

Jacobus du P. Bothma

Carnivore Ecology in Arid Lands

With 18 Figures



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Family Felidae

3.1

Taxonomy, Distribution, and Status

Many cat species occupy diverse habitats. The same species sometimes ranges from deserts to tropical forests. This requires great adaptability, a characteristic of all cats. All felids rely on their physical environment for successful prey-use, which is a major facet of survival (Kruuk 1986). They are also more strictly carnivorous than other carnivores, and markedly more so than canids (Kleiman and Eisenberg 1973).

Felids spread from Europe throughout Africa. The Eurasian dirk-toothed cat *Megantereon cultridens*, for example, is found in South African fossil deposits along with a form of leopard *Panthera pardus* which was the most common predator of its time, although it was larger than modern leopards. This was some 1.8 to 1 million years ago. The cheetah *Acinonyx jubatus* is also present in these fossil deposits (Turner 1993). Today the family Felidae is diverse and occurs over much of the world. The felids are divided into three subfamilies, the Acinonychinae which is represented by the cheetah only, the Felinae and the Pantherinae. Eighteen genera and 36 species are currently recognized (Wozencraft 1993).

The threat to the conservation of all 36 cat species excluding the Pampas cat *Oncifelis colocolo* is such that they are either listed in Appendix I or II of CITES (Wozencraft 1993). Furthermore, the following cat species or subspecies are considered by the IUCN to be critically endangered (Nowell and Jackson 1995): the Asiatic cheetah *Acinonyx jubatus venaticus*, Florida panther *Puma concolor coryi*, eastern cougar *Puma concolor cougar*, Anatolian leopard *Panthera pardus tulliana*, Arabian leopard *Panthera pardus nimr*, Amur leopard *Panthera pardus orientalis*, North African leopard *Panthera pardus panthera*, Amur tiger *Panthera tigris altaica*, Sumatran tiger *Panthera tigris sumatrae*, and the South China tiger *Panthera tigris amoyensis*. In addition, 11 more cat species or subspecies are considered endangered. They are: the northwest African cheetah *Acinonyx jubatus hecki*, North African serval *Lynchailurus serval constantinus*, Iberian lynx *Lynx pardinus*, iriomote cat *Prionailurus bengalensis iriomotensis*, Asiatic lion *Panthera leo persica*, Caucasus leopard *Panthera pardus ciscaucasica*, Sri Lankan leopard *Panthera*

pardus kotiya, North Chinese leopard *Panthera pardus japonensis*, Javan leopard *Panthera pardus melas*, tiger *Panthera tigris* and the snow leopard *Uncia uncia* (Nowell and Jackson 1995). Further details on the status and distribution of the world's cats can be found in Nowell and Jackson (1996).

Ten cat species occur in Africa, but only the black-footed or small spotted cat *Felis nigripes* and the African golden cat *Profelis aurata* occur in Africa only. The leopard *Panthera pardus* has the widest range of all large cats, occurring from deserts to moist tropical forests in Africa, the Middle East and Far East, northwards to Siberia and southwards to Sri Lanka and Malaysia (Hes, 1991). There has recently been a suggestion that the current 27 subspecies of leopard be reduced to 8, but this suggestion is not yet generally accepted (Anonymous 1996a).

The cheetah belongs to a subfamily that was previously much more diverse, and even had two extinct species in America (Caro 1994). As recently as 2000 years ago, four cheetah species still roamed open habitats in Africa, Asia, Europe and North America (Hunter 1996). The extant cheetah has been the subject of some controversy regarding its poor conservation future because of its relative genetic poverty. Of the current cheetah subspecies, the Asiatic cheetah probably numbers less than 50 individuals in Iran, while of the northwest African cheetah there are only several dozen left in the mountains of southeastern Algeria and possibly southern Morocco, and some 150 on the Aïr and Termit Mountains in Niger (Nowell and Jackson 1995, 1996). The cheetahs of the Sahara Desert are smaller and paler than cheetahs elsewhere (Nowell and Jackson 1995). Genetically, the cheetah is interesting for the occurrence of the so-called King cheetah genetic coat colour variation which is mainly found in the more arid parts of southern Africa (see below).

It is now accepted that all cheetahs are genetically similar with virtually no genetic diversity (eg. Hunter 1996), having a mean polymorphism of 3.2% and a mean heterozygosity of 0.013 as opposed to 14.7% and 0.036 respectively in other felids (Caro and Laurenson 1994). Another study shows no allelic diversity in 55 cheetahs at 52 loci with a polymorphism of 0% and a heterozygosity of 0. This has to be compared with the considerable allelic diversity in seven other felids which have a polymorphism range of 8 to 28.8% and a heterozygosity range of 0.029 to 0.072. These values are typical of mammals generally (Hunter 1996).

The cheetah's skull characteristics also reveal a high level of asymmetry, with the left, lower jaw longer than the right one. Such asymmetry is a common result of inbreeding, and the cheetah is the most genetically impoverished species ever examined. This is probably the result of a series of population bottlenecks, one of which occurred about 6000 to 20 000 years ago. It may also be because of a great interchange between subpopulations (Caro 1994; Nowell and Jackson 1996) at a time when many other large mammal species became extinct (Hunter 1996). The factor(s) which would or could have led to these bottlenecks are unknown (Nowell and Jackson 1996). In comparison,

the cheetah's closest relative, the puma or cougar *Puma concolor*, has abundant genetic variation (O'Brien 1994).

The cheetah's lack of genetic diversity seems to be linked to semen with spermatozoal concentrations seven to 10 times less than those of domestic cats, and abnormal spermatozoa levels of 70 to 80% compared to 29% in domestic cats. Such lack of genetic diversity may explain the 29.1% rate of infant mortality in captive bred cheetahs (Hunter 1996). However, the cheetah has survived for at least 10 000 years despite its genetic impoverishment. Merola (1994) therefore believes that genetics are no real threat to cheetah conservation. Caro and Laurenson (1994) add that it has yet to be shown that inbreeding has led to the extinction of any wild population of cheetahs. They also believe that genetics have been overemphasized and environmental causes underemphasized in cheetah population dynamics. The real threat to the cheetah therefore seems to lie in a combination of genetic and environmental factors. Moreover, successful cheetah breeding by means of artificial insemination and other ways (Lindburg 1989), contributes to the cheetah's survival.

The King cheetah coat pattern mainly occurs in arid southern Africa. It is one of several known mutant skin patterns in cheetahs, and it is controlled by a single recessive gene (Lindburg 1989). Once regarded as a separate species *Acinonyx rex*, this genetic variant of *Acinonyx jubatus* has softer, longer and silkier hair than normal. The spots are also replaced by dark bars or stripes on the dorsal surface (Van Aarde and Van Dyk 1986). Almost all King cheetah sightings are from relatively arid areas in southern Africa between latitudes 17 and 25 °S and longitudes 24 and 33 °E. This area includes Zimbabwe, Botswana and South Africa, an area where the cheetah's coat pattern varies much between localities. The King cheetah coat pattern was at one time erroneously thought to represent an aberrant leopard or even a leopard-cheetah hybrid (Hills and Smithers 1980). There are recent reports of a King cheetah patterned skin from Burkina Faso too (Frame 1992; Nowell and Jackson 1996).

Of the other cats, the Asiatic lion *Panthera leo persica* of western India also has low genetic variation, leaving it vulnerable to survival. Genetic studies suggest that these lions separated from African lions 55 000 to 200 000 years ago. Visible differences include the belly fold of Asiatic lions, which is rare in African lions, sparse manes in male Asiatic lions, and even differences in skull shape (Johnsingh and Chellam 1991). In this context it is interesting to note that the Somali lion, which is geographically the closest of the African lions to the Asiatic lion, lacks a mane even in large, adult males (Fagotto 1985). In contrast, the two extinct subspecies, the Barbary or Atlas lion *Panthera leo leo* of Morocco, and the Cape lion *Panthera leo melanochaitus* of southern South Africa, occurred on the northwestern and extreme southern opposite ends of the continent from the Somali lion. These subspecies had dense, well-developed manes extending over the shoulders and chest to the belly (Mazak 1964, 1970; Smithers 1983; Anonymous 1996b). The Asiatic lion population, al-

though resident in a relatively humid area with a rainfall of 650 mm in the east and 1000 mm in the west, also went through a major genetic bottleneck in the late 19th and 20th centuries with an estimated population low of no more than 20 individuals compared with an estimated 221 individuals in 1990 (Chellam and Johnsingh 1993). By 1995 there were an estimated 304 Asiatic lions, all in the Gir Lion Sanctuary of India or its adjacent areas (Singh 1995).

3.2

Social Behaviour

3.2.1

Group Formation

Felids range from totally solitary to highly social animals. Most wild cats are solitary as adults for most of their lives, the African lion (Fig. 3.1) being an exception. In the Kruger National Park, the largest lion pride recorded by Smuts (1982) is 21, but Aiken (1987) has recorded as many as 39, but possibly more, lions in a pride there. One or two large males usually dominate the pride (Grobler et al. 1984). In the Etosha National Park, an area receiving <400 mm of rain per year, the mean density of lions is lower (1.6 to 2 subadult and adult lions per 100 km²) than anywhere else in Africa, yet the mean pride size is 8.8 (range 5 to 16) (Stander 1991). This compares with the modal group size of 2, and a mean pride size of 2.8 lions (maximum 13) which is found in the more mesic Serengeti National Park (Schaller 1972). In the Etosha National Park, lion densities correlate directly with the number of available water points (Stander 1991). The lions there also live in social groups with no clear social hierarchy among pride lionesses as is found elsewhere in Africa (Stander 1992a). In the southern Kalahari, which is more arid than Etosha, the density of lions is estimated at 1.3 lions per 100 km² (Smuts 1982) and this density and the mean pride size of 4.2 individuals (maximum pride size 21) are smaller than in the lions of Etosha (Eloff 1973a, c). Density and group size apparently were also low in the Barbary lion (Mazak 1970). It is believed that these variations in group size reflect a selective capacity of social animals to adjust group size to a hierarchy of ecological conditions. Primarily, these differences reflect the temporal and spatial patterns of resource availability, which in turn influence foraging efficiency, mating probability and reproductive success (Caraco and Wolf 1975).

A further factor influencing optimal lion group size in the Savuti Marsh may be the influence of competition by other predators such as the spotted hyaena. There, the lion prides suffer from a shortage of adult males: one male per 5.7 females compared with one male per 1.7 to 2.4 females in the southern Kalahari and Serengeti. Consequently, groups of female and subadult

lions lose almost 20% of their food to spotted hyaenas. Such losses are most frequent for lions living in smaller groups (Cooper 1991). Increased food availability in lions is known to lead to increased pride size because of higher cub survival rates. However, it also leads to new prides being formed (Hanby and Bygott 1979). Therefore it can be expected that lion group size in arid areas, with relatively sparse food resources, will not be overly large. Also, as in the Serengeti, the onset of the dry season may cause larger lion groups to break up into smaller groups which are energetically more efficient (Caraco and Wolf 1975).

The only other felid that occasionally forms social groups is the cheetah. Their male offspring born together may remain together for life to form a male group. Also, a female and her dependent subadult offspring move around together. However, non-relatives may occasionally join forces if such a larger group allows the take-over of an existing territory or the fending off of a challenge from intruders (Caro 1994). Larger group size in male cheetahs seems to be related to greater prey availability as happens with lions and cheetahs in the Serengeti (Caro and Collins 1987a,b). Moreover, male sibling cheetah groups seldom number more than three to four individuals because there is seldom more than such a number of male siblings in a given litter (Caro and Collins 1987a,b). Male cheetahs in the arid southern Kalahari, however, seldom move around in groups of more than two individuals (Labuschagne 1979). Grouping in male cheetahs is most probably a response to intraspecific competition, with greater food intake in groups being a secondary consequence (Caro 1994). However, group hunting as such in felids will be discussed later.

3.2.2

Nomads

In the Kalahari Gemsbok National Park, many subadult male lions leave the park and therefore do not remain in established prides (Smuts 1982). These nomads wander widely, often following migrating game in the Kalahari as they do in the Serengeti (Schaller 1972). However, in the Etosha National Park, solitary hunting lions are the only ones who do not meet the estimated minimum daily food requirement per lion (Stander 1992b). In the Serengeti, any male lion cubs which survive to adulthood leave the pride together, and remain together as a group of breeding males in a different pride (Bertram 1979). There the nomads of the lion population form about 20% of the entire population. It occasionally includes one, or a few, nomadic females of any age, which may settle in an area and build up a pride by recruitment of young. As environmental conditions improve, however, the number of nomadic lions decreases because fewer subadults leave their prides and more subadult females form new prides. Mortality is usually high among nomads (Hanby and Bygott 1979). In the southern Kalahari, adult male lions often move

between prides which contain females and young of both sexes. At least three different prides shared a common area with a single roving male on one occasion there (Eloff 1973a). In the Savuti, adult male lions in resident prides are rare (Cooper 1991). Some females also become nomads, although these in turn may form small groups (McBride 1990).

Single, male cheetahs are at a great disadvantage in fights when attacked by a group of males. However, there is a lack of dominance in a group of males, who probably share in mating opportunities (Caro 1994). Nomadic, male cheetahs generally live shorter lives, are in poorer physical condition, and weigh less than territorial ones (Caro and Collins 1987b).

3.2.3

Communication

Most mammals display an array of vocal and visual communication systems, but especially so in the more social species. In some carnivores, such as the mongooses, this has led to highly specific messages about the location of food and predators (e.g. Beynon and Rasa 1989) and to intergroup activities in hyaenas (Mills 1990).

As most cats live solitary lives, vocal and visual communication between them has developed to varying degrees. In cats, complex expressive movements are highly developed, despite most cats being solitary (Schaller 1972). As the body postures and vocal expressions within one species are likely to be relatively similar from area to area, this section will deal more with chemical communication, which, intuitively viewed, may be influenced by the aridity of the environment and its sparser resources. However, no such evidence could be found in the literature.

Communication among African lions has been dealt with extensively by Schaller (1972) in Serengeti lions. There it includes vocalizations, facial expressions, postures and scent. Long-range signals in these lions mainly involve scent-marking and roaring, the intensity or frequency of which varies with circumstances (Schaller 1972). Both of these are also more frequent when intrusion pressure by nomadic lions is the greatest (Hanby et al. 1995).

Among the glands used by cats in scent-marking, the highly-developed ones above the tail, the anal and praegenital glands, the circumoral and sub-mandibular glands and the glands between the footpads are used often (Verberne and Leyhausen 1976). As little is known specifically about scent-marking by lions in arid areas, the information on Serengeti lions (Schaller 1972) will mainly be summarized here as it should probably also occur in the lions of more arid environments. Furthermore, there are also long, dry periods in the Serengeti ecosystem.

Any lion will leave its tracks, urine and faeces in the environment as it moves about. These may serve as signals to other lions passing by later. Lions spray-urinate a musky-smelling substance on vegetation. This substance is

expelled from their anal glands and is mixed with the urine squirted. The resulting mixture is used in small quantities, and distributed widely (Verberne and Leyhausen 1976). The mixture is squirted upward and backward at an angle of 30 to 40° for a distance of up to 3 to 4 m. Urine-spraying is predominantly done by male lions. When spray-urinating, male lions prefer to do so against vegetation, often a tree trunk at least 1 m high.

Several felines scrape on the ground or wipe with their feet (Verberne and Leyhausen 1976). Such scrapes or wipes are used by male and female lions for chemical communication. When scraping, a lion rakes the ground from two to 30 times with the claws of the hind feet, undoubtedly leaving a concentration of scent in the process. African lions often spray-urinate while scraping (Schaller 1972; Verberne and Leyhausen 1976) or do so immediately afterward. Such urination usually consists of spurts which often wet the animal's hind legs. There is evidence that lions can distinguish the scents of individuals within the pride, and between prides (Hamilton 1976). However, lions have never been observed to defecate on scrapes as tigers often do. This suggests that scraping in lions is not as important in scent-marking as it may be in tigers. The frequency of scraping in lions varies with the habitat. Male lions in prides spray urine or scrape at a constant rate throughout the year. Spraying and scraping by one lion frequently stimulates others to do the same. Previously used sites may become permanent landmarks. Lions of all ages also sharpen the claws of their forepaws by raking tree trunks, scarring some trees repeatedly. Such trees also serve as chemical sign posts (Schaller 1972).

Apart from the contact between adults when mating, and between a female and her cub, there is little physical contact between leopards (Fig. 3.2), although adults may occasionally fight (Scott 1985). Scraping, tree-scratching and urination are all forms of communication found in leopards (Smith 1978; Bothma and Le Riche 1984). In the Serengeti, the faeces of a leopard is not used to mark range boundaries as in the Masai Mara National Reserve (Scott 1985). However, ground scraping and tree-clawing occurs occasionally in the Serengeti, as it does in the Matobo National Park (Smith 1978). In the latter area, one specific tree was clawed repeatedly by a specific male leopard. Tree-clawing in the Masai Mara National Reserve leaves an odour-tainted visual and olfactory mark establishing the leopard's whereabouts to itself and to conspecific individuals. It also stretches the muscles involved and keeps the animal's claws sharp by peeling off loose flakes (Ewer 1973; Scott 1985). Female leopards in the Masai Mara claw trees regularly, occasionally scrape the ground and mark the edges of their ranges by defecating. These females also spray-urinate on low bushes (Scott 1985).

Tree-clawing by leopards varies between regions. In the Tsavo National Park for instance, tree-clawing was only observed once in a detailed study on leopards. However, spray-urination, faeces and scrapes were all used in marking the area. Scrapes are less common among African leopards than in those of India (Hamilton 1976). In the southern Kalahari, scraping is infrequent

among leopards as elsewhere in Africa; but chemical communication is used extensively. There both sexes claw trees; females doing so less often than males. Regularly used scratch posts are rare, possibly because of the large ranges used by these leopards and the relatively infrequent use of a given area of habitat by a certain leopard over a given period of time (Bothma and Le Riche 1984, 1995).

Both sexes of leopard spray-urinate against shrubs or trees, and scrapes are often associated with urination (Eisenberg and Lockhart 1972). In the southern Kalahari, males repeatedly scent-mark trees by urination prior to mating. However, females seldom scent-mark trees and shrubs. In males, this activity seems to be aimed more at females than at other males. Both sexes use trees as rubbing posts, males doing so more often than females. Rubbing is done presumably for grooming, and coarse-barked *Acacia erioloba* tree trunks are clearly selected as rubbing posts over other trees (Bothma and Le Riche 1995). In the Kruger National Park, a leopard sometimes ascends a tree and urine-marks the branches (Pienaar 1969).

Apart from scent, the leopard female uses her tail as a visual guide or signal when leading her cubs somewhere (Schaller 1972). Leopards also roll on the dung of other species, or do so on the ground, possibly where other animals have urinated. Whether this is a form of communication is unknown (Scott 1985; Bothma and Le Riche 1984).

Tree-scratching has never been observed in cheetahs in the arid South African bushveld (Kruger 1988), and rarely so in East Africa (Eaton 1970a). However, cheetahs in the southern Kalahari urine-mark trees on average every 1.6 km moved, using the same tree repeatedly to do so (Labuschagne 1979).

Verberne and De Boer (1976) refer to flehmen in a male cheetah after smelling a female's urine, suggesting some sort of chemical communication. Male cheetahs are as capable of directional urination as tigers and lions. Cheetahs pass small quantities of urine throughout the day onto objects in their range. Female cheetahs usually spray-urinate widely and frequently, but seldom urinate heavily. The urine of a female cheetah in oestrus relays a definite message to males (Eaton 1970a). Marking locations of cheetahs are regularly marked over and over in the same location, but the density of such markings increases with the openness of the environment (Eaton 1970a). Cheetahs in the southern Kalahari regularly defecate next to specific trees in a scent-marking action (Labuschagne 1979). Cape wild cat males also spray-urinate against bushes (Mills et al. 1984).

3.3

Reproduction

None of the cats maintain permanent pair bonds (Eltringham 1979). The urine and cheek gland secretions of female domestic cats generally appear to

contain pheromones which inform males about their hormonal phase. The same may be true for cats in the wild. Males commonly show flehmen in response to these messages. Both male and female cats spend much time in exploring the urine and skin gland secretions of foreign cats who may come into their range (Verberne and De Boer 1976).

3.3.1

Lions

Nomadic, male African lions often move between prides consisting mostly of females and their offspring. In the southern Kalahari there is no clear mating season, but lions stay together for several days, copulating two to three times every hour. Occasionally, two males may share a female, but this is rare. Whilst mating, lions seldom hunt (Eloff 1973a).

Infanticide by immigrating males occurs regularly in African lions. Males who take over a pride, kill the resident infants when they first encounter them, but are unlikely to kill their own offspring subsequently. Such infanticide is clearly disadvantageous to the females. These females, such as those in the Serengeti, adapt in various ways to reduce their cub losses due to infanticide. Such adaptations involve various behavioural responses aimed at minimizing losses if they cannot be prevented at all. Females whose young are killed through infanticide, resume sexual activity soon after the killing of the cubs (Packer and Pusey 1983). This often leads to synchronised breeding of all females in a pride which has been taken over by a new male (Packer and Pusey 1987).

The act of infanticide by immigrating lion males could be a reproductive strategy allowing such males to stop females from investing in the offspring of evicted males. Females, often assisted by other females, respond to this threat aggressively, attacking the male lion. In doing so, they allow some of the cubs to escape. Sometimes older cubs one-and-a-half to two years of age are evicted from the pride without being killed. They may be accompanied by some of the females, resulting in only a partial take-over of a pride. However, despite these adaptations, cub losses to infanticide may be high (Packer and Pusey 1983).

The gestation period of an African lion is about 90 to 110 days (Schaller 1972; Rudnai 1973). Large foraging groups of six to eight female lions in the Serengeti ecosystem enhance reproductive success. This happens because the births tend to coincide, and the females protect and feed each other's young, leading to increased cub survival (Caraco and Wolf 1975). Nevertheless, only 20% of the matings there lead to successful conception (Schaller 1972). In the Serengeti and the Ngorongoro Crater, the sex ratio of cubs born during the first 300 days after a male take-over of a pride favours males. It also differs significantly from that of cubs born subsequently. Therefore, more males are born when females breed synchronously after a male take-over (Packer and Pusey 1987). A lion cub is weaned when 10 weeks old (Grobler et al. 1984).

All pride males in the semi-arid bushveld of the Kruger National Park are between five and nine years old. No males younger than five years old associate sexually with the females, despite the fact that males become sexually mature at a median age of 30 months. Females become sexually mature at 48 months of age, and by the age of 5.5 years, all females sampled there had ovulated previously (Smuts et al. 1978).

Of all parous female lions in the Kruger National Park, 20% are pregnant at any given time, 21.7% are lactating and 6.7% are sterile. In one study, the two oldest females capable of reproduction were 12 and 13 years old. Lactation continues for 8 to 9 months post-partum and the mean litter size is 3.08 at birth, 3.02 when 1 year old and 2.71 when between 1 and 2 years old (Smuts et al. 1978). These parameters are similar to the mean litter size of 3 at birth in the southern Kalahari lions (Eloff 1973a), and to those in the Nairobi National Park (Rudnai 1973). However, they are higher than that of 2.3 (maximum: seven) found in the Serengeti where litter size of lions seems to be independent of food abundance (Schaller 1972). The overall conclusion that litter size in African lions is independent of food abundance agrees with the presence of large litters as are found in some arid areas.

Pregnancy control in the lions of the Etosha National Park was practised successfully by implanting a tiny capsule into the neck muscle of a lioness. This capsule releases a constant, minute amount of pregnancy-simulating hormones. This prevents ovulation for up to 5 years (Berry 1983). Under given circumstances, lions are also able to increase their reproductive rate. Cub survival in lions seems to be related to the abundance of food resources (Schaller 1972; Rudnai 1973; Smuts et al. 1978). The presence of abundant food decreases the time that mothers have to spend away from their cubs while hunting. Consequently, the culling of lions in the Kruger National Park, which significantly decreased lion numbers and led to more food available per given remaining lion, also led to increased reproduction (Smuts 1978b).

Male lions play no direct role in cub rearing in the Savuti Marsh (McBride 1990). A lioness never brings food to her cubs (Scott 1985) and these eat more relative to their weight than adult lions do (Smuts 1979). Lion cubs in the Savuti do eat meat from an age of 2 weeks, however, if available and while still suckling (McBride 1990). However, lion cubs usually only start to hunt when close to a year old (Schaller 1972; McBride 1990). Subadult males leave their natal pride at between 27 and 36 months of age in the Kruger National Park, but females either remain with the natal pride, or emigrate as early as 24 months of age (Smuts et al. 1978). A lion reaches its asymptotic weight at 7 to 8 years of age (Van Jaarsveld et al. 1988). The mortality rate of lion cubs in the southern Kalahari is high, probably the highest in Africa, particularly as the prey base there is relatively low (Eloff 1973a, 1980). Hofer and East (1993a) believe that, apart from spotted and brown hyaenas, the cubs of other carnivores cannot survive without nutrition for more than 24 to 36 h. However, it often happens that a lioness in the southern Kalahari will leave her

cubs unattended for 2 to 3 days while out hunting. During this time the cubs are at the mercy of the harsh environment as well as marauding predators. Despite this, they can and do survive, as can leopard cubs there (Eloff 1973a). Although it is known that allo-suckling occurs in lions, other lactating females must still be available in a pride if the cubs are to survive in this way. This is especially so if their own mother should die or abandon them (Eloff 1980). Nevertheless, in the southern Kalahari, predators and starvation are the main causes of mortality in lion cubs (Eloff 1973a).

On the arid Serengeti Plains west of the Ngorongoro Crater, the low survival rate of lion cubs is also related to the harsh environment. It is less than half of what it is in the wetter and adjacent Ngorongoro Crater. Most cub mortality on these arid plains occurs before the cubs are a year old (Hanby et al. 1995). An overall cub mortality of 67% occurs for lions in the Serengeti (Schaller 1972). In the central part of the Kruger National Park, lion cub mortality is estimated at 29%. Only 40% of the cubs in the Etosha National Park reach maturity (Pienaar 1960; Eloff 1980). In the southern Kalahari, lion cubs may also die of scorpion stings, particularly as the area is rife with them. The disease rickets is another cause of lion cub mortality in this harsh environment (Eloff 1980).

Further evidence for the influence of prey abundance on lion cub survival is found in the Serengeti. When conditions which prevailed from 1966 to 1969 are compared with those from 1975 to 1977, the available prey biomass doubled. At the same time the number of cubs in each lion pride increased significantly. This was probably because the cubs survived better, and the fact that that more cubs remained with their natal prides as there was enough food. Cub survival to two years of age increased from 14% to 44% in this interval. Once a lion cub has reached 2 years, its chances of premature death decrease considerably (Hanby and Bygott 1979). It is possible that cub mortality may be a good indicator of population condition and the physiological condition of lions as in the Etosha National Park (Melton et al. 1987).

3.3.2

Leopards

There are no in depth data on the reproduction of leopards in the wild, and especially so in arid areas. The gestation period is 90 to 106 days (Grobler et al. 1984; Scott 1985; Le Roux and Skinner 1989; Hes 1991). Oestrus lasts six to seven days, and will recur every 20 to 50 days. A female in oestrus travels widely and calls often. Hormonal changes are relayed to males by way of substances in her urine (Scott 1985; Bothma and Le Riche 1995). There is no clear mating season and the mating pair stays together for only 24 to 48 h (Scott 1985; Bothma and Le Riche 1989). When mating, leopards copulate frequently, and a mean interval between copulation of 30 min has been recorded (Baker 1982). Copulation itself is brief (Scott 1985). Female leopards produce

their first young when about 3 years old. In the arid bushveld of South Africa, there is an interval of 17.1 months between successive litters (Le Roux and Skinner 1989).

The cubs of leopards in the southern Kalahari are usually born in aardvark burrows taken over by the leopard. The cubs spend their early life under dense vegetation such as the shepherd's tree *Boscia albitrunca*, or in the burrows of mammals like the springhare and various mongooses (Bothma and Le Riche 1986). In East Africa, leopard cubs are known to home in on their dens by its odour. The eyes of a leopard cub are closed at birth, opening at 6 to 10 days of life (Grobler et al. 1984; Scott 1985). The female stays close to the cubs for the first few days, then moves about to hunt (Bothma and Le Riche 1986).

Cubs start to wean when about 42 days old, start to feed on meat when about 4 months old, being led to food by the female (Scott 1985), and will begin to kill their own prey when about 5 months old (Smithers 1983). They will eat meat brought to them by their mother before reaching 8 weeks (Scott 1985), but remain totally dependent on their mother for the first 11 to 18 months of life (Scott 1985; Le Roux and Skinner 1989). After this time the cubs continue to associate with their mother on a less permanent basis (Scott 1985). Litter size usually varies from one to three (Bothma and Le Riche 1986; Hes 1991) but it can be as high as six (Hes 1991), although such big litters are rare.

Unweaned cubs are moved frequently to new sites of seclusion (Scott 1985; Le Roux and Skinner 1989). In the southern Kalahari, female leopards only cover their faeces and kills with sand when close to their own young cubs, possibly in cub-defence. Other defecations are not covered (Bothma and Le Riche 1994a).

Female leopards make a chuffling sound consisting of three or more short, sharp puffs as a vocal greeting to communicate with their cubs. Cubs remain relatively inactive when the female is away, but other predators such as eagles, lions, spotted hyaenas, jackals, baboons and even male leopards still regularly find and kill them (Scott 1985). In more prey-abundant areas, females usually return to their cubs every day, even when hunting is unsuccessful (Scott 1985). Nevertheless, even in the prey-rich Chitwan National Park in Nepal, a female leopard may be absent from her cubs for a day or more, her period of absence being determined by the time required to search for and kill prey (Seidensticker 1977). In the prey-poor southern Kalahari, females may leave their cubs alone for as long as 2 nights while out hunting, considerably increasing the chances of cub mortality (Bothma and Le Riche 1984, 1986). When a female is close to her cubs, she will suckle them several times per day (Scott 1985). Nevertheless, it is clear that among leopard cubs there is an adaptation for a "feast and famine" food regime which operates from a very early age (Seidensticker 1977).

Leopard cubs at play use a sequence of instinctive behaviour patterns common to all cats. However, from an age of about 8 months, the cubs start to

socialize less with each other, spending little time together after an age of 11 months or more, being fully grown and solitary by 30 months of age (Scott 1985), and sexually mature at a mean age of 3 years (Hes 1991).

Mortality in leopard cubs usually is high (Scott 1985) and few cubs survive to adulthood. Young, male leopards leave their natal range when 15 to 16 months old, dispersing gradually until they can establish an own territory (Sunquist 1983). In the southern Kalahari, a subadult male leopard dispersed over a straight line distance of 112.6 km over a period of three months before establishing a permanent home range (Bothma unpubl.). The timing of dispersal in young leopards is a function of a variety of social and environmental factors because the age at which leopards disperse varies from area to area (Sunquist 1983).

3.3.3

Cheetahs

Cheetahs have considerable problems in reproducing successfully, including congenital mortalities (O'Brien 1994). In addition, they have extremely high cub mortalities (Eaton 1970a; Schaller 1972; O'Brien 1994; Caro 1994; Laurenson 1995). Cheetahs are induced ovulators with no marked peak in breeding. A high percentage of the spermatozoa show abnormalities, but the effect of these on fertility is still largely unknown (Caro 1994). Cheetah females are highly selective of their mates. Gestation lasts for 90 to 95 days, and the cubs are born with closed eyes (Grobler et al. 1984).

In the wild, one to six cheetah cubs are born to a litter, and they remain dependent on their mother for more than a year, although they are weaned when two to three months old (Mills 1990; Caro 1994). Most adult females give birth, but even in a prey-rich area such as the Serengeti only 28.8% of all cubs born eventually survive to emerge from the den, and only 8.8% survive till four months old. Predation by lions is the primary mortality agent. Of all cubs born in the Serengeti, 4.8% have a chance to reach independence (Caro 1994).

About 50% of all cheetah cubs in the southern Kalahari die before they are 6 months old, primarily because of predators and starvation. The known predators of cheetah cubs in the southern Kalahari include the black-backed jackal and occasionally the brown hyaena *Parahyaena brunnea*. These predators usually find and kill cheetah cubs while the female is away hunting. As a given female cheetah once left her cubs alone and unattended eight times in 22 days to go away and hunt in the southern Kalahari, cheetah cubs there are highly vulnerable to predation (Labuschagne 1979). Of all cheetah cubs born in the Serengeti, 7.7% are eventually abandoned by their mothers and starve to death. The difficulty of successful hunting and the availability of prey at certain times of the year are major reasons for such abandonment. Where other predators are virtually absent, such as on farmland in Namibia, however, cheetahs do well and litter size at independence can be as high as four.

This clearly illustrates the devastating potential effect of predation on cheetah cub survival in a variety of ecological conditions (Laurenson 1995).

Cheetah cubs start moving with the female when six weeks old, reach sexual maturity when 15 months old and leave their mother when 18 months old (Grobler et al. 1984). Young cheetahs learning to hunt already possess a fair degree of innate predatory behaviour, but the training which they receive from their mother is essential for the eventual development of the entire predatory sequence (Eaton 1970b). Hunting success in cheetahs increases with age (Caro 1994).

Female cheetahs rapidly conceive again following the loss of unweaned cubs. Conceptions when food is abundant are usually most successful. Cubs losing their mothers sometimes join unwilling females and steal food from them to survive. Cheetah cubs remain with their mothers until about 18 months old. They are nursed for the first 4 months, a period in which their mothers double their food intake in the Serengeti (Caro 1994).

On the Serengeti Plains, cheetah cub recruitment is not enough at present to maintain the cheetah population there (Laurenson 1995). This suggests a variable pattern of recruitment and survival over considerable time for the population to have survived to date.

3.3.4

Other Cats

The African caracal occurs extensively in arid areas, but little is known about it there. However, it seems that the sexes only associate when mating (Pringle and Pringle 1979). The litter size varies from one to four (Grobler et al. 1984). In the arid Eastern Cape Province areas of South Africa, young are born in late autumn, spring and summer (Pringle and Pringle 1979). The gestation period is 76 days (Grobler et al. 1984). In the even more arid West Coast National Park, caracal litters are born mainly in summer, with a mean litter size of 2.25 (Avenant 1993). The eyes are closed at birth. Kittens stay with their mothers for their first 4 months of life (Avenant 1993). In the arid Karoo regions of South Africa, caracal in the Mountain Zebra National Park disperse from their natal ranges when 7 to 9 months old. One young, dispersing male there moved 10 km in 8 months, and another one 22 km in two months before settling in an own territory (Moolman 1986). In the Cape wild cat, litters of two to five are born in the wet season after a gestation period of some 58 days (Smithers 1971; Grobler et al. 1984). The kittens hide in thickets by day and only the female raises the young. For the black-footed cat, litters of one to three are born in burrows, mostly in the summer. The kittens are cared for by the female only (Grobler et al. 1984).

3.4

Area Use, Movements, and Activity

The basic pattern of felid social organization is one in which males occupy large, exclusive ranges that encompass several females' ranges. In range use, the females in turn are keyed to resource availability (Sunquist and Sunquist 1989).

3.4.1

Lions

Contrary to popular belief, the African lion (Fig. 3.1) typically is an animal of dense, dry habitat (Smuts 1982). African lion individuals can either be nomads or residents and members of a pride living in a given area. These categories are not mutually exclusive, and a nomad can become a resident and vice versa, but the two ways of life differ vastly. A pride occupies a given range or territory, and a nomad one of up to ten times that of a pride. The size of the range of a lion pride in the Serengeti ecosystem is related to the size of the pride and the resources available: pride territories often overlap extensively in space but usually not in time (Schaller 1972).

Nomadic African lions in the Serengeti wander widely, often following the migrating game. Nomads there defend no given area and are remarkably tolerant of strange lions (Schaller 1972). In the southern Kalahari, most lions tend to have territories, but territory size varies. One pride there hunted in a known area of 120 km², another in one of 273 km². However, there are also



Fig. 3.1. The African lion is a typical animal of dense, dry habitats

nomadic lions in the southern Kalahari which move between prides or may stay alone for some time (Eloff 1973a). In the Etosha National Park, lion prides use areas ranging from 150 to 2075 km² in size. Area size used there is related to pride size, the larger the pride, the larger the area used (Stander 1991). In the Savuti Marsh, lions occupy territories as large as 300 km² for life, but the territories may shift over time and the size of each territory depends upon the number of prey present on a year-round basis (McBride 1990).

Some Asiatic male lions may live in coalitions of two to six animals. These actively defend a territory which usually includes one or more prides of females and young (Johnsingh and Chellam 1991). In the Gir forest of India the mean range of prides (50 km²) is much smaller than those of lions in the southern Kalahari (Eloff 1973a). However, they are larger than the 20 to 30 km² territories of prides in the Serengeti (Hanby and Bygott 1979).

Lions in the southern Kalahari at times hunt in definite circuits, one pride completing a circuit of 120 km in 4 days. The greatest individual daily distance moved by any lion in the southern Kalahari, is a female who moved 41.2 km in one night. A pride of three females moved a mean of 22.3 km per night on eight consecutive nights, the greatest mean distance recorded there (Eloff 1984). This compares with up to 21.5 km in 24 h in the Serengeti (Schaller 1972). Although covering great distances when moving, lions seldom hurry, and often lie or sit down to rest for a while (Eloff 1973a). In the Etosha National Park, the mean daily distance moved by prides of lion is 13.2 km in 24 h (Stander 1992b), a distance which is similar to that of the lions in the southern Kalahari.

The African lion seldom climbs trees, but it may do so occasionally to escape danger. However, in the Lake Manyara National Park, lions often rest by day in trees, possibly to evade biting flies. The southern Kalahari lions also occasionally rest in trees, possibly to avoid ground-living, biting invertebrates such as the sand tampan *Ornithodoros savignyi* (Smuts 1982).

Female lion pride members in the Serengeti defend their territories against female intruders, and males against males (Hanby and Bygott 1979). In the Kruger National Park, the territory tenure of a male lion starts at an age of 5 years, and continues at most for a few years (Smuts et al. 1978).

Lion numbers, and hence their density, are related to resource abundance and availability. This means that they also have to be influenced by aridity. In the resource-rich Serengeti ecosystem, there is one lion per 6.3 km² in the woodland areas (Schaller 1972), compared with one lion per 12.5 km² in the Selous Game Reserve (Rodgers 1974), one lion per 7.7 km² in Kruger National Park (Smuts 1982), one lion per 35.7 km² in the Etosha National Park (Stander 1992a) and one lion per 76.9 km² for the southern Kalahari. The arid Masai Steppe of Tanzania has the lowest known lion density of one lion per 306 km² (Mills et al. 1978). In the Etosha National Park, there is a clear and direct correlation between lion pride size, and hence density, and the number of waterpoints, and hence prey availability (Stander 1991).

3.4.2

Leopards

The leopard (Fig. 3.2) is an agile cat which moves with ease and can leap gaps of up to 6.0 m (Scott 1985). It has adapted to life in diverse environments (Smithers 1983). This habit also reflects its available prey-base and hence its area use and movements. The leopard has an exclusive range for a given sex, which is probably a territory, although it is not as much defended against as avoided by other leopards (Eltringham 1979). Hes (1991) believes that these ranges are territories. Female leopards usually have overlapping ranges, shared with one male (Eisenberg 1970; Schaller 1972). Male leopards will become involved in fierce physical territorial disputes (Grobler et al. 1984). In moist, tropical areas such as Sri Lanka, leopards have small ranges, varying from 8 to 10 km² in prime habitat, and 29 km² in more marginal areas (Muckenhirn and Eisenberg 1973). This compares with ranges of 40 and 60 km² (maximum 262 km²) in two females in the Serengeti (Schaller 1972), 10 to 60 km² in the Tsavo National Park (Hamilton 1976), a mean of 18 km² (range 10 to 19 km²) in the Matobo National Park (Smith 1978), a range of 23 km² (possibly 33 km²) for a single female in the arid bushveld of the Sabi-Sand Game Reserve (Le Roux and Skinner 1989), and mean ranges of 2182.4 km² (n = 3; males) and 488.7 km² (n = 5; females) in the extremely arid southern Kalahari (Bothma et al. In Press).

Where prey is scarce, a leopard patrols its range regularly, unconsciously giving the prey a time of respite from predation pressure (Turnbull-Kemp



Fig. 3.2. The leopard has the widest range of all large cats

1967; Bothma and Le Riche 1984). Apart from food abundance and availability, the density of other competing predators influences the size of a leopard's range (Schaller 1972). In the Tsavo National Park, male leopards are at times as close as 0.8 km to each other, but are usually much further apart (Hamilton 1976).

Leopard ranges have a high degree of stability (Hamilton 1976). Some areas of the range, the core areas, are used more intensively than others (Smith 1978). In the southern Kalahari, the mean core-area size of adult female leopards is 26% of the total range, and 21% in males (Bothma, unpubl.). Transient leopards may occasionally move through a given leopard's range (Ewer 1973; Smith 1978). Individual leopards spend several months in the core area of their range, but at other times they are active elsewhere.

In the Sabi-Sand Game Reserve, a male leopard visits a given part of its range once every 17.8 days, and a female once every 8.8 days. However, this varies seasonally (Kruger 1988). In the southern Kalahari, leopards move significantly longer distances per 24-h period as hunger increases (Bothma and Le Riche 1990). The long-term, mean distances moved by leopards there are 13.4 km in 24 h for adult females and 14.2 km for males (Bothma and Le Riche 1984). On the basis of hunger, those leopards in the southern Kalahari, that had recently killed prey moved a mean distance of 10.1 km in 24 h; those that had gone without food for one day 14.2 km; those that had been without food for two consecutive days 20 km, and those that had had no food for three or more consecutive days, 21.8 km (Bothma and Le Riche 1990). The maximum known distance covered in 24 h by an adult male leopard in the southern Kalahari is 33 km and 27.3 km by a female with cubs (Bothma and Le Riche 1984).

Male leopards in the southern Kalahari, where summertime day temperatures reach the mid-40s in °C, are influenced significantly by ambient temperatures in their movements. On colder nights with minimum air temperatures of 0 °C or less, leopards of equal hunger status move a mean distance of 29 km in 24 h, compared with 19.1 km on nights of between 1 and 15 °C and 15.2 km on nights of 16 °C or more. Overall, male leopards with equal hunger status in the southern Kalahari move significantly longer distances (mean: 24.9 km) in 24 h in winter than in summer (mean: 17.2 km). These data probably reflect a combined influence of higher temperature and shorter nighttime in summer (Bothma and Le Riche 1994b).

When disturbed, leopard flight distances in the southern Kalahari are minimal, the mean flight distance being 91 m (range 15 m to 2.7 km) (Bothma and Le Riche 1993). Moving leopards in the southern Kalahari rest frequently, but they especially do so just after the onset and before the cessation of activity for any given day. The main daytime resting place is the shady and dense cover of the shepherd's tree, or an aardvark *Orycteropus afer* or porcupine *Hystrix africaeaustralis* burrow (Bothma and Le Riche 1984).

3.4.3

Cheetahs

Little is known about cheetah range use in arid areas. However, cheetah females usually have undefended ranges with considerable overlap, while territorial males are limited to small territories. In the Serengeti ecosystem, the females follow migratory game and the males remain behind. In consequence, there is a large mean range of 833 km² for female cheetahs there, compared with a small mean range of 37.4 km² for males. There are also, however, non-territorial males which range over areas with a mean size of 77.2 km². Territorial males occasionally make excursions outside their territories (Caro 1994). Some males also leave their territories during the dry season in search of food. There are large, vacant areas between established territories, even when all are occupied (Caro and Collins 1987a). Furthermore, the length of tenure of a territory increases with the group size of cheetahs involved. The territory occupants are usually all large animals for their age group (Caro and Collins 1987b).

Among the Serengeti cheetahs, body size and age are two crucial factors influencing whether cheetahs become territorial or not. Single males have to form groups with other males before being able to displace resident territorial males. Larger coalitions are, however, never displaced by smaller ones. Only adult males hold territories, but territorial males are not more likely to encounter females than non-territorial ones (Caro and Collins 1987b).

In the southern Kalahari, data on cheetah area use reveal a mean range in two adult males of 300 km², which is considerably larger than that found in East Africa. These two adult males moved a mean distance of 12.6 km in 24 h, often being inactive by day, when they usually rested in deep shade (Labuschagne 1979). An inactive period by day for cheetahs is also found in the arid bushveld areas in South Africa (Kruger 1988).

Cheetahs generally live in low densities compared with most other carnivores, but the reasons for this are still unknown. One possibility, however, is the high cub and juvenile mortality rates of cheetahs in the wild. These are mainly due to predation by other large carnivores (Eaton 1970a; Laurenson 1995). The Nairobi National Park has the highest density of one cheetah per 5.12 km² known anywhere (Eaton 1970a). The cheetah population in arid Namibia is considered to be the most viable one of any in Africa, possibly in part due to the relative absence of other large predators on farmland where most of Namibia's cheetahs occur and thrive (Phillips 1993).

3.4.4

Other Cats

Area-use by the caracal in arid regions has been studied in detail in two locations in South Africa. These are the Mountain Zebra and West Coast National Parks (Moolman 1986; Avenant 1993). In the mountainous Mountain Zebra

National Park, four adult caracal males used a mean range of 15.2 km² and four adult females one of 5.5 km², a significant difference. On adjacent sheep farms, three adult male caracals used a mean range of 19.1 km². This is significantly larger than that of males in the national park. The ranges of males and females overlap within and between the sexes. Some ranges are confined to the national park, others to the farming area, while yet others include both farmland and land in the national park in their range. Although some areas of each range are used more extensively than other parts, no data on core-area size are given. When a vacant range develops, a young caracal will establish itself there and the boundaries of that range and of the neighbouring ones may be adjusted (Moolman 1986).

In the arid West Coast National Park, with its succulent to semi-succulent scrub vegetation, the mean range of two adult male caracals was 27 km² and that of three adult females 7.4 km² (Avenant 1993). The West Coast National Park is more arid than the Mountain Zebra National Park and also does not have as high a herbivore biomass. Hence the prey base is poorer. The caracal of the West Coast National Park have larger ranges than in the Mountain Zebra National Park. In both cases, however, the range of adult males is approximately three to four times that of the females. In the West Coast National Park, caracal ranges also overlap within and between the sexes (Avenant 1993).

The mean spacing between resting adult male caracals in the Mountain Zebra National Park is 4 km, and 2.2 km in females. This difference is significant. The mean, straight-line distance moved by adult males in a given 24-h period there is 2 km. This is significantly different from the mean of 0.9 km moved by adult females. The males travel mainly along the brush of the upper slopes, while the females with cubs prefer the lower, dense riverine thickets where there is an abundant rodent prey base. These rodents are their primary food. Females without cubs use the same habitat as males (Moolman 1986).

The caracal of the Mountain Zebra National Park are often blamed for stock depredation on the adjacent farmland. However, their area use and density in the park clearly show that the park can never sustain or produce the number of caracal killed annually on the adjacent farms. Consequently, the farmers must be producing their own problem caracals which live on these farms, and the park is not a main reservoir for such caracal (Moolman 1986).

In a semi-arid area of Spain, the activity cycles of the Iberian lynx *Lynx pardinus* were studied in the Doñana National Park. Photoperiod there has a major influence on the circadian patterns of activity of the lynx throughout the year. In winter, maximum temperature, high barometric pressure (decreased activity), evaporation and moon phase all influence lynx activity significantly. In summer, maximum temperature (decreased activity), high barometric pressure, moon phase and hours of moonlight are important determinants of lynx activity. In spring, rainfall and maximum and minimum temperatures play a major role in lynx activity. Some climatological factors affect

the lynxes directly in terms of activity, while others such as moonlight, act indirectly by influencing the activity cycles of the Mediterranean rabbit *Oryctolagus cuniculus* which is the lynx's main prey there (Beltrán and Delibes 1994).

Overall, the activity patterns of the lynx in the Doñana National Park is part of the adaptation of this felid to its environment. Lynxes there are more active as the photoperiod decreases. This results in seasonal activity cycles. However, the greatest photoperiod influence occurs in winter. Barometric pressure and evaporation changes also influence the circadian activity cycle of lynxes, and movements increase on warm nights in winter (Beltrán and Delibes 1994).

The nocturnal African wild cat *Felis silvestris* in an arid area near Elmenteita in Kenya has a mean range of 1.6 km² in a mixed habitat of dry woodland and grassland (Fuller et al. 1988). Like the African wild cat, the black-footed cat is also nocturnal (Smithers 1971).

3.5

Feeding Ecology

The evolutionary fitness of any predator depends largely upon the quantity and quality of its diet (Sunquist and Sunquist 1989). Felids are more strictly carnivorous than other carnivores, but especially more so than canids. This leads to more peaceful feeding in the canids in comparison with felids, where it is rare (Sect. 2.5.4; Kleiman and Eisenberg 1973).

Most felids are solitary. In terms of feeding ecology, a solitary existence is compatible with felid specializations. Such specializations have developed to deal with the ecological constraints which prey place upon being preyed on. These deal with aspects such as prey abundance, the temporal and spatial distribution of the prey, the size of prey, and prey defence. These factors all contribute to the most beneficial balance of energy expended while hunting, and energy gained from successful hunts (Sunquist and Sunquist 1989).

Felids use prey of a modal size, which varies considerably between different geographic areas, even for the same species. The modal prey size used in a given area is primarily related to prey availability and vulnerability. Usually, however, the modal prey size is less than the given predator's body mass (Sunquist and Sunquist 1989).

Like carnivores generally, felids are primarily predators, but some of them scavenge food whenever it is available. Most of the food of large felids comes from ungulates (Houston 1979). Felids eat little bone, and there seems to be a negative relationship between the size of a carnivore and the need to chew its food. Especially in socially feeding carnivores, such as lions, speed of ingestion may be more important than precision in the use of teeth. This lack of precision also explains the tendency towards breaking the teeth, particularly the canines, when feeding (Van Valkenburgh 1996).

In the big cats, the moods of prey-catching and consuming food seem to be relatively independent of each other (Leyhausen 1979). However, in the leopard, hunger is a motivation for hunting (Bothma and Le Riche 1990). Nevertheless, surplus killing of prey independent of hunger or nutritional needs is known in felids. Surplus killing is defined in Section 2.5.3. It usually is a waste of a carnivore's energy unless it stores its prey to return to feed later (Kruuk 1972a).

All felids rely extensively on the physical features of their environment when hunting. Almost any type of cover may be used to get as close as possible to a potential prey before making a final attack (Eltringham 1979; Leyhausen 1979; Sunquist and Sunquist 1989). Felids never rush at their intended prey with as much unrestrained eagerness as do many other predators (Leyhausen 1979). Identification of its prey is important if the predator is not to "bite off more than it can chew". Of the cats, the two stalking specialists in Africa are the lion and the leopard, both of which take prey with more stamina than themselves (Eltringham 1979). Intraspecific competition for kills among solitary felids seems to be rare. The possibility of felids meeting at a kill is reduced by temporal and spatial dispersal (Sunquist and Sunquist 1989).

3.5.1

Food

Lions. The African lion hunts opportunistically, but it does scavenge part of its diet, usually stealing carcasses from other predators (Houston 1979). However, predation by lions is complex, and the feeding habits of lions are conspicuously influenced by the size of the prey and the availability and density of food for scavenging (Kruuk and Turner 1967; Schaller 1972; Eloff 1973a,c, 1984). In the Serengeti ecosystem, lions on the plains have difficulty in acquiring sufficient food in the dry season (Hanby et al. 1995). In the whole area there, the size of the prey of lions appears to increase with the size of the hunting group (Kruuk and Turner 1967).

The African lion occasionally kills young elephants *Loxodonta africana* (Pienaar 1969; McBride 1990). Other carnivores are not usually used as food by lions as they are by leopards, even when the lions are hungry. However, carnivores such as spotted hyaenas, brown hyaenas, jackals, cheetahs and leopards may occasionally be killed by lions, but are usually not eaten (Schaller 1972; Eloff 1973a, 1984). Cannibalism occurs in lions, but the reason for this is unknown (Schaller 1972). In the Krüger National Park, lions remove over 50% of the biomass of prey killed by all the large predators (Mills and Biggs 1993). Lions in the Kafue National Park take a higher proportion of prey that is in poor condition, but fewer juvenile prey than any of the other predators (Mitchell et al. 1965).

In the Serengeti, prey selection by lions varies between seasons, across habitats and from year to year. Most of this variation can be attributed to the

annual migration of some important prey, a migration which is driven by varying amounts and patterns of rainfall from year to year (Scheel and Packer 1995). In the southern Kalahari, moisture-rich plants such as the tsama melon *Citrullus lanatus* are eaten by lions to obtain moisture, especially when prey is scarce (Eloff 1973a). In the Savuti Marsh, lions eat prey from as small as a springhare to the occasional young elephant (McBride 1990).

Lions in the Namib Desert feed extensively on fur seals, but it is not clear if the seals are killed by the lions, or scavenged along the coast. The distribution of the prey of lions in the Namib Desert is generally sparse. These lions do feed on another carnivore, the black-backed jackal, which is relatively abundant there. The lions also feed on white-breasted and Cape cormorants, both of which are abundant in rookeries along the coast. Namib Desert lions therefore clearly show the high degree of food selection opportunism present in lions generally (Bridgeford 1985). The same is true for lions in Somalia which depend heavily for food upon the warthog *Phaecochoerus aethiopicus* which is locally abundant there (Fagotto 1985). In comparison, 85% of the food eaten by lions in the Serengeti are buffalo *Syncerus caffer*, wildebeest *Connochaetes taurinus* and Burchell's zebra (Saba 1979).

The Asiatic lion is equally opportunistic in its food selection. A comparison of the food used from 1986 to 1990, to that eaten in earlier times, shows increasing use of wild ungulates, especially chital *Axis axis* and sambar *Cervus unicolor* (Chellam and Johnsingh 1993). The availability of these species also increased over these years after livestock were removed from the Gir National Park. Before 1971, the lions in that region mainly depended upon livestock for food (Johnsingh and Chellam 1991).

Surplus killing is known in lions, both in Africa and in India (Pienaar 1969; Kruuk 1972a), especially if a herd is weak from drought (Pienaar 1969). Both the African and the Asiatic lion also on occasion deliberately eat grass (Schaller 1972; Johnsingh and Chellam 1991). Male lions in particular are known to be cannibalistic (Pienaar 1969).

Leopards. The leopard is opportunistic in its food choice, killing prey of specific size classes rather than specific species (Bothma and Le Riche 1984, 1986; Kruger 1988). Leopards also have a variable diet between individuals (Kruuk and Turner 1967). Because leopards occur over a wide geographic range, their diet is more varied than that of any other large felid (Sundquist and Sundquist 1989). The prey of leopards in the arid bushveld of South Africa usually weighs from 20 to 70 kg, although the impala *Aecypyceros melampus* there forms 88% of the leopard's prey, mainly because of its local abundance (Kruger 1988). In food choice, leopards are adaptable. They sometimes become habit-killers by taking only or mainly a single food resource (Turner and Watson 1964). For example, in the Kafue National Park, a leopard which was re-located from a temporary island in Lake Kariba in Zambia, where it had become entirely adapted to a fish diet, continued to catch *Clarius* sp. after its

relocation to the park (Mitchell et al. 1965). Leopards are also cannibalistic, but rarely so (Pienaar 1969).

Local prey abundance appears to be a common factor in the selection of food by leopards elsewhere too. In The Matobo National Park, for example, the hyraxes *Procavia capensis* and *Heterohyrax brucei* are abundant, and form from 55 to 61% of the leopard's diet (Smith 1978). In the Serengeti, a leopard hunts mainly from good cover, hence its diet seldom includes small animals from the open plains (Kruuk and Turner 1967). In the southern Kalahari, on the other hand, there is no dominant food resource in terms of numbers and distribution, and the leopards there use a variety of prey. However, prey items weighing 70 kg or less are taken most often (Bothma and Le Riche 1984). In the arid Au-grabies National Park, no clear single prey species preference by leopards is also evident, although a relatively high incidence of porcupines, duiker *Sylvicapra grimmia* and gemsbok calves *Oryx gazella* occur in the leopard's diet (Bothma and Le Riche 1994a).

Other carnivores, but especially the black-backed jackal, aardwolf and bat-eared fox, are hunted and eaten regularly by leopards in the Kalahari Gemsbok and Au-grabies National Parks (Bothma and Le Riche 1984, 1994a). In the Ngorongoro Crater, leopards occasionally even prey on African wild dogs (Wright 1960).

In areas such as Matobo National Park (Grobler and Wilson 1972; Smith 1978) and Tsavo National Park (Hamilton 1976), rodents are often used as food by leopards. Elsewhere rodents are rarely used (Le Roux and Skinner 1989). In more arid areas such as the southern Kalahari, rodents do not form part of a leopard's diet (Bothma and Le Riche 1994a). However, it is not impossible that rodents will be used in years of abundance. Even the snow leopard *Uncia uncia* of the arid rain shadow area of the Annapurna Mountain Range, eats rodents fairly regularly (Oli et al. 1993). Birds are seldom eaten by leopards in the southern Kalahari. Even when eaten, only the ostrich *Struthio camelus* is involved (Bothma and Le Riche 1989). In the Tsavo National Park, however, phasianid birds especially are eaten by leopards (Hamilton 1976). Reptiles (Hamilton 1976; Le Roux and Skinner 1989), invertebrates (Fey 1964; Ewer 1973; Hamilton 1976), fair quantities of grass (Smith 1978) and wild fruits (Bothma and Le Riche 1994a) are also eaten by leopards, but rarely so. Leopards also readily eat putrid meat (Smith 1978; Scott 1985). As a consequence, leopards can be trapped with such bait. Leopards will also scavenge food from other carnivores, and feed on animals that have died a natural death (Kruger 1988). In the Judean Desert the leopards are relatively small (males: 30 kg; females: 20 kg) in size, and their limited food resource leads to a diet of 63% ibex *Capra ibex* and 37% rock hyrax and porcupines *Hystrix africaeaustralis* (Skinner and Ilani 1979).

Cheetahs. This cat eats different prey species in different localities, but in the Serengeti young prey are taken in preference to adults (Caro 1994). There is

also no clear evidence in the Serengeti that when adult prey are taken, old or sick animals are deliberately selected (FitzGibbon and Fanshawe 1989). In the Nairobi National Park, cheetahs use 25 types of prey, ranging from hares and warthog piglets to adult wildebeest and zebras. Specialization on particular prey by individual cheetahs occurs (Eaton 1970b). In contrast, cheetahs in the southern Kalahari mainly hunt springbok, but they also often hunt ostriches and duikers, and to a lesser extent five other prey animals. Attempts to hunt bat-eared foxes, black-backed jackals and the fleet-footed red hartebeest *Alcelaphus buselaphus* calves are invariably unsuccessful (Labuschagne 1979). In the Etosha National Park, cheetahs use the springbok as an important source of food (Phillips 1993). Although Bertram (1979) considers the cheetah to be the only large African carnivore that does not scavenge, this has been reported in isolated cases by Caro (1982) in the Serengeti, and by Pienaar (1969) in the Kruger National Park. Cannibalism by cheetahs also occurs (Pienaar 1969), but rarely so, and then probably only as a result of territorial disputes (Hunter and Skinner 1995).

Other Cats. The caracal is an opportunistic feeder, but it usually takes smaller mammals as food (Grobler et al. 1984). Caracal in the Postberg Private Nature Reserve make use of small rodents as their main source of food, concentrating heavily on the bush Karoo rat *Otomys unisulcatus* and the striped field mouse *Rhabdomys pumilio*. Also often eaten, however, is the steenbok, duiker, springbok, rock hyrax, hares *Lepus* sp., rodent moles (Bathyergidae) and smaller carnivores such as the otter *Atilax paludinosus*, Cape grey mongoose *Galerella pulverulenta*, polecat *Ictonyx striatus* and some birds (Avenant 1993). Some of these prey are taken abundantly only on a seasonal basis. In the Mountain Zebra National Park, the rock hyrax and mountain reedbuck *Redunca fulvorufula* are the main prey of caracals, followed by a variety of other mammals, birds, reptiles and invertebrates. However, on neighbouring farmland, rock hyraxes and rodents are the main food of caracal. This diet differs significantly from that of caracals in the adjacent national park (Moolman 1986).

In the mountainous regions of the Western Cape Province of South Africa, rock hyraxes, small antelope and vlei rats *Otomys irroratus* are also the main prey of caracals (Norton et al. 1986). In the Karoo National Park, the prey base available consists of fewer and larger mammals. Consequently, rodents form the main prey of the caracal there, with some use of the rock hyrax and the grey rhebuck *Pelea capreolus* (Palmer and Fairall 1988). In the Bedford farming area of the Karoo region, caracals switch to an almost exclusive diet of rock hyraxes following the elimination of other prey (Pringle and Pringle 1979). In Botswana, murids are the food most often eaten, but other animals such as birds, antelopes as large as adult springbok, hares, springhares and reptiles are also eaten (Smithers 1971). The caracal occasionally also scavenges food (Skinner 1979).

The nocturnal African wild cat in the Karoo National Park eats rodents mainly, with birds and invertebrates being taken occasionally (Palmer and Fairall 1988). Springhares and hares are the largest prey of this cat, while murids form 50% of all wild cat food in Botswana. Insects, reptiles and birds are also eaten. The black-footed cat eats insects, spiders, frogs, lizards, small birds and murids (Smithers 1971; Grobler et al. 1984). The sand cat *Felis margarita* digs for fossorial rodents, one of its main food items. The diet also includes birds, reptiles and arthropods (Nowell and Jackson 1996). The sand cat has a reputation as an adept snake hunter, particularly of horned and sand vipers (Dragesco-Joffé 1993; Nowell and Jackson 1996).

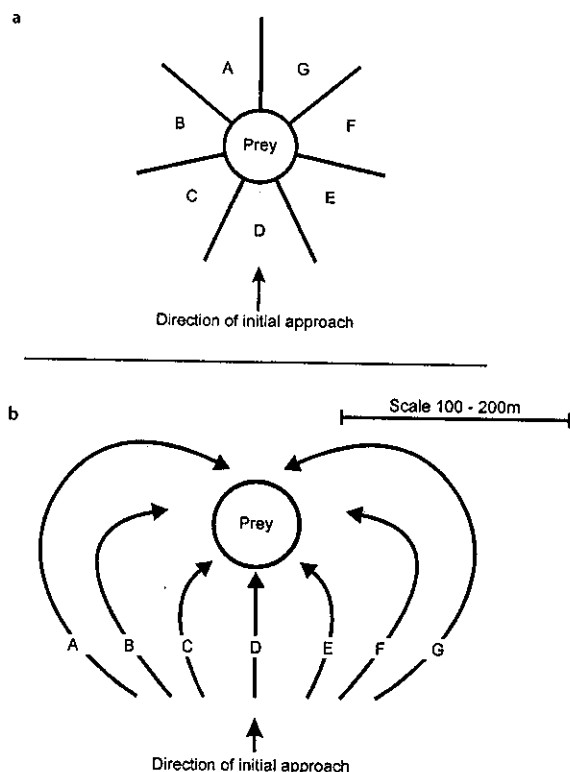
3.5.2

Hunting

Lions. The cats differ widely in their hunting methods. This in part is the result of habitat diversity, prey availability and the size and social structure of the species involved. The African lion pride often hunts as a group, with individuals spreading out to take different routes to the intended prey (Stander 1992a; Fig. 3.3). Lions hunting as a pride in the Savuti Marsh will deliberately hunt any small animal cooperatively. In doing so, however, the individual making the kill generally also eats it without sharing it (McBride 1990). Group hunting occurs mostly at night and is believed to require less cover than solitary hunting (Bertram 1979). However, the success or failure of a given hunt depends as much upon the response of the prey to the hunting lion or lions as it does upon their hunting prowess. As long as hunting lions are visible to them, prey are quite casual in their response. Therefore, a lion must seek every possible advantage to kill its intended prey. Lions are believed by some authors seldom to hunt by using the prevailing wind direction, but the height and density of vegetation influence the ease of stalking. Sight and smell are used extensively in stalking (Schaller 1972). Nonetheless in the Etosha National Park, lions do hunt significantly more often and more successfully downwind (Stander 1992b).

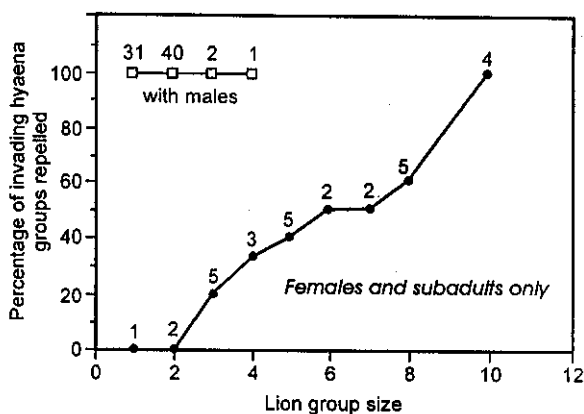
Female lions hunt proportionately more often than males. Opportunistic hunts have the highest success rate (61%) in the Serengeti ecosystem. Group hunting by lions increases the chances of success, especially against larger prey (Schaller 1972; Caraco and Wolf 1975), although males are less likely to hunt in groups than females. Both male and female lions in the Serengeti often refrain from participating in a hunt depending upon the type of prey, and ease of killing it (Scheel and Packer 1991). For small prey, the optimum hunting group size and the maximum allowable group size, based upon energetic balances, are the same (Caraco and Wolf 1975). In exceptionally dry years in the southern Kalahari, a larger pride kills much more frequently than a smaller one (Eloff 1973a).

Fig. 3.3 a, b. Typical stalking routes of individual lions (A to G) in the Etosha National Park in Namibia, intended to surround a the prey for the final kill (Stander 1992a)



McBride (1990) believes that the lions of the Savuti, where 90% of all hunts occur at night, do so, as they do elsewhere, because of high heat stress of the African day. Actual hunting by a lion begins with a systematic search, not directed towards a particular animal but intended to scan the environment generally. This is followed by a stalk of varying distance, using as much cover as possible. Depending upon the terrain and the behaviour of the prey, the lion gets close to its intended prey, making a high-speed, final charge towards the victim. Chases are generally believed to seldom last for more than 100 m or so (Kruuk and Turner 1967). However, McBride (1990) believes that the African lion is capable of sustained bursts of speed over distances of as much as 1 km. Stalking can occur in bouts, with the lion stopping at times, or it can be a slow, sinuous and continuous action (Kruuk and Turner 1967). In the Kafue National Park, hunting conditions for lions are easy and physical strength more than any other factor will determine the success of a hunt. For example, the lechwe *Kobus leche* is hunted with great difficulty there, whereas the buffalo is a major buffer species in the dry season, easing the predation pressure on other prey species (Mitchell et al. 1965). Prey availability influ-

Fig. 3.4. The proportion of kills at which lions of different group sizes were able to repel spotted hyaenas of different group sizes from their kills in the Savuti Marsh of the Chobe National Park in Botswana. Sample sizes appear above the data points (Cooper 1991)



ences the focus of a given hunt. The relatively prey-poor southern Kalahari, for example, is the only area where lions consistently hunt small mammals (Smuts 1979). In the southern Kalahari, lions mostly (69%) kill small prey or the young or subadult segment of the available prey population (Eloff 1973a). Lions of the Savuti also mostly (62%) kill young or subadult prey (McBride 1990).

In the Savuti, there is also preliminary evidence that kleptoparasitism by spotted hyaenas may influence the optimal hunting group size in lions (Fig. 3.4). The Savuti lion population suffers from a shortage of adult males. In their absence (44% of feeding groups have no adult male close by), spotted hyaenas can drive female and subadult males from their kills, provided that they outnumber such lions by a ratio of 4:1. The larger the lion hunting group, the better it defends the kill. The lions there lose almost 20% of their food to spotted hyaenas, but these lions are often already satiated by the time that the hyaenas acquire the kill. Also, these lions often hunt in groups large enough to defend their kills, even in the absence of a large adult male. The hyaenas therefore do not cause an immediate need, but they do constitute a constant energy drain on the Savuti lions by forcing them to hunt more frequently than they would have done in the absence of this interaction (Cooper 1991).

In the arid and relatively open southern Kalahari, hunting lions take advantage of every possible cover, even small shrubs and tufts of grass. To make use of the relatively abundant, but potentially lethal, gemsbok (Fig. 3.5) as a prey resource (Eloff 1973a), the Kalahari lion has altered the focus of its attack by approaching gemsbok from behind and attacking the lumbar region, instead of using the normal throat and neck attack. The lion then jumps onto the haunches of the gemsbok out of reach of the lethal horns, and breaks its prey's back by snapping the spinal chord, before seizing its throat and crushing the neck. The back is not broken by the impact of the attack, but by a sharp upward jerk with the jaws, focusing on what seems to be a weak link



Fig. 3.5. In the southern Kalahari, the gemsbok is a potentially lethal prey of large carnivores

in the anatomy of this and many other ungulates in which vertebral anatomy has sacrificed stability for mobility. A gemsbok's horns are lethal weapons and cases are known in which an attacking lion has been gored and killed by a gemsbok (Eloff 1964, 1973a).

Lions of the southern Kalahari also show clear, cooperative hunting as is found elsewhere, with the females being especially important. However, the method used to kill a gemsbok indicates a prey-specific, learned hunting technique resulting from the smaller abundance and variety of prey in the southern Kalahari. In contrast, the lions of the Etosha National Park also kill gemsbok, but do so with the customary throat and neck bite. This difference probably reflects the greater abundance and variety of prey in Etosha compared with the southern Kalahari (Eloff 1973a).

In the Etosha National Park, group hunting by lions involves the circling of prey by some females of the pride (Fig. 3.3), while others wait for the prey to move to them. The circling lions frequently initiate the attack, while the waiting animals move relatively short distances and usually capture the fleeing prey. In Etosha, a lioness in a pride usually occupies the same position in the hunting formation repeatedly. Hunts where most of the lionesses present occupy their preferred position in the hunting formation have a higher probability of success than others. However, hunting behaviour is flexible, varying from group to group (Stander 1992a,b).

Cooperative hunts by lion groups are more common where prey are difficult to catch. On the open plains of the Etosha National Park, lions have low

overall capture success rates (15% for all prey species in both the wet and dry seasons). Single lionesses have the lowest success rate (2.3%), while cooperative hunts have a high success rate (27%). During successful, cooperative hunts most prey are caught from an ambush. The individual that captures the prey, always also kills it (Stander 1992a,b).

Cooperative or group hunting by the lions of Etosha clearly benefits the individual member's efficiency and per capita food intake, especially during the dry season when prey is scarce (Stander 1992a). During this season, in fact, group hunting is essential for lions to gain sufficient food. A pair of lions is the optimum group size for hunting. In the wet season, hunting groups of all sizes obtain more than their daily food requirements. Etosha lions rarely scavenge as they seem to obtain sufficient food by hunting at most times (Stander 1992b).

Asiatic lions live in conspicuous groups in open habitat. Females prefer to hunt near water where natural prey congregate, avoiding livestock which are usually associated with human presence. Male lions frequent hilltops in the wet season, probably because the cool breezes there reduce the impact of insects. Unlike African lions, male and female Asiatic lions seldom congregate or even hunt together. The Asiatic male lion will only join a female to mate or to feed at a large kill (Johnsingh and Chellam 1991).

Leopards. The leopard usually hunts and kills in one continuous action. It hunts from cover more so than any other predator (Kruuk and Turner 1967). A stalking leopard uses every bit of available cover (Eltringham 1979). In the Serengeti ecosystem, leopards may hunt from an ambush or by stalking, rushing at the prey in a high-speed dash for the kill (Kruuk and Turner 1967; Bailey 1993). Attacks are apparently never launched from trees (Le Roux and Skinner 1989; Bailey 1993). Leopards hunt opportunistically, mainly at night, dawn or dusk, but they will hunt in broad daylight if the opportunity arises. When doing so, they often watch their intended prey for some time before starting to hunt (Scott 1985; Bailey 1993).

In arid areas with limited resources, adaptive hunting behaviour has an important survival value for a large predator such as the leopard (Bothma and Le Riche 1989). In the southern Kalahari, leopards hunt opportunistically and are therefore number maximizers as opposed to the leopards of more mesic areas which are energy maximizers because of greater prey abundance (Bothma et al. 1997; Karanth and Sunquist 1995). As in other places where prey is scarce (Turnbull-Kemp 1967), southern Kalahari leopards only hunt in any specific part of their range once every four to six days, thereby giving the prey in a given area time to settle down again before their return (Bothma and Le Riche 1984).

When hunting, the leopards of the southern Kalahari use a flexible approach based upon the vigilance, vulnerability and aggression of their prey. Vigilant prey such as the ostrich, and potentially dangerous or lethal prey

larly by male leopards, and are usually merely pounced upon, often while lying down, presumably resting (Bothma and Le Riche 1984, 1986). When prey is chased, the distances involved vary according to prey type. Porcupines go into a stationary defence mode with raised quills and are only chased for a mean distance of 14.2 m ($n = 13$) by male leopards. They are hunted infrequently by females. In comparison, the mean chase distance of all prey is 48.5 m ($n = 146$) for male leopards and 36.8 m ($n = 61$) for females. For all prey, 14.6% ($n = 137$) of chases by males end in kills, 27.9% ($n = 61$) do so in females (Bothma et al. 1997).

Although the southern Kalahari is an arid, open landscape of shrub and woodland savanna, hunting cover is not a limiting factor for leopards in this region. What cover there is, is sufficient to allow stalking leopards to get within striking distance of their prey. A stalking leopard can conceal itself behind a shrub or tuft of grass as low as 200 mm. Moreover, although it is an open environment, the density of 58.5 woody plants per ha (shrubs and trees) in the interior tree savanna habitat is sufficient to allow successful stalking (Bothma et al. 1994).

Hunger, which is one of the basic behavioural motivations for hunting by various types of predator (Schaller 1972; Leyhausen 1979), does not seem to influence the stalking or chase distances of southern Kalahari leopards (Bothma and Le Riche 1989, 1990). However, as hunger levels increase, southern Kalahari leopards do increase their hunting intensity. This, however, manifests itself by increased distances moved per 24-h period rather than by increased frequency of hunts. The evidence suggests that southern Kalahari leopards, whose prey is scarce, are already utilizing their available prey resource maximally by hunting every available item in any given hunt. With the number of hunts per km remaining constant, a leopard can only increase the overall number of hunts per 24-h period by moving increasingly longer distances as its hunger grows. A recently satiated leopard moves a mean of 10.2 km per 24-h period. In comparison, a leopard that has gone without food for one day, moves a mean of 14.2 km over the same period, one that has been without food for two consecutive days, moves a mean of 20 km, and one that has had no food for three or more consecutive days, moves a mean distance of 21.8 km in 24 h. This difference is significant. It increases the total number of prey contacts as hunger increases without changing the rate of prey contacts per kilometre moved (Bothma and Le Riche 1990).

Cheetahs. The hunting success of the cheetah varies with habitat, prey type, sex and age, herd size, cheetah group size and the individual cheetah's or group's hunting experience. The cheetah depends mostly upon vision and speed and not smell to hunt (Eaton 1970a). When chasing prey, a cheetah is said to be able to reach a speed of up to 110 km/h (Grobler et al. 1984). In reality, such speeds are rare in the field with all its obstructions, and prey jinking and swerving to avoid capture. In the wild, 78 chases measured by Frame and

Frame (1981) yielded a top chase speed of 87 km/h in cheetahs. Antelopes can reach top speeds equal to that (Garland 1983; Nowell and Jackson 1996). A hunting cheetah watches its prey intently, stalking with a slow walk and not a crouch as other large cats do. No division of labour occurs in a group of cheetahs, and hunting is the same when the cheetahs are in a group as when they are single. The chase, once begun, ends when the prey escapes or is knocked over and killed (Eaton 1970c). The cheetah is a sprinter rather than a courser (Nowell and Jackson 1996). Male cheetahs that live in groups also hunt together. The weight of prey taken increases with the size of the hunting group (Caro 1994), as in spotted hyaenas. Cheetahs in the Nairobi National Park select juvenile or female prey (Eaton 1970b).

In the southern Kalahari, single cheetahs successfully kill in 32.4% of all hunting attempts when single, 25% when hunting in pairs of adults and 71.4% when a female with cubs younger than 12 months old is hunting. In one instance, a female with young cubs is known to have hunted nine times in 22 days, being successful in 77.7% of these attempts. As the southern Kalahari is poor in prey, there is no selection for prey type or attributes, and all potential prey are hunted opportunistically with no obvious preferences being shown (Labuschagne 1979).

Cheetahs in the southern Kalahari move a mean distance of 10.2 km between unsuccessful hunts and 30.7 km between successful ones. This translates into a successful hunt every 2.5 days or a mean hunting rate of once in every 7.6 km travelled. Single cheetahs there successfully hunt once every 24.4 km and adult pairs once every 39.9 km. In terms of energy gained, however, pairs are more successful because they hunt and kill more larger prey than single cheetahs (Labuschagne 1979).

The difference in the size of prey selected by single, adult cheetahs as opposed to pairs in the Kalahari is evident from the following: in increasing order of size, the prey animals killed by single cheetahs were, Cape hares *Lepus capensis* in 25% of all kills, springhares 33.3%, steenbok 12.5%, duikers 8.3%, springbok 8.3%, and ostriches 12.5%, while gemsbok adults and calves were never killed. In contrast, adult cheetah pairs killed Cape hares in only 5% of all cases, they never killed springhares and duikers, killed steenbok in 10% of all cases, frequently killed springbok (45%) and ostriches (30%), and they even killed adult gemsbok and calves (10%) (Labuschagne 1979).

In the southern Kalahari, cheetahs find prey in three ways: by chance, by a purposeful search using vantage points such as trees or termite mounds, or by ambushing prey from concealment. The prey is located mainly by sight. Successful kills involve a longer chase distance (mean: 218 m) than unsuccessful ones (mean: 122 m). The maximum distance recorded is 650 m for an unsuccessful chase of an ostrich. The maximum successful chase distance recorded is 550 m for an adult springbok. A close approach before launching the attack apparently does not ensure greater chances of hunting success (Labuschagne 1979).

As for southern Kalahari leopards (Bothma et al. 1997), steenbok (Fig. 3.6.) are hunted frequently by cheetahs, but are equally infrequently killed thanks to their vigilance and fleet-footedness (Labuschagne 1979). Similarly, gemsbok are aggressive especially when their calves are threatened, although they are frequently killed by leopards (Bothma et al. 1997) and by cheetahs (Labuschagne 1979). Cheetahs do chase smaller carnivores such as black-backed jackals and bat-eared foxes in the southern Kalahari, but this seems to be without any real hunting intent (Labuschagne 1979).

Other Cats. Few data exist on hunting by other cats in arid areas. However, caracal in the Mountain Zebra National Park are known to hunt by stalking or from an ambush (Moolman 1986).

3.5.3 Killing

The canines of felids display relatively fewer features (pits) of microwear than canids or hyaenids, suggesting that felids deliver deep, strong bites when killing their prey. These bites result in less abrasion of the canines than in other large carnivores (Anyonge 1996).

The African lion is well equipped for grasping and killing its prey with its claws and teeth, despite lacking great speed (Schaller 1972). The prey is usually killed with a throat or muzzle bite leading to suffocation (Kruuk



Fig. 3.6. The steenbok is hunted often, but infrequently killed, by cheetahs and leopards in many parts of southern Africa

and Turner 1967) or a broken neck (Eloff 1973 a, c). However, the killing method is adaptable and, as already said, the lion in the southern Kalahari kills gemsbok by jumping onto the victim's haunches and breaking its back at the lumbo-sacral joint. It seldom breaks the neck of other animals, but the prey taken in the southern Kalahari is generally small and easily killed with a few bites (Eloff 1964, 1973a, 1984). Compared with the leopard there, the lion in the southern Kalahari has a high success rate as it kills 38.5% of all prey hunted. However, kill rates vary with the prey selected. For example, lions in the southern Kalahari kill only 13.6% of all aardvark hunted, 15% of all adult gemsbok hunted, but 85% of all porcupines hunted (Eloff 1984).

The leopard commonly kills its prey with a throat or neck bite, or one to the base of the skull (Kruuk and Turner 1967; Smith 1978; Bothma and Le Riche 1984, 1986; Scott 1985). Leopards are proficient hunters and can kill prey three to four times their own weight (Bailey 1993). Southern Kalahari leopards most often kill early in their daily movements. This coincides with the early evening (Bothma and Le Riche 1986). In the Serengeti ecosystem, leopards kill 11% of all prey hunted (Schaller 1972). In contrast, male Kalahari leopards kill 18.5% of all prey hunted and females 21.8%. However, prey in the southern Kalahari are not killed in proportion to the frequency with which they are hunted. For example, the steenbok, an abundant, fleet-footed and vigilant small Kalahari antelope is the focus of 22.2% ($n = 410$) of all hunts by male and female Kalahari leopards, but it only represents 7.5% ($n = 80$) of all prey killed by them (Bothma et al. 1997). In the Matobo National Park, the steenbok is also common, but it is infrequently killed by leopards, being found in only 2% of all scats (Grobler and Wilson 1972). In the arid bushveld of South Africa, steenbok are also abundant but are never killed by leopards there (Kruger 1988). In the southern Kalahari, the steenbok is by far the prey hunted most unsuccessfully, requiring 27.5 hunting attempts for every successful kill by male leopards, and 9 attempts by females. In contrast, it requires a mean of 5.4 and 4.6 hunts respectively per successful kill for all prey (Bothma et al. 1997).

The cheetah commonly kills larger prey by suffocation through a throat or muzzle bite (Kruuk and Turner 1967) after a high-speed chase. This chase usually ends when the cheetah slaps the hindlegs of its prey to unbalance and overpower it (Eaton 1970c; Phillips 1993). Smaller prey, however, are simply pounced upon, pinned to the ground and killed with a single bite (Eaton 1970c; Labuschagne 1979). In the southern Kalahari, suffocation of larger prey by a cheetah may take up to 10 min. Moreover, the prey sometimes recovers from the initial suffocation attempt, usually only to be suffocated again (Labuschagne 1979).

A caracal catches prey with a sideways swipe of the front paws (Smithers 1971) and usually bites its prey in the throat or at times in the nape of the neck. The lower incisors of a caracal are reduced. Coupled with its large dia-

stema, this allows the canine teeth to penetrate the prey almost to their full length (Pringle and Pringle 1979; Moolman 1986).

Surplus killing as defined elsewhere, occurs occasionally in felids but it seems to be rare. Nevertheless, in the Gir Forest of India, a single leopard once killed 17 of a group of 60 domestic goats that went astray in a monsoon (Kruuk 1972a). In the Mountain Zebra National Park a caracal once killed small livestock en masse, but no natural prey are known to have been killed in a similar way (Moolman 1986).

3.5.4

Feeding

Lions. The carcasses of killed prey are eviscerated before feeding starts. In feeding, lions eat some bones, but they eat muscle mainly, using their front paws in 35% of all cases to aid in feeding (Van Valkenburgh 1996). When feeding at a kill, lions are quite socially organized. The larger males are dominant over the females, but there is considerable squabbling (Bertram 1979). Lions consume large prey as completely as possible. In the Serengeti ecosystem, lions sometimes cover the disembowelled viscera of their prey with vegetation or soil (Schaller 1972). However, in the southern Kalahari, they regularly cover these remains by scraping sand over them. The viscera are often removed from the carcass and is then dragged some distance away before being covered. The remainder of the food may then be moved a short distance to suitable cover before feeding starts, or it may be eaten where it is (Eloff 1973a). Lions in the Serengeti pluck out the long hair of furry prey with their incisors before beginning to feed (Schaller 1972). When a porcupine is killed in the southern Kalahari, it is carefully dequilled to a fair extent before being eaten. Nevertheless, southern Kalahari lions may at times sustain fatal injuries from quills when attacking or eating porcupines (Eloff 1973a). Usually, however, through its feeding habits and daily pattern of life, the lion of the southern Kalahari is able to meet its habitat's greatest challenge: that of lack of water and excessive heat (Eloff 1973a).

Near the coast in the Namib Desert, lions drag carcasses considerable distances from the kill site (mean: 1100 m; range 100 to 2600 m) before starting to feed. Dragging carcasses from a kill site before feeding is common felid behaviour, but in the Namib Desert the carcasses are usually dragged by lions away from exposed, windy beaches to the shelter of vegetated hummocks, or into the reedbeds of the dry river courses. Away from the coast, the carcasses are usually dragged to the shelter of some isolated small tree or bush. This action also hides the carcass from possible scavenging spotted hyaenas (Bridgeford 1985).

The mean daily food intake of an African lion indicates an optimum lion group size for the ecological conditions of a given area. Prey biomass and lion feeding group size define the limits of acceptable energetic expenditure or

gain, (Caraco and Wolf 1975). In the Kruger National Park, lions feed only once every four days (range 1 to 13 days), while 47.1% of all lion stomachs are empty at any given time (Bryden 1978).

Leopards. Before feeding, the leopard usually also drags the carcass to some form of acceptable cover (Smith 1978; Bothma and Le Riche 1984, 1986). In areas of high terrestrial predator density, leopards often store their food in a tree to avoid it being scavenged by other predators, especially spotted hyaenas (Scott 1985). For example, 31% of all kills by leopards in the arid bushveld of South Africa are stored in trees (Kruger 1988). However, actual interference by scavengers is not the only cause of leopards storing prey in trees as they often do this, possibly as a preventive move or for some other reason (Kruger 1988). In the southern Kalahari, where large predators are not abundant, leopards only store 17% of their kills in trees before feeding (Bothma and Le Riche 1984). Especially, but not necessarily only when eating furry prey such as young antelope, hares or other carnivores, leopards also use their incisor teeth to pluck out small bundles of hair so as to gain access to the meat, dropping the hair in a neat pile (Bothma and Le Riche 1984; Scott 1985; Kruger 1988). Porcupines are dequilled as lions do before being eaten (Bothma and Le Riche 1986). Most prey are eviscerated en route to the feeding site or at the kill site (Smith 1978). Only female leopards in the southern Kalahari, however, are known to cover the eviscerated remains of their prey with vegetation, and they only do so when the kill is made close to small cubs (Bothma, unpubl.). However, in areas of higher scavenger density such as the Matobo National Park, such remains are covered more frequently, but not regularly (Smith 1978). In the arid bushveld of South Africa, leopards never cover the intestines of their prey with sand or vegetation (Kruger 1988) despite the abundance of scavengers.

In the Matobo National Park, kills made in the wet season are usually dragged to higher ground for a mean distance of 260 m. In the dry season they are only dragged a mean distance of 120 m (Smith 1978). In the southern Kalahari, male leopards drag their prey longer distances away from the kill site (mean: 410 m) than females (mean: 57 m). The reason for this difference is unknown (Bothma and Le Riche 1984). Leopards in the southern Kalahari occasionally drag or carry their prey considerable distances before starting to feed. In the Matobo National Park, a leopard once carried a rock hyrax 1.6 km before starting to feed (Smith 1978). In the southern Kalahari, a male leopard once carried a bat-eared fox 4.9 km before doing the same (Bothma and Le Riche 1984). There is no apparent preference for the type of vegetation used by leopards for feeding (Kruger 1988).

Usually a leopard starts to feed on the buttocks around the anus of its prey, but occasionally it starts on the chest or shoulders (Smith 1978; Scott 1985; Bothma and Le Riche 1986; Kruger 1988). The tongue of a leopard is covered with hair-like papillae which are used to rasp meat particles from

bone (Scott 1985). The muzzle, part of the cranium, feet and viscera of prey are seldom eaten (Smith 1978; Bothma and Le Riche 1986).

Leopards will sometimes feed on a kill for several days. In the southern Kalahari, only a few kills are big enough, however, to satisfy a leopard for longer than a day. The maximum feeding duration recorded there is four days for a female that had killed a large aardvark. Male leopards in the southern Kalahari consume approximately 3.5 kg of meat per day; females with cubs 4.9 kg, but the males only kill once every 3 days as opposed to once every 1.5 days by females with cubs (Bothma and Le Riche 1984). In the Matobo National Park, a leopard once fed on a yearling blue wildebeest for six days (Smith 1978). Leopards which are disturbed at a kill in the southern Kalahari usually return to it later (Bothma and Le Riche 1993).

Cheetahs. Cheetahs only feed on food killed by themselves (Bertram 1979). When doing so, they feed as rapidly as possible to avoid competition from scavengers, although they may stay with a kill for up to 11 hours. When feeding, cheetahs in the Etosha National Park eat all the bones, except the skull, of prey weighing less than 10 kg. Even young cheetahs six to 16 months old have no difficulty in crushing and consuming most bones of a kill (Phillips 1993). Cheetahs do not use their front paws to aid in feeding as lions do (Van Valkenburgh 1996). Cheetahs feeding in groups are less likely to be harassed by scavenging spotted hyaenas in the Serengeti ecosystem than individuals feeding alone. A male cheetah will also occasionally scavenge food from a female there (Caro 1994). In the Etosha National Park, feeding cheetahs seldom pay attention to scavenging jackals, but may lose much or all of their prey to other scavengers. The cheetahs there feed in bouts lasting a mean of 82 min, with usually less than 15 min between bouts. If undisturbed, large prey such as an adult springbok are fed on for up to six feeding bouts. Each feeding bout lasts several hours. Adult cheetahs in the Etosha National Park require 3 to 4 kg of food per day to maintain good health (Phillips 1993).

In the southern Kalahari, cheetahs usually carry or drag their prey to shade before beginning to feed. The rump or ribs are eaten first, but little skin is eaten (Labuschagne 1979). When several cheetahs feed at one kill, they position themselves in the shape of a star around the kill, sometimes threatening each other as the food supply becomes reduced (Labuschagne 1979).

Other Cats. Before feeding, the caracal plays with its food (Smithers 1971). In the Mountain Zebra National Park, the prey is usually jerked about with the paws for five to 20 min before feeding begins: the reason for this is unknown. The caracal usually starts to eat the ribs and the breastbone, but it never touches the stomach or intestines (Smithers 1971; Pringle and Pringle 1979; Moolman 1986). The hair of certain prey is not removed before feeding as it is in the case of the leopard (Moolman 1986). Although the caracal does not eat carrion (Pringle and Pringle 1979), it will leave and then return to its own

fresh kill for a second feeding bout later (Moolman 1986). Caracals do not cache or bury unconsumed parts of their prey, but occasionally a kill may be dragged into the fork of a tree for feeding (Pringle and Pringle 1979).

3.5.5

Food Passage and Defecation

Data on food passage and defecation rates in felids in the wild are scarce, but it is known that lions in the Kruger National Park have a slower rate of digestion of food, and that they also eat less frequently, than do spotted hyaenas (Smuts 1979). In the southern Kalahari, most remains of the food of leopards appear in the scat on the first day following ingestion, but some appear as much as five days later. There is no differential passage rate for different types of prey (Bothma and Le Riche 1994a). Leopards that feed on large prey, deposit most of their faeces near the feeding site (Eisenberg and Lockhart 1972).

The mean interval between successive defecations by a leopard in the southern Kalahari is 0.6 days for males and 1.2 days for females. The difference is significant, but the reason is unknown. It contradicts the general belief (McNab 1989) that carnivores with smaller body sizes (here the females) have higher basal metabolic rates (and hence defecate more frequently) than those with larger body sizes (here the males). The distance travelled between successive defecations by male (mean: 12.4 km) and female (mean: 21 km) leopards is random, but there is a significant difference between the sexes. Seasonal climatic differences do not appear to influence defecation frequency as a measure of metabolic rate in leopards in the Kalahari (Bothma and Le Riche 1994a).

3.5.6

Water Use

Like most carnivores, felids are independent of free water, but will utilize such water when available (Grobler et al. 1984). In the Umfolozi Game Reserve, lions do not derive any significant fraction of their water intake in cool weather from drinking. However, in hot weather about 50% of their water intake is obtained from drinking water (Green et al. 1984). Lions in the northern Sudan have no access to surface water and must obtain moisture from their prey (Schaller 1972). In the southern Kalahari, lions are found up to 250 km away from the nearest open water and are independent of drinking water (Eloff 1973a). While southern Kalahari lions drink regularly when water is available, they can be completely independent of water under extreme desert conditions, obtaining sufficient moisture from the body fluids of their prey, and from wild fruits such as tsama melons when available. Loss of water in southern Kalahari lions is further reduced by long rests in the shade during the hot hours of the day. When it rains, these lions lap up water form-

ing in pools or lick the moisture from each other's pelage. Lionesses with cubs, however, drink water more frequently than other lions (Eloff 1973b).

Where available, leopards make use of caves as an important survival strategy to escape high daytime temperatures in hot climates, and to reduce water loss. In the Namib Desert, some caves may be used for many years by successive generations (Bailey 1993). Where caves are absent, as in the southern Kalahari, leopards rest underground by day in porcupine or aardvark burrows, or do so under the dense shade of vegetation such as the shepherd's tree (Bothma and Le Riche 1984, 1986). In desert areas, leopards are independent of free water but will drink it when it is available (Bailey 1993). Moisture is obtained through the body fluids of the prey, and by eating wild fruits when available (Bothma and Le Riche 1984, 1986). In the Masai Mara National Reserve, leopard cubs lick moisture from each other's fur when it rains (Scott 1985).

When water is available in the southern Kalahari, male leopards drink at a mean interval of 3.9 days, or once every 58 km moved. The male leopards move a maximum recorded distance of 113.4 km between drinks, while females with cubs seldom drink. However, they kill prey on average once every 1.5 days. On one occasion, an adult male leopard did not drink water for ten consecutive days in summer (Bothma and Le Riche 1986). Leopards lose little moisture through sweating, but pant rapidly as a cooling device (Scott 1985).

In the southern Kalahari, two adult male cheetahs are known to have moved 127 km in 12 days without drinking water. During this time they failed 15 times, but succeeded twice in killing prey. As with lions and leopards, wild fruits such as the tsama melon are used when available as a water source by cheetahs (Labuschagne 1979). No data on water use by other felids in arid areas are available.

3.6

Population Ecology

Little solid data regarding population ecology exist for felids in arid areas. What is known is fragmented and scattered in the literature. This area of study needs considerable scientific attention and is as yet a wide open field of study.

3.6.1

Lions

Mortality seldom targets adult African lions, but cubs are at risk. Most cubs die when still young. In the Serengeti ecosystem, most lions die from disease, starvation, abandonment, violent contacts with rival lions or other animals, or a from combination of these factors. Only 10% of all lions reach old age

there (Schaller 1972). In a recent outbreak of canine distemper, 33% of an estimated 3000 lions in the Serengeti died (Packer and Kock 1995). Lions are immune to anthrax probably because the pathogens of this disease cannot flourish in the highly acidic digestive tract of lions, even when they feed on the carcasses of animals that have died of anthrax (Berry 1983). Healthy, adult lions seldom starve to death, but cubs often do. Abandonment of cubs is a major cause of death. In various areas of the Serengeti, more than 50% of all cubs die before reaching adulthood (Schaller 1972).

Of the lions in the southern Kalahari, 68% are adults and 32% cubs (Mills et al. 1978). However, cub mortality may be as high as 90% especially in years of extreme drought when prey is scarce (Eloff, pers. com.²). Females outnumber males by 1.8:1 in subadults and by 2.1:1 to 2.8:1 in adults (Eloff 1973a; Mills et al. 1978). Female lions in the Savuti Marsh outnumber males by a wide margin. There the sex ratio is 5.7 females per male, a ratio which has serious foraging implications for these lions as has been explained earlier (Cooper 1991). In more mesic regions of Africa, the sex ratio of adult lions is closer to unity. This is the case in the Selous Game Reserve where cubs form a smaller proportion (21%) of the population (Rodgers 1974). In the Nairobi National Park, adult female lions are also more abundant than adult males (Rudnai 1973), as they are in the Etosha National Park (Stander 1991). These variable sex ratios indicate that survival in African lions is dependent upon age and sex, but variable between populations.

Prey abundance is a major factor in lion population dynamics, especially in respect of mortality (Schaller 1972; Bertram 1979; Hanby et al. 1995). In the arid bushveld of South Africa, lions disperse in response to diminishing prey in times of drought. They use the giraffe as staple food because this herbivore is little affected by anything except prolonged drought (Kruger 1988). In the Serengeti, prey biomass doubled over a recent decade, leading to a 33% increase in the number of lion prides in the area. At the same time, the mean pride size increased from 15 to 19, while cub survival also increased (Hanby and Bygott 1979).

When culled, lion numbers are soon restored by infiltration from surrounding areas in the Kruger National Park, and by increased reproduction. Short-term culling of many lions over a large area creates many vacant areas that attract strange lions. These lions interact aggressively, probably suppressing the birth rate and cub survival in their own prides. A more gradual culling of a few lions at a time from neighbouring prides, or even the gradual removal of an entire pride over time, produces fewer vacant areas, a lower influx of new lions and more sustained reproduction. However, both methods are followed by a rapid recovery of the lion population in a given area. Culling of lions in small parts of their range is therefore of questionable value as an aid to increasing prey productivity in large conservation areas. Culling

² Prof. F.C. Eloff, Research Associate, Centre for Wildlife Management, University of Pretoria, South Africa 0002.

increases the proportion of cubs or subadults to adult lions, and these younger lions eat proportionally more on a body mass basis than do adult lions (Smuts 1978b). For culling of lions to be effective for increasing prey numbers in large conservation areas, the culling will have to be sustained for several years over most of the lion range (Smuts 1982). Furthermore, lions in the Kruger National Park can only regulate the numbers of their major prey when populations of the latter are low (Mills and Shenk 1992). In the southern Kalahari, all the predators present have an influence on their prey populations. However, the food supply available to the prey might be the eventual regulator of the prey populations in an area where the amount and distribution of rain has a great influence on the overall availability of food resources (Eloff 1984).

3.6.2

Leopards

Data on most of the population ecology of leopards in arid areas are virtually non-existent. Cub survival is low. Probably most adult leopards die of starvation. Cubs are also prone to starvation and predation by other predators (Bailey 1993). Infanticide of cubs has also now been confirmed in the Judean Desert where at least three different male leopards killed 11 cubs over a 9-year period (Ilani 1990; Bailey 1993). In the southern Kalahari, where a female has to fend for herself and her cubs, hunting for food may take the female away for up to 2 nights at a time. During this time, the cubs frequently die of starvation, thirst or are taken by other predators. Although solid data are still lacking, it is estimated that cub mortality may be as high as 90% there, especially in times of drought when prey is scarce (Bothma and Le Riche 1986). Young leopards are rarely seen in the southern Kalahari (Bothma, unpubl.).

Predation by other predators on leopard cubs is not rare. For example, in the Kruger National Park the remains of young leopards have been found in the stomach contents of spotted hyaenas (Bailey 1993). Several lions once treed a female leopard in the Serengeti National Park and devoured her two cubs (Schaller 1972). Adult leopards are occasionally killed by other large predators such as lions, spotted hyaenas, wild dogs, crocodiles and even by their own intended prey such as baboons *Papio* spp., warthogs or gemsbok (Eloff 1973a; Scott 1985; Bailey 1993). Porcupine quills lodging in the palate of a leopard when feeding may well lead to death (Bailey 1993).

In the Kruger National Park, the leopard population is probably self-regulated thanks to abundant food and a stable population of adults (Bailey 1993). In the wild, a female leopard might live to about 12 years of age (Scott 1985). When she dies, she is replaced by a female from the same area. However, when an adult male dies, he is replaced by a younger male from an adjacent area (Bailey 1993).

3.6.3

Cheetahs

Cheetahs have the highest juvenile mortality rates yet recorded for any cat that is not hunted by man (Caro 1994). It has already been shown that cheetah cubs have high mortality rates with less than 50% of all cubs surviving. This is especially due to predation by lions, which take 73% of all cheetah cubs between birth and independence (Laurenson 1995). In addition, some 50% of all the subadult male cheetahs in the Serengeti are killed by intraspecific fights when competing for territories. Usually, however, predation by lions, spotted hyaenas and leopards are only a secondary cause of cheetah mortality. Other causes such as disease, starvation or injuries are more important. To compensate for these high mortality rates, cheetahs reach maturity earlier, and have higher mean litter sizes than do other felids (Caro 1994).

The mean life expectancy of a female cheetah reaching three years of age in the Serengeti, is 3.9 years (Laurenson 1995). In the Nairobi National Park, there appears to be a relationship between the size of the cheetah population and the numbers of other large predators (Eaton 1970a). Cub recruitment of cheetahs in the Serengeti is currently insufficient to maintain the cheetah population found there (Laurenson 1995). However, increases in food resources may increase cub survival (Hanby and Bygott 1979).

3.6.4

Other Cats

In the arid Karoo region, the caracal selects rock hyraxes as a food resource in a density-dependent way. Although nomadic, the caracal is considered to be a main regulator of the rock hyrax and rodent numbers there (Palmer and Fairall 1988).

3.7

Interaction with Other Carnivores

Different carnivores usually interact to varying degrees, depending mainly upon their food requirements and the food resources available. In an ecosystem such as the Serengeti, the different sizes of the predator species present, their distribution over different habitat types, and the variety of their hunting or foraging methods all lead to a low degree of overlap in the food resources eaten. The extent of exploitation competition when carnivores compete for the same prey is therefore slight. Pursuit hunters, such as cheetahs, wild dogs and spotted hyaenas, take the slower individuals of their prey spe-

cies, while ambushers such as lions take a more random selection. Interference competition, when carnivores compete for the same prey individual is usually more severe (Bertram 1979).

In adaptive carnivores, increasing prey scarcity may result in range expansion by the predators dependent upon them. For example, during one severe drought in the southern Kalahari, the available prey became widely dispersed and one lion pride once increased its range from 702 to 3900 km² in response to this (M.J. Owens and Owens 1984). Such conditions bring the predators involved into increasing contact with other predators into whose range they would not normally intrude.

Whether scavengers are a constraint upon predation by large felids, depends upon the abundance of these scavengers in a particular ecosystem, and upon the number of prey lost to them. Intraspecific competition for kills among solitary felids seems to be rare, and the possibility that they will meet at a kill is reduced by their temporal and spatial isolation (Sunquist and Sunquist 1989).

Of the felids in the arid bushveld of South Africa, the lion is the leopard's closest competitor, and there is a considerable degree of prey overlap (Kruger 1988). In the Etosha National Park, however, it is the spotted hyaena which seems to evoke most aggression from lions (Stander 1992b). In the Savuti Marsh, kleptoparasitism by spotted hyaenas of lion kills is a major competitive force. The prides there lose almost 20% of their food to spotted hyaenas, which live in clans of up to 50 members each. These hyaenas locate 78.5% of all lion kills, usually within 30 min of the kill having been made, and before much feeding has been achieved by the lions. On 82.4% of these occasions the hyaenas mob the lions at the kill, provided that the hyaenas outnumber the lions by at least 2:1. Complete take-over occurs regularly when they outnumber the lions by 4:1 (Fig. 3.4; Cooper 1991). Even in the Serengeti, lions may lose 10% of their food to spotted hyaenas if there are fewer than four lions on a kill (Caraco and Wolf 1975).

In the Kruger National Park, there is relatively little contact between lions and leopards, but given the opportunity, lions will take a kill away from a leopard. However, such a leopard may just escape with its prey up a tree (Bailey 1993). In the Masai Mara National Reserve, lions kill leopards irrespective of age or size. Even a group of olive baboons *Papio anubis* can chase a leopard from its prey (Scott 1985). Spotted hyaenas discover about 50% of all leopard kills, which they are easily able to take away if the leopard does not succeed in caching, or has already cached in a tree. A single spotted hyaena attracted to a leopard kill is occasionally killed by the leopard and is not normally able to appropriate the kill. However, two or more spotted hyaenas will usually take over a leopard's kill (Scott 1985; Bailey 1993). African wild dogs in the Kruger National Park occasionally pursue leopards with the obvious intent to kill them. The leopards there are also occasionally robbed of their kills by wild dogs (Pienaar 1969).

Leopards occasionally kill and eat an adult cheetah in the Kruger National Park, but contact between these two predators seems to be rare (Bailey 1993). However, leopards and black-backed jackals take a particular interest in each other in many areas (Scott 1985). In the Kruger National Park, black-backed jackals are never observed scavenging around leopard kills (Bailey 1993), possibly because of the danger of being preyed upon by leopards (Pienaar 1969) as in the southern Kalahari (Bothma and Le Riche 1984).

Black-backed jackals often follow foraging leopards around in the southern Kalahari, barking at them in a peculiar way as if notifying all and sundry about their whereabouts. The leopard will occasionally turn on them and kill them. Brown hyaenas also follow the tracks of foraging leopards at times in a possible attempt to scavenge food remains. A large, male leopard in the southern Kalahari, however, is able to defend its kill with varying success against up to two spotted hyaenas that may harass it simultaneously (Bothma and Le Riche 1984). Smaller carnivores such as the black-backed jackal, bat-eared fox, aardwolf and even on occasion the cape fox and genet *Genetta genetta* are preyed upon by leopards in the southern Kalahari (Bothma and Le Riche 1994a).

The competition between leopards and cheetahs for food in the dry riverbeds of the Kalahari Gemsbok National Park is reduced by the proportional selection of age cohorts of the springbok killed. Also, in the dunes away from the riverbeds, the leopards use a wider selection of prey than cheetahs. Furthermore, the cheetah hunts mainly by day and the leopard by night. This further reduces interference competition (Mills 1990). Bertram (1974) suggests that the leopards of the Serengeti are an unobtrusive, but integral part of the food chain.

The cheetahs of the Serengeti lose 12.7% of their kills to spotted hyaenas, and even more food to other large carnivores (Caro 1994). Competition between cheetahs and lions is not rare in the arid bushveld of South Africa, but these lions do not rob the cheetahs of their prey as they are known to do elsewhere. This is probably because the lions and cheetahs there are separated in time but not in space, as are cheetahs and leopards (Kruger 1988). In these bushveld areas, as they do elsewhere, cheetahs most often hunt during the day when other large predators are inactive (Schaller 1972; Eltringham 1979; Bertram 1979). This reduces competitive exploitation. In the southern Kalahari, most other predators, including the black-backed jackal and even some vulture species, rob cheetahs of their food. The main food source for the cheetahs there is young springbok lambs. This food resource is also used by at least eight other types of predator in the southern Kalahari, from martial eagles to lions (Mills 1990). The African wild cat is preyed upon by larger carnivores and birds of prey (Grobler et al. 1984).

The ethology of predation has been reviewed by Curio (1976), and the interactions between predators and prey in arid lands by Cloudsley-Thompson (1996).