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Abstract: A description of common traits, distribution, ecology, and predation, social, sexual and parent/offspring behaviour of all African Felidae, including cheetahs

The Behavior Guide to African Mammals

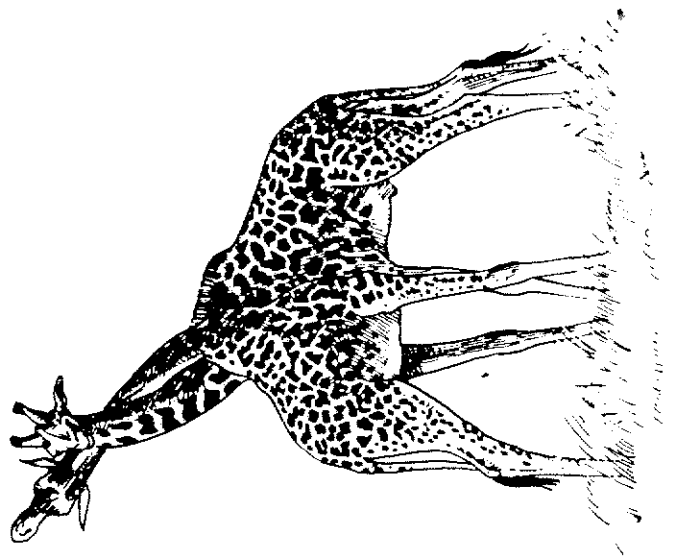
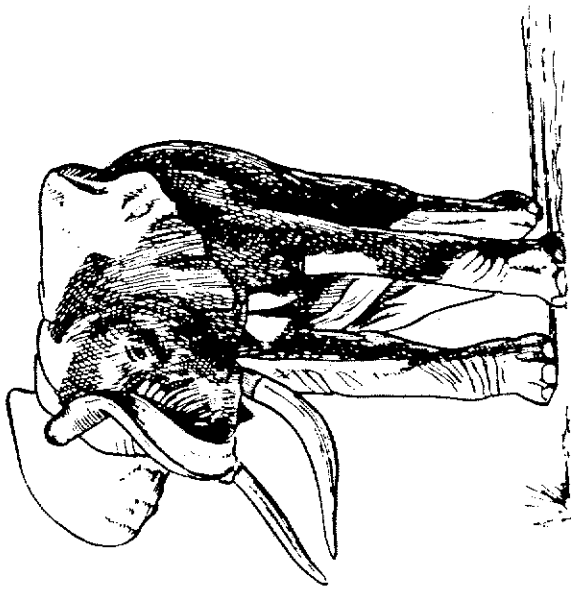
Including Hoofed Mammals, 1991
Carnivores, Primates

Richard Despard Estes

Drawings by Daniel Otte

Foreword by E. O. Wilson

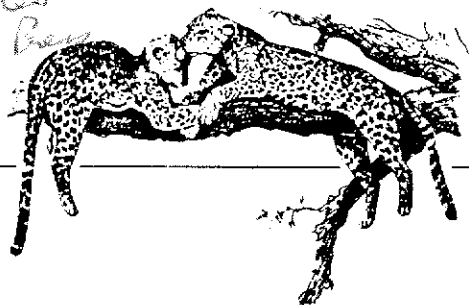
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Chapter 21

Cats

Family Felidae



African Species

Felis lybica, African wildcat
F. margarita, sand cat
F. nigripes, black-footed cat
F. aurata, golden cat
F. chaus, swamp cat
F. serval, serval
F. caracal, caracal

Panthera pardus, leopard
P. leo, lion

Acinonyx jubatus, cheetah

FAMILY TRAITS. Carnivores resembling the domestic cat, with long, lithe body and long tail, or shorter body and bob-tail (lynx type), males somewhat larger and more muscular than females, otherwise minimal sexual dimorphism (except lion). Legs short (sand cat) to long (serval, cheetah); big, soft-padded feet with 5 front toes and 4 rear toes armed with hooked, sharp claws normally retracted in sheaths (except cheetah). Head rounded, with large cranium and short jaws; big, frontally placed eyes; ears triangular to rounded, \pm prominent; conspicuous whiskers on upper lip. Teeth typically reduced to 30, specialized for eating meat: large, shearing carnassials and only 1 small upper molar, small, chisel-like incisors, canines long and laterally flattened; tongue rough, covered with horny papillae. *Coloration:* cryptic, pale gray to brown, sometimes black (especially leopard and serval), with pale or white underparts, most species spotted, striped, or blotched, some plain-colored (lion, caracal); many with black and/or white markings on ear backs, face, and tail. *Scent glands:* paired anal glands, scent glands in foot pads, chin, and cheeks of at least some *Felis* species. *Genitalia:* short, barbed penis situated just below testes with urethral opening facing backward, bone present but reduced.

