.

Lions are known to hunt singly or in prides. Hunting as a pride requires less cover for a given lion, and it is done most frequently under the additional cover of darkness. When hunting as a pride, the individual pride members spread out in different directions to stalk a common prey. In doing so, the prey may or may not be surrounded. Often some pride members will circle the prey, while others wait to ambush any prey that moves towards them. The circling females usually initiate the attack, causing the prey to flee into the path of the ambushing females who make the kill. Pride hunting also seems to require an optimum pride size for maximum hunting efficiency. In the dry season in Etosha the optimal size for hunting would appear to be two females, while during the wet season female prides of all sizes each obtained more than the minimum daily food requirement for survival. When hunting in a pride, each lioness in Etosha repeatedly occupies the same position in the hunting formation. This preference for a specific hunting position seems to ensure a higher degree of success than when a position is chosen at random. However, the hunting behaviour of an individual pride member will differ according to variations which may occur in the composition of the pride over time, and in response to the hunting behaviour adopted by other pride members. Whatever the case, hunting as a pride will increase the feeding efficiency of each of the members of that pride, especially during the dry season.

In Serengeti male lions do not participate in hunting as a group, and also pursue their migrating prey less frequently than females. Nevertheless, they clearly benefit from any prey which has been hunted by the female members of the pride, and can therefore be construed to be cheating. Such cheating by refraining to help in the hunt is common in lions, and some females also do it sporadically, but especially when the prey is relatively common or easy to kill. In Etosha where prey occurs at low densities in isolated pockets, the females of a pride will probably cooperate more often and cheat less frequently.

When making a kill the lion is both a stalker and a runner, and the killing method used varies with prey type and size. Even when hunting as a pride, the actual kill is usually done by a single lioness when hunting easily killed prey such as a warthog or a wildebeest *Connochaetes taurinus*. However, when the prey is more difficult to kill, several individuals may cooperate in making the kill. The prey base of a given area therefore influences the degree of cooperative hunting practised by lions. In the flat, open savanna of Etosha, for example, lions often hunt

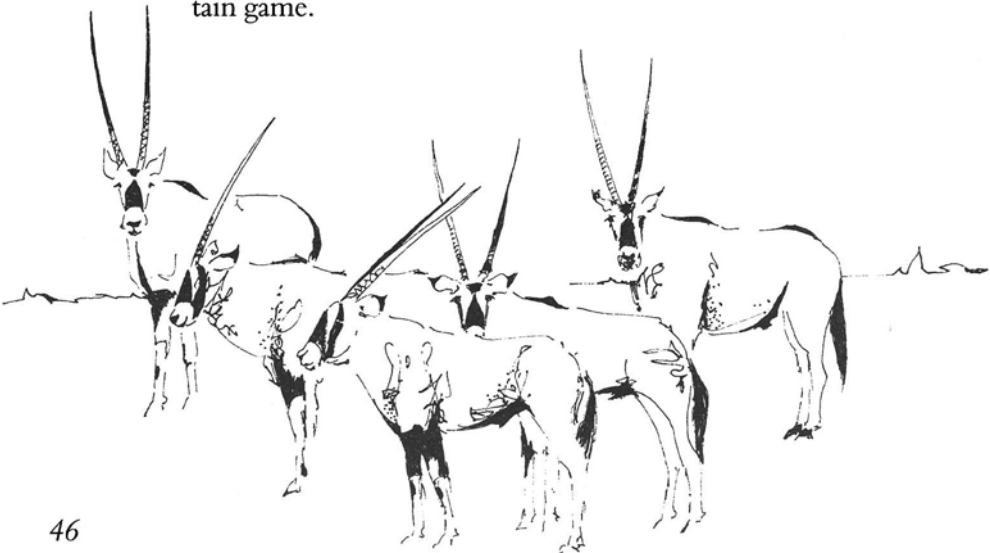
THE AFRICAN LION

With its long canines, a lion kills its prey easily.
Photo: C.H. Walker.



the fleet-footed springbok *Antidorcas marsupialis*, which requires a great deal of teamwork. By contrast, the hunting of massed prey during migration in Serengeti can be quite opportunistic and disorganised.

A lion is extremely powerful and when making a kill even the smaller lionesses can grab and pull down large prey such as a zebra *Equus burchellii* by simply using a grip on its rump. The prey may be stunned by a blow to the head, but it is usually suffocated with a muzzle grip, although its neck may also be broken occasionally. The killing method may vary, however, as the lion may adopt a special technique to kill certain game.





In the southern Kalahari savanna the lion has developed a special technique which allows it to kill a gemsbok which could easily kill its attacker with its long, rapier-like horns.

Photo: J. du P. Bothma.

For example, the potentially lethal gemsbok *Oryx gazella* in the southern Kalahari savanna is never attacked from the front. Instead, it is attacked from behind, with the lion jumping on to the gemsbok's haunches, breaking its back at the lumbosacral joint, and then seizing it by the muzzle or throat to suffocate it or crush its neck. The back is not broken by the impact of the attack but by a deliberate, sharp upward jerk. This is an adaptation to a type of prey which has long been known to be able to kill an attacking predator with its rapier-like horns. The fact that lions which kill gemsbok in Etosha do not adopt the same approach as in the southern Kalahari, has been ascribed to the smaller occurrence and diversity of the prey base available in the Kalahari, which makes killing gemsbok a more frequent necessity there.

Elsewhere lions also adopt special killing techniques for specific prey. For example the giraffe *Giraffa camelopardalis* is killed with a specialised technique which has been developed to knock this animal off its feet, pulling it down in such a way that the hooves of its powerful front feet are avoided. A giraffe uses these feet to chop down at an attacking lion with deadly accuracy and even its hind legs can be employed to dangerous effect in a powerful backward kick. In attacking dangerous prey, lions may be killed or injured. Although temporarily injured lions will be cared for by other pride members, they must still attempt to avoid injury at all costs. When their prey is not caught at once, lions usually do not pursue the victims for long distances, although C. McBride believes that Savuti lions are capable of sustained bursts of speed over

In attacking a porcupine, a lion may sustain potentially debilitating injuries, which may eventually lead to starvation and death. Photo: J. du P. Bothma.



distances of as much as 1 km. In Etosha fleet-footed prey is usually hunted cooperatively, during which 73% of the prey killed is hunted from an ambush involving a chase of less than 10 m.

The lion's killing rate varies from area to area depending upon the terrain, pride size, prey composition and abundance. In Ruwenzori, only 28,8% of all the lion hunts are successful, but hunts involving an ambush are more successful (57,1%) than others. In Serengeti opportunistic hunts without much preparation are the most successful (61%), followed by hunts involving stalking by single lions (17 to 19%), and then by those of single lions chasing prey (8%). However, almost half of all the hunts there involve two lions hunting together, with a killing success of 30%. For larger prey, the killing rate increases with increasing pride size. Single lions in Serengeti kill 15% of all the large prey they hunt, whereas prides of 6 to 8 lions kill 43% of the prey hunted. In Etosha lions kill 15% of all prey hunted, but single females are mostly unsuccessful (2,3% success) in capturing large, fleet-footed prey. Cooperative hunts in the region have a mean success rate of 27%, but this also increases with increasing pride size. Multiple kills sometimes occur too. During 12 hunts recorded in Etosha, a pride killed two prey animals in the same hunt, and three prey animals in each of three different hunts.

Lions occasionally kill unnecessarily. This happens in predators when many more prey are killed in one attack than could possibly be eaten, and may occur because of unusual circumstances when the prey

is not reacting to normal stimuli, such as during a violent thunderstorm. Surplus killing in the wild is rare among lions, but a pride of lions did once kill 15 buffalo in a single attack in the Kruger National Park. Also, a severe drought in the southern Kalahari System in 1985 led to the concentration of thousands of game at waterholes where lions would lie and wait to attack the milling mass. As these lions were usually already satiated, they ate little of their kills. Once the surplus killing trigger has been released, the impulse seems to continue to operate until all vulnerable prey have been attacked, or the lions have become exhausted.

When feeding at a carcass, lions are well organised socially, although there is considerable squabbling. The larger males are dominant over the females, but in the Kruger National Park large territorial males are present with pride females for only 6,1% of the time, and at only 13% of the kills of such prides. Young cubs usually get whatever food happens to remain after the adults have fed, but they may occasionally be allowed to feed with the males. A small kill or a piece of a larger carcass can also be claimed by a single lion, especially if the lion can carry the food away on its own. Heavy carcasses are pulled backward into some shade by one or more of the lions. They feed while lying on their bellies, and are the only cats which habitually do so. Most of the others sit, crouch or stand while feeding. The prey may or may not be gutted before feeding begins. Unlike most other cats, lions seldom eat the stomach, but they do eat the intestines of their prey. The viscera are sometimes covered with soil and vegetation. The lion that made the actual kill usually rests for a while, allowing the other lions in the pride to start feeding first. When feeding, males usually start on the buttocks, while the females and cubs start on the internal organs. Porcupines are frequently hunted in the southern Kalahari savanna, and they are partially dequilled by lions and leopards before being eaten. Lions consume their large prey as completely as possible, and a pride of lions can take up to 4 days to finish a big carcass such as a buffalo.

In Savuti a lion's food intake is 1,6 times higher in the rainy season when more large prey is available than in the dry season. In Serengeti lone females may often eat more than the individual females of a pride. The main food intake per sitting for a Serengeti lion is 16 kg, but one of the males is known to have consumed an estimated 53 kg of food in one night. In Etosha, however, lions that hunt alone during the prey-poor dry season do not get the estimated minimum of 5 to 8,5 kg of food required daily for long-term survival, and experience food stress periodically as a result.

A porcupine is partially dequilled before a lion or leopard starts to feed on it.
Photo: J. du P. Bothma.



In the Kruger National Park lions have a slower rate of digestion, and they also eat less frequently than spotted hyaenas. Lions generally experience some degree of competition for food from spotted hyaenas and they may lose a portion of their food to these hyaenas, but this is dependent upon the lion pride size. In Serengeti lions may lose 10% of the meat from a carcass to scavenging spotted hyaenas if the pride consists of fewer than four lions. The Savuti lion prides often have a shortage of adult males and therefore prides consisting of females and subadults only, may have almost 20% of their food stolen by spotted hyaenas. In studies of animal behaviour this is known as kleptoparasitism. The losses are most frequent in small prides. In the absence of large male lions, spotted hyaenas can drive female and subadult lions away from their kills, provided that they outnumber the lions by at least 4:1. Consequently the larger the pride, the more successfully it can defend its kill. Nevertheless, even those lions which are driven off their kills have usually fed well before they are deprived of their food, although such action does constitute a constant energy drain which forces these lions to hunt more frequently than would otherwise be necessary.

When water is available, lions will drink regularly, and there is no apparent preference for water quality. However, even when water is available, they may go without drinking for up to 5 days. In the southern Kalahari savanna lions are found up to 250 km away from the nearest water and are consequently independent of free water. They make use of metabolic water, the fluids of their prey and the moisture in wild fruit, and may even lick moisture off each other's fur when it rains. In



It can take a pride of lions several days to finish a large carcass.
Photo: C.H. Walker.

Kenya they are also known to chew *Sansevieria* plants and to pull them out of the ground to get at the moisture-rich roots. In cool weather the lions of the Hluhluwe-Umfolozzi Park do not obtain a significant portion of their water from drinking although it is available. However, in hot weather about 50% of their water intake is from drinking. Females with cubs have a greater need for moisture than other lions. When lions do drink water, it becomes a social event for pride members. They also pant rapidly at a rate of up to 140 pants per minute to avoid heat stress.



Relationship with other wildlife

The question of whether lions and other large predators can influence their prey negatively has often been debated. In the early years of conservation in Africa, lions were shot as a deliberate management strategy because it was believed that prey populations could be increased in this way. In the process thousands of lions were shot in the Kruger National Park alone up to 1946. From 1974 to 1979 lions and spotted hyaenas were again shot there in an attempt to stop a major decline in blue wildebeest and zebra numbers. This culling was later stopped when habitat change from years of excessive rainfall, and not predation, was found to be the significant cause of the decline in these prey animals. The lions soon restored their numbers by immigration and increased reproduction.



It is now generally known that predators cannot regulate their prey numbers in natural areas, unless such prey is already low in number. The prey is regulated mainly by their dry-season food supply, and to a lesser extent by parasites and disease. Where man intervenes in the system, however, by creating artificial waterholes or introducing prey strange to an area for example, lions can severely influence their prey at times. In Serengeti lions are only responsible for a small portion of all the mortalities of their most common prey, the wildebeest. In the Klaserie Private Nature Reserve, the lion population dispersed after prolonged droughts caused their prey to diminish considerably in numbers.

Although lions kill the occasional elephant, they are generally wary of these large herbivores which can easily intimidate them.

Photo: C.H. Walker.



The lion of the African savannas does not compete much with other carnivores because all the larger carnivores in these savannas are usually separated ecologically. Although the lion is the leopard's closest competitor where there is some prey overlap, the degree of competition in Serengeti is reduced because the leopard usually has a much more varied diet than the lion. Lions readily appropriate spotted hyaena kills, but the reverse is equally true. It all seems to be a matter of group size and aggression. In Savuti, for example, lion prides often suffer from a lack of large males. Consequently they may lose as much as 20% of their food when outnumbered 4:1 or more by spotted hyaenas. Even when outnumbered 2:1, the lions are mobbed and disturbed by scavenging spotted hyaenas who may often feed alongside the lions in the absence of a large pride male. Therefore prides without a large male tend to hunt in groups of females and subadults which are sufficiently large to defend a kill against spotted hyaenas for long enough to satiate themselves. Nevertheless, this competition is a constant energy drain on these lions.

Population dynamics

Lion population dynamics varies from region to region because of environmental and other variables. For example, the lions of Serengeti clearly have a harder life than those of the Ngorongoro Crater. On the Serengeti Plains the large migratory prey herds make the lion's food supply more ephemeral, water is scarcer in the dry season, and denning sites are more widely scattered than in the Ngorongoro Crater. Consequently cub mortality in Serengeti is highly seasonal, and also much higher than in the Ngorongoro Crater. In the Kruger National Park the oldest lion collected was a 16-year-old male. The oldest known female collected was 14 years old, and there are considerably more old females than males in the population. All lions older than 12 years are also in poor condition. It is believed that wild lions in Serengeti can live up to 18 years.

The sex ratio of lions also varies from region to region. In the Kruger National Park male lions were found to be vital to pride functioning, although they spend the majority of their time away from the pride females, either as male coalitions or alone. There are usually two territorial males per pride and 2,9 females per male. In the southern Kalahari savanna the sex ratio of adult lions is 1,4 to 2,1 females per male. In cubs it is 1,6 females per male. The sex ratio of adult lions in Etosha is almost equal, as it is in Selous and Serengeti. However, other

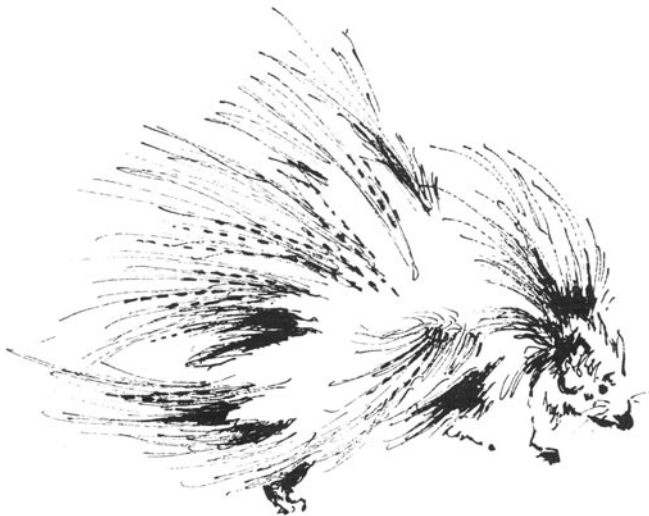
authors believe the sex ratio in Etosha to be 1,4 females per male which is similar to what it seems to be in most of Africa. In a deciduous woodland elsewhere in Namibia females outnumber males by 1,4:1.

In Serengeti adult lions form 57% of the population, and in the subadults the males are almost twice as abundant as females. The annual recruitment rate there is 11%. Cubs form 17% of the population and subadults 26%. In Selous juvenile lions make up 21% of the population. By contrast, 60% of the lions in the Nairobi National Park are juveniles, possibly because of the higher reproductive rates and better cub survival. Some authors believe that cub mortality rates may be the best indicator of lion population dynamics. In Serengeti 67% of all the lion cubs die each year. In one area 28% died of starvation, but more cubs probably die of starvation when the prides follow the migrating



herds of prey than for any other reason. Of all the lions, most die of disease, starvation, abandonment, old age or violent conflict with other large predators, including other lions. In Serengeti 41% of the lions which die are adults in their prime and only 10% of all the lions born there eventually reach old age. Buffaloes and elephants occasionally trample lion cubs and some adults are crippled when they attack dangerous prey. The type of prey resource available obviously influences lion survival, because some prey are more difficult or dangerous to capture than others. Mortality rates also differ between the sexes, with males being more vulnerable as was found in the Kruger National Park. There the adult males are not necessarily territorial, and intraspecific competition is high among the males.

Lions are prone to various diseases but immune to others. In southern African lions there is widespread infection from the canine distemper virus, but there are usually no catastrophic mortalities. Nevertheless, in a recent outbreak of canine distemper in the Serengeti-Mara ecosystem 33% of its estimated 3000 lions died of this disease. In Namibia, Botswana and Zimbabwe isolated cases of rabies are found in lions, but it remains a rare and sporadic disease in the lions of the African savannas. Although lions are sometimes exposed to anthrax from affected herbivores, they are fairly resistant to this disease. A recent severe outbreak of tuberculosis amongst the African buffalo in the southern part of the Kruger National Park is now threatening the survival of some of the lions which prey on them there. Lions are also heavily parasitised by all manner of external and internal parasites.



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