Cats are so much alike in nearly every way except size that all but the cheetah could

arguably be placed in the same genus, *Felis*. They are so close genetically that species within the same size range can interbreed and even produce fertile hybrids (e.g., tiger \times lion, leopard \times lion, domestic cat \times various wildcats). But most taxonomists separate the 7 big cats, lumping 5 in the genus *Panthera*. This group shares an anatomical specialization that enables them to roar: the hyoid apparatus (voice box) is suspended by an elastic ligament that permits vibration and sound magnification (3, 5).

Senses. Vision is highly developed in the Felidae. Apart from good binocular vision of the frontally placed eyes and cone receptors providing visual acuity (and possible color perception) equal to the human eye by daylight, cats can see at least 6 times better in the dark, partly because of the light-reflecting layer (the tapetum lucidum) behind the retina, and the very large pupil (3). The iris varies in color from orange and yellow to green, gray, or brown; under bright light the pupil contracts to a small dot in the big cats and caracal, a vertical slit (wildcat, black-footed cat), or spindle shape (serval). Hearing is also acute in most felids, especially the smaller species that use their large mobile pinnae like dish antennae to locate hidden prey precisely (see serval account). The sense of smell is least important for predation but preeminent in felid social interactions (see under Social Organization and Olfactory Communication), and urinalysis with the vomeronasal organ enables males to monitor female reproductive condition. The presence of prominent whiskers and other sensory vibrissae indicates the importance of the tactile sense in this family (6).

DISTRIBUTION. Worldwide except Australia, the Antarctic, Madagascar, and other oceanic islands. *Felis* is one of the most widespread mammal genera, and the leopard is one of the widest-ranging land mammals in the Old World.

ANCESTRY. The first recognizable felids date back 40 million years to the upper Eocene, and representatives of modern cats, subfamily Felinae, have existed since the Miocene, a good 24 million years ago. However, from then until just a couple of million years ago the family was dominated by saber-toothed cats. True cats (*Felis*), the size of a large wildcat, date from the late Miocene of Eurasia and the Pliocene of South Africa (table 1.1, fig. 18.1). The modern big cats arose (probably from a leopard-like prototype) as predators on modern ungulates, which the saber-tooths, apparently specialized for grappling and killing ponderous, primitive mammals, were poorly adapted to capture (3).

The seldom-seen but common golden cat of Africa's rain forests may be close to the prototype from which modern cats evolved as they moved into more open habitats. The golden cat and the caracal are considered to be survivors of an earlier radiation (3, 5). The cheetah has been running down gazelles since the late Pliocene, but the other big cats only became dominant in the early Pleistocene, during the Golden Age of Mammals.

ECOLOGY. Found in all major habitat types from desert (sand cat) to equatorial rain forest (golden cat, leopard), to swamp and marsh (swamp cat, fishing cat), to high mountains (leopard). Apart from the cheetah and the adult tiger and lion, probably all cats are good climbers; yet Africa, unlike Asia and South America, has no specialized arboreal hunters (7). Most cats climb trees for their own safety; those that live on treeless plains take refuge underground.

DIET. Of all the carnivores, cats are the most committed meat-eaters. Although reptiles, amphibians, fish, shellfish, and even insects are included in the diet, rodents, rabbits, and hares are no doubt the mainstay of most small cats. The bigger ones prefer ungulates, but take whatever is most readily available.

SOCIAL ORGANIZATION. Because of their secretive and nocturnal habits, few cats have been closely studied in the wild. But judging from those few and observations of others in captivity, social organization and behavior are as similar as felid morphology. The familiar assertion that a housecat is simply a miniature tiger is essentially true. Knowledge of this domestic feline provides insights into the psyche of all cats.

With few exceptions, cats are truly soli-

tary animals which avoid one another except when sexually attracted. In closed habitats, prey species are usually dispersed and best hunted alone, and mostly too small to be shared by a group. Relying mainly on scent-marks, which carry information about when the mark was made and the sex, reproductive status, and identity of the marker, individuals can share a hunting range without meeting unless they choose to do so (1, 6). Adult males of probably all species defend at least part of their ranges against other males. The ranges of females are generally smaller and several may be included within a male's territory. The extent to which females are territorial is unclear in most cases, but even when their ranges overlap, adult females usually avoid both one another and males. The African lion is the only social cat and has evolved an elaborate clan-territory system based on close kinship bonds among females (9). The pride owns an extensive range frequented by large, open-country ungulates, which pride members hunt and eat cooperatively. But latent sociability may be seen in the fact that tigers, normally solitary, summon one another to share large kills (8), and adult male cheetahs, like lions, form coalitions. Furthermore, feral housecats subsisting on an abundant food supply such as a garbage dump develop a social organization comparable to the lion's, including baby-sitting by subadult males and communal guarding, suckling, and feeding of kittens (7).

ACTIVITY. Although many cats can be active in daytime, all but the cheetah are primarily nocturnal, night being the time most favorable for stalking and ambushing predators to go hunting.

POSTURES AND LOCOMOTION. Although few cats are truly arboreal, they have retained much of the freedom of movement associated with climbing, which terrestrial carnivores have sacrificed in becoming more cursorial (4). The use of the claws in capturing prey and in fighting also requires limb mobility, as well as a muscular build. In acquiring the strength to overpower large prey, cats sacrificed speed and endurance. Most prey of rabbit-size and up can outrun their felid predators, which accordingly have to rely on stealth to get close enough to capture them. If their quick rush or pounce misses, they usually quit, for cats (including even the cheetah) are notoriously short-winded. A comparatively small heart (e.g., amounting to only 0.36% of a

leopard's body weight) partly explains the felid's lack of endurance (cf. canids, Postures and Locomotion). But they cover long distances at a walk or trot, and they are also good swimmers and jumpers. The tail is important as a balance organ, especially in the more arboreal species.

PREDATORY BEHAVIOR. All cats capture and kill prey in basically the same way as the domestic cat [6]. The different steps involved in hunting, capturing, killing, and eating prey are traits shared by the whole family which appear at the appropriate time in the development of each individual. Yet practice is needed to perfect these innate motor patterns, and experience leads to individual variations and improvements on the basic techniques. Interestingly enough, each link in the predatory chain exists as an independent drive: the urges to stalk, to catch, and to kill can each stand alone and separate from the urge to eat [6]. Once this is understood, some of the inconsistencies in the predatory behavior of cats become less puzzling: for instance, why gorged lions can't resist the chance to make another easy kill, why cats often abandon a quarry after killing it and even when hungry usually don't begin eating right after killing their prey, and why cats play with and may not even kill the animals they catch.

Considering that the usual prey of most cats is small, why do they need to be so powerful? The capability of killing animals their own size or bigger increases the food resources that are available to the predator and the areas where it can subsist. There is always the risk of injury, though, particularly from well-armed prey. The cat's strength and killing techniques minimize the risks of bringing down and immobilizing large animals while administering the coup de grace. Cats hardly ever jump out of trees upon formidable prey. They spring or rush forward and grab the quarry by the rump, back, or shoulder with a forepaw; both paws are used when pouncing on small prey and to grapple large prey. The back feet remain on the ground, providing purchase to pull the quarry off its feet. The unsheathed claws sink through the skin like meathooks when the cat pulls the prey toward itself. But while chasing at full speed behind a fleeing animal, the claws remain sheathed when the cat adroitly trips it up with an extended foreleg—to be attached to a large animal as it falls would be dangerous. This technique is practiced by cheetahs and lions as well as by other cats [6].

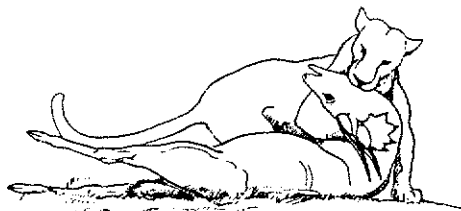


Fig. 21.1. Leopard strangling gazelle (redrawn from Leyhausen 1979).

Cats use a very precise bite to kill small prey: a canine tooth is deftly inserted between 2 cervical vertebrae, wedging them apart and partially or completely severing the spinal cord, bringing instant death. But the big cats dispatch large prey by suffocation, holding the throat or muzzle with jaws designed to clench with maximum sustained force (fig. 21.1) [3, 5]. Small prey is always eaten beginning at the head. Large prey, with skull too large to crack, is eaten beginning at the belly or chest, although there are minor differences among species [9]. Meat is sheared from the bones with the carnassials or pulled off with the incisors and swallowed without chewing. *Felis* species eat in a crouched position and rarely use their paws to hold their food, whereas *Panthera* species normally lie down and hold their meat between or beneath their paws [6]. Most cats partially pluck the feathers before eating birds.

Cats tend to be frugal with their food, caching the remains of a kill by covering it with leaves or grass and returning to feed on it as long as it lasts. Leopards and sometimes caracals take their kills up trees. Many species will eat carrion, and many can go for days between meals, making up for a fast by gorging up to $\frac{1}{4}$ their own weight. Their catholic choice of prey species extends to all smaller cats, sometimes including members of their own species.

SOCIAL BEHAVIOR

COMMUNICATION. Felids have the most mobile lips and changeable facial expressions of all carnivores. Why should cats need a more complex communication system than other solitary animals? Perhaps because of the unusually dangerous consequences of fighting between animals armed both with long fangs and sharp claws [9, 10]. The ability and readiness of cats to defend themselves with these weapons tend to inhibit outright attack. Instead, cats employ discrete distance signals (scent-marks and loud calls) to avoid surprise meetings, and variable, graded visual and vo-

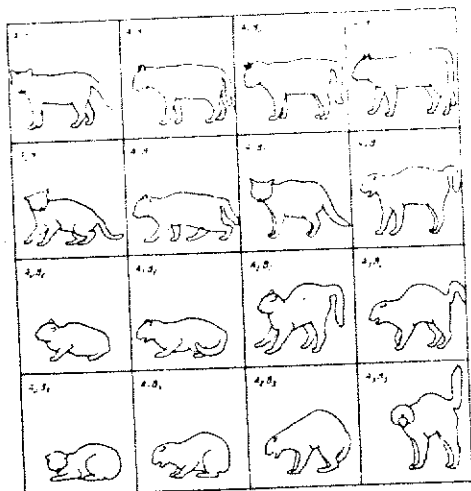


Fig. 21.2. Felid offensive and defensive body postures: A_0B_0 denotes a normal, relaxed posture, A_0B_1 a posture of offense unmodified by fear, A_0B_1 a purely defensive posture. Other illustrations show postures assumed when offensive and defensive emotions are both present, in varying degrees, culminating in A_1B_1 when a cat is strongly and equally motivated by offensive and defensive tendencies. (From Leyhausen 1979.)

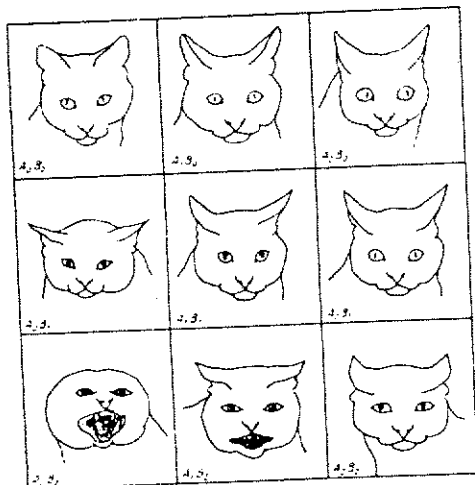


Fig. 21.3. Offensive and defensive facial expressions: same arrangement as in fig. 21.2, but to a less extreme degree. Here A_0B_0 denotes a relaxed expression, A_0B_1 an offensive mood unaffected by fear, A_1B_0 a purely defensive threat, and A_1B_1 equally strong offensive and defensive moods. (From Leyhausen 1979.)

cal signals, plus olfactory and tactile messages, to communicate their feelings and intentions at close range under any and all conditions [9, 11]. The domestic cat, a typical small feline virtually identical to the African and European wildcats, uses at least 9 facial expressions and 16 different tail and body postures for a total of 25 visual patterns, 16 of which occur in combination. It has 8 distinct calls, 3 kinds of scent-marks, and about 7 contact patterns [rubbing, clapping, patting, etc.] [2, 11]. The lion's communication system employs at least 17 visual patterns, 13 calls, 5 olfactory signals, and 7 contact patterns. To make the positions and movements of the ears, tail, eyes, and lips as plain as possible, these organs have contrasting markings in most cats.

Visual Communication

Offensive and Defensive Facial Expressions and Postures. Some of the possible variations in feline visual signals are shown diagrammatically in figures 21.2 and 21.3, where facial expressions and postures associated with offensive and defensive moods are illustrated in the domestic cat. The upper left-hand drawings represent the face and body in the relaxed, neutral state; the upper right figures represent the strongest threat and the lower left figures the greatest readiness for defense. Note that the ears are erect and turned outward, presenting a triangular shape, in the most intense offensive threat, and the eyes are wide open with small pupils (fig. 21.3 A_0, B_0); whereas the ears are flattened, presenting no silhouette, and the eyes are narrowed with dilated pupils in a purely defensive mood [A_1, B_1]. The other drawings show gradations between the 2 extremes when a cat is activated by both emotions to varying degrees and intensities. The lower right drawing in figure 21.2 (A_0, B_1) shows what happens when motor patterns associated with flight, defense, and attack are all superimposed, at high intensity. This is the classic posture of a cat confronting a dog. Only at highest intensity are facial expressions and body postures completely synchronized. Otherwise the face registers changes of mood quicker and more subtly than does the body [6]. Consequently it is necessary to illustrate expressions and postures separately.

The mildest expression of aggression is a bland unwavering look (fig. 21.3 A_1, B_0), as if the cat was looking through or past its opponent [9]. Conversely, the mildest expression of an intimidated cat is *looking away* or *looking around*. When a cat in strange surroundings is approached by an-



Fig. 21.4. Consummatory expression of fully fed lion licking its bloody paws.

other cat, it sits or crouches and calmly surveys its surroundings in every direction but that of the other cat. The stranger often appears more at ease than the resident. In like manner, a stalking lion sits up and looks around indifferently when it is spotted by its intended victim. In both situations cats are seen to be disconcerted by a direct stare, and indeed a cat on the defensive can also halt the approach of an aggressive opponent by looking directly toward it [6].

Nonaggressive Facial Expressions

Consummatory face (fig. 21.4). Associatable with certain activities apparently pleasurable to the animal, notably eating contentedly, urinating and defecating, sharpening the claws, rolling in carrion, catnip, or dung. The eyes may be closed, or open but "dreaming" or "staring into space," the ears partially flattened.

Alert face. An expression of intentness as a cat surveys its surroundings, particularly after sighting potential prey; mouth closed or slightly open, ears cocked, and eyes wide open.

Play face. Mouth slightly open, corners drawn back and slightly raised without showing teeth; ears and eyes as in relaxed face or fairly alert.

Urine-testing (flehmen). Wrinkling up nose with mouth open and eyes closed, after smelling urine, estrous females, and sometimes carrion. Given mostly by males.

The flehmen grimace is much more pronounced in *Panthera* than in small cats. Otherwise facial expressions and ear movements are very similar in all cats. So are the postures and behaviors associated with defense, although the big cats do not arch their backs. The greatest differences are seen in the postures and movements asso-

ciated with offensive threat and attack. For instance, threatening lions keep their heads low, backs stretched, and rib cage lowered so that the shoulder blades stand out prominently [6].

Vocal Communication. A wide range of different calls is represented in the family, including the cheetah's birdlike contact chirp. Other monosyllabic short sounds include panting, inspiratory gasp (leopard only), expiratory bursts, "knocking," and guttural hissing. Examples of variable, longer calls are yowling, meowing, roaring, cooing, snorting, rumbling, growling, grunting, gargling, snarling, and purring. Mothers use a special call to summon kittens when bringing home live prey. Call intensity is clearly different when the prey is small and harmless (mouse) or large and potentially dangerous (rat), and the young respond accordingly [6].

Most small cats lack distance calls comparable to the roars of *Panthera* species, although some *Felis* females announce the onset of estrus with loud calls, and males of seasonal-breeding species may call more often then or utter special mating calls. As in visual signals, most vocal signals are concerned with offensive and defensive behavior [11]. Thus, most small cats have 6 calls in common: hissing, spitting, growling, screaming, purring, and meowing, of which all but the last 2 are hostile [11]. Several of these calls grade into one another and express rising excitement by increasing noise and pitch: growling—yowling—screaming (the highest, noisiest vocalization), followed by a volley of spitting.

To demonstrate how calls are often linked with visual, olfactory, or tactile signals as part of a complex display, consider growling and snarling, the one offensive and the other defensive in character. It is basically the same vocalization, but when given with the mouth closed during offensive threat it comes out as a growl, and when the mouth is opened with lips retracted in a defensive threat it becomes a snarl [9]. In this way, the vocalizations of an aroused, angry cat express every shade of emotion from pure aggression to pure fear while precisely tracking the visual signals.

Meowing signals mild distress, especially in kittens, helping to remind mothers of their whereabouts, whereas purring, as everyone knows, expresses contentment, as when kittens are suckled or licked, or when adults greet or groom one another. Felines have no special alarm calls; they simply growl [9].

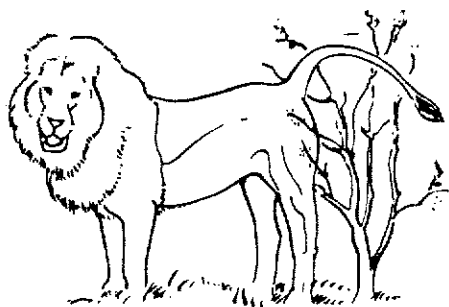


Fig. 21.5. Lion patrolling and scent-marking defended part of pride territory by *urine-spraying*.

Olfactory Communication. The main form of scent-marking is *urine-spraying* directed backward against objects at nose level or higher. The placement and form of the penis seem specifically adapted for this purpose (6), and indeed adult males are the main practitioners. But adult females also spray, in some species more frequently than males, particularly during estrus (6). The basic marking technique is as follows: first the cat sniffs the place to be marked intently, especially if it has been marked before, in which case it often *grimaces*. Next, or after urinating, it rubs its head against the object, thereby anointing itself with its own or another's urine, meanwhile wearing the *consummatory face* (fig. 21.4). Finally, it backs up and sprays its own urine on the spot (figs. 21.5, 21.13). Feline urine has a potent smell, especially the male's, but there is no evidence that anal-gland secretions are sprayed or otherwise mixed with the urine (11), as sometimes asserted (9). Indeed, the function of the cat's anal glands is still a mystery.

Scuffing. A rhythmic treading and forward-kicking motion of the back feet with claws extended is performed by many of the bigger cats (fig. 21.6). If, as commonly occurs, the cat also urinates, the urine becomes mixed with soil and impregnates

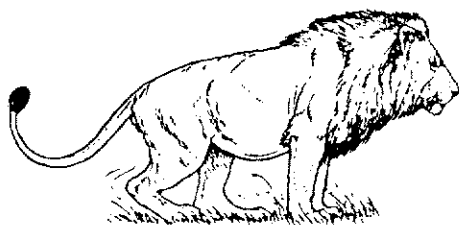


Fig. 21.6. Lion *scuff* marking (from Schaller 1972b, drawing by R. Keane).

the hindfeet. Scuffing visibly disturbs the ground.

Rubbing and rolling. *Head-rubbing* is stimulated by odors other than urine [e.g., catnip] and may serve to deposit glandular secretions as well as to anoint the animal with scent. After sniffing, or licking and biting the place, and often after *grimacing*, the cat proceeds to rub its lips, cheeks, head, and neck on the spot. Copious amounts of saliva often appear on the lips during a vigorous rubbing bout, soaking the spot and the rubbed areas of the cat (11). Cats are also stimulated to rub their cheeks and neck on smelly, decomposing substances such as carrion and dung, followed sometimes by rolling and writhing of the whole body on the spot. The parts of the body which are most commonly rubbed, namely the forequarters, are also the places most commonly sniffed and rubbed during social encounters between cats (more under Tactile Communication).

Defecation. The act of defecation is similar among species and sexes, but other associated acts vary. Feces are apparently unimportant for scent-marking, at least in many smaller cats that rake soil or litter over their scats. *Panthera* species make no attempt to cover theirs and a few deposit dung at specific or conspicuous sites (see leopard account).

Display claw-sharpening. Probably all cats rake the claws of their forepaws on trees. Aside from removing loose claw sheaths, clawing leaves visual and possibly scent marks (assuming glands described in the feet of domestic cats exist in other cats [11]). The act of clawing may also be a visual display.

There are few clues to the significance of these different marking behaviors, either for the sender or the receiver. *Urine-spraying* is often considered territorial behavior, but if so there is no evidence that these marks intimidate or deter other individuals from using the same areas, although cheetahs have been seen to alter course after checking fresh scent-marks (1, 6). Such marks may well be signposts from which cats find out who is ahead and how far. *Spraying* and *scuffing* may also be assertions of self-confidence if not space claims, since cats often scent-mark during or following aggressive encounters, around kills, and so on (6, 9, 11).

Tactile Communication. Nonaggressive meetings between cats begin with *mutual sniffing* of noses, head and neck stretched forward and ears erect in friendly curiosity (6). They proceed to sniff and touch light-

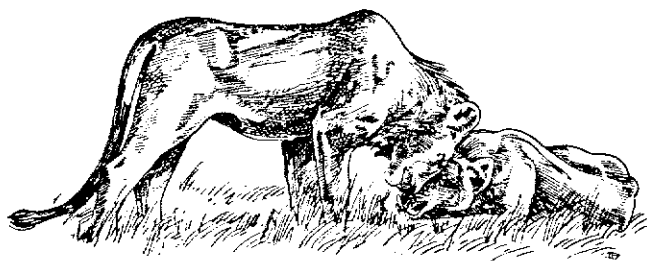


Fig. 21.7. Lion greeting ceremony.

ly with their whiskers the nape and flanks, and finally the anogenital area. A friendly cat raises its tail to allow this inspection, but often one is more fearful, keeps its tail down, and sidesteps, so the pair ends up circling.

Greeting ceremony. When family members meet they go through a ritual that begins with sniffing noses, followed by rubbing their heads and often their sides together (fig. 21.7). The tail is erected with the tip bent toward or draped over the partner. Small kittens rub against the mother's chest and throat. The similarity between greeting and the sexual presenting of an estrous female is striking, and comparable to social presenting in primates [6]. The ceremony is more frequent and pronounced in some of the larger cats, above all in the lion.

AGONISTIC BEHAVIOR. See also Vocal and Visual Communication. The following account of aggressive interactions, based on studies of feral housecats [6], applies with minor variations to probably most small and at least some of the big cats.

The intensity and outcome of hostile encounters between cats vary according to circumstances and the sex and motivation of the participants. Ranking among males whose ranges overlap or adjoin is usually settled by fighting. *Rival fights* are serious combats with the underlying intent of inflicting damage by delivering a neck

bite. A single fight between adult males usually settles the issue of dominance, but young adults may go through many fights before their standing is established. Dominance determines which of the males attracted by the calls and scent of a female in heat ends up mating with her.

The approach of an aggressive male is made in the posture shown in figure 21.2 A₁, B₀. The animal moves very slowly and stiffly and when close, raises and moves its head from side to side, meanwhile growling deeply and yowling. The tail tip twitches rapidly and spasmodically. The defensive cat gets ready to roll onto its back, first by turning its forequarters, freeing a forepaw, and raising it to strike the enemy on the nose if it continues to advance. The attacker can only press home a biting attack by disregarding the risk of injury to itself. Usually the aggressor stops, draws in its own neck, and hits out with a forepaw, indicating that it is on guard and ready to repel a counterattack. The defender immediately responds by rolling onto its back, with all 4 paws ready for action (fig. 21.8). Should the aggressor follow through, the defender clutches and pulls him toward his open jaws while his hindfeet trample and rake his exposed underside. The aggressor has no choice but to follow suit and they now roll on the ground, the aggressor yowling, the defender hissing,



Fig. 21.8. In a dispute over food, a lion (right) resorts to the characteristic felid rollover self-defense, which often inhibits an aggressor's attack.

spitting, and growling, culminating in hair-raising shrieks. After breaking off, the winner typically sniffs the ground (*displacement sniffing*) and slowly moves away. The loser remains crouched until its rival is out of sight (6).

Territorial and maternal defense. Both types feature a sudden, swift attack, chasing, and hitting without preliminary displays. If the trespasser stops and defends itself, both stand or rear with paws raised to strike, showing that territorial and maternal attacks are defensive and not purely offensive. Mothers of small cubs are the most determined and fearless.

Long chases are associated only with territorial defense and *mock pursuit* during mating. In *rival fights*, the stiffness associated with offensive threat display actually prevents the aggressor from pursuing a rival that elects to flee (6).

REPRODUCTION. Gestation ranges from about 2 months in small cats to over 3 months in the lion and tiger. Litters include 1–8 offspring, with 2–4 the usual number. The smaller species may reproduce yearly beginning at a year or younger; the larger ones begin a year later (males later still), and reproduce at intervals of no less than 1½ years. But when a litter is lost, females reenter estrus within a few weeks (see lion account), and keep cycling every few weeks until fertilization occurs, either during a regular mating season or, particularly in the tropics, at any time of year. Estrus may last anywhere from a day to 2–3 weeks (6).

SEXUAL BEHAVIOR. Frequent copulation over a period of days is a felid characteristic (see lion account). Cats are induced ovulators and repeated copulation is necessary before ova are produced and conception can occur (3, 9).

A female coming into heat advertises her approaching receptivity by become hyperactive, calling, scent-marking, *rubbing against objects*, and *rolling* sinuously on the ground. This behavior disrupts the usually solitary existence of mature but sexually inactive cats, attracting the local males who proceed to compete for the right to mate. They engage in a lot of display and some combat (6). The female's courtship behavior is alternately coquettish and defensive. She *rubs against the male, presenting her posterior with tail raised* invitingly, but when he makes bold to approach, she turns upon him *spitting*, scratching, and yowling. The next moment she writhes on the ground at his feet or invites pursuit. A female in

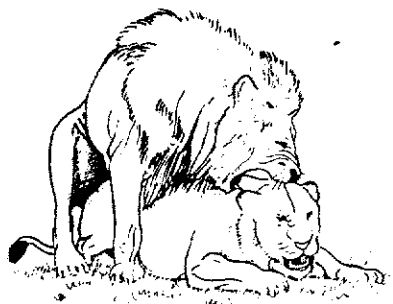


Fig. 21.9. Felid copulation (lion), with female crouching, male making biting movements at her neck.

full estrus adopts the *copulatory crouch* (fig. 21.9), head low, eyes narrowed, ears slightly back, rump elevated, tail raised and deflected. Sometimes a female *treads* with the hindfeet.

Male courtship behavior features frequent *urine-spraying*, *rubbing heads* with the female, frequent licking of the erect penis, long pursuits, and patient waiting. When the female invites copulation, the male tries to grip her neck before mounting. This may induce passivity in the female, in the same way that kittens go limp when so gripped. But quite often a female will try to escape, twisting and scratching. Once the male straddles the female, instead of grasping her with the forelegs as in most carnivores, copulation is usually accomplished with a few pelvic thrusts. Small cats commonly maintain the *neck grip* the whole time, whereas in *Panthera* species the bite has been reduced to a mere baring of the teeth or a *symbolic bite* a moment after ejaculation (6). Immediately afterward the female screams or snarls, and often twists and hits out at the male, which jumps back, growling. The female then licks her vulva and/or rolls. Within a few minutes courtship is resumed. After several days of this, the initiative shifts increasingly to the female, which uses *rubbing*, *rolling*, and *presenting* to renew the male's flagging interest. Not infrequently males lose interest while the female is still going strong, and another male takes over (see lion account). This could explain the observation that males of solitary species tend to be more tolerant of one another than are females. Waiting may be a more viable strategy than all-out fighting to gain mating opportunities (6).

PARENT/OFFSPRING BEHAVIOR.

The young are born blind, deaf, and barely able to crawl. In probably all species but

the lion, the mother bears sole responsibility for feeding and rearing them. Males play no paternal role. Cubs remain hidden in a den or nest for several weeks until they become mobile. During this time the mother's normal flight response may be blocked, leading her to attack even against impossible odds.

Older cubs are warned to take cover by the mother's hissing and slapping at them; in this way they learn which animals are to be feared (6). The mother readily changes hiding places if much disturbed, carrying 1 kitten at a time by the head, nape, or back skin. The mother retrieves and vigorously licks strayed babies—but only if they meow loud enough to be heard.

Felid mothers train their young to fend for themselves, prior to separating from them shortly before the next litter is born. While her offspring are still very young, the

mother begins bringing prey back to them, first dead, later still alive. At first the kittens are more frightened than attracted, but the escape attempts of live prey soon stimulate their hunting urge. All the motor patterns of prey catching and eating are practiced long before the young become independent. The neck bite is the last link to be perfected. Seemingly 1 or 2 experiences in delivering the bite are necessary before the pattern "clicks" into place and becomes automatic (6).

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The only 2 strictly African cats are the serval and black-footed cat. The others also occur in Eurasia or did until very recently. Because of their extremely secretive habits, too little is known about the behavior and ecology of these small cats to present comprehensive species accounts. Dissimilarities in their form and distribution clearly indicate still unstudied differences in their ecology. However, observations in captivity reveal relatively minor differences between species in displays and other basic behavior patterns. Descriptions in the family introduction should be consulted to fill gaps in the species accounts.



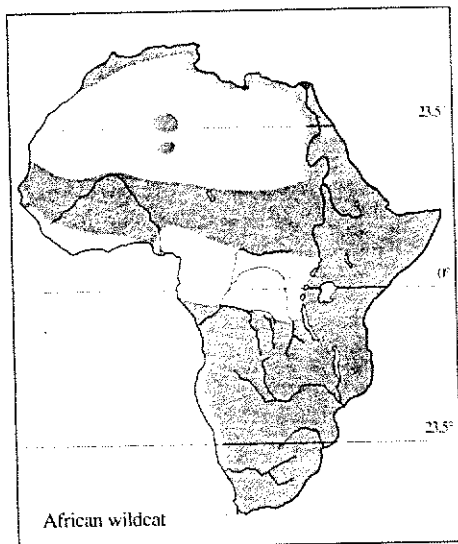
Fig. 21.10. African wildcat, resting in a disused hole, its refuge in open grassland.

African Wildcat *Felis lybica*

TRAITS. A wild tabby cat. *Weight and length* (head and body): (Botswana population) males 5 kg (3.7–6.4) and 58 cm (53–

63), females 4 kg (3.2–5.4) and 55 cm (51–58), tail 31–37 cm (7). *Coloration*: geographically and individually variable, lighter in dry and darker in wet regions, usually gray or tan but varies from orange to black; dark garters on upper limbs, outer tail ringed, ending typically in black tip; striped forehead and cheeks, fainter stripes on torso and indistinct spots on chest; underparts lighter. Distinguished from domestic tabby by rufous, unmarked ears and longer legs, resulting in more upright seated posture (8). *Scent glands*: anal glands, also chin, cheek, and possibly foot-pad glands. *Mam-mae*: 8.

DISTRIBUTION. Pan-African outside the Lowland Rain Forest and the Sahara, it is the commonest African cat. The wildcat of Europe and Asia, *F. silvestris*, is considered by some authorities to be the same species, despite a heavier build, shorter legs, and long hair (3). Embalmed cats retrieved by thousands from Egyptian tombs show that the wildcat was domesticated probably as early as 4000 B.C. The Egyptians worshiped Bast, the cat goddess of the hunt, love, and pleasure (3). Egyptian drawings and figures of cats depict the distinctively upright seated posture of *F. lybica*, an indication that domestic cats descend from the African wildcat. But the long legs that account for the posture disappear, along with the translucent, unspotted ears, when the wild form crosses with modern-day housecats from African villages and towns (8).



ECOLOGY. The wildcat occurs in virtually all places where rats and mice are plentiful, including the outskirts of villages and towns. Attraction to human habitation may have led to domestication in the first place. Wildcats even live in treeless open grassland, as on the floor of Ngorongoro Crater. Here they depend on holes dug by other species for refuges against a host of bigger, faster predators [fig. 21.10]. One orange-colored cat with greenish eyes, seen occasionally sunning, lived in a burrow complex that also housed hyenas, porcupines, and bat-eared foxes (author's observation).

The food habits of the wildcat differ little from those of free-ranging housecats. Rodents are the mainstay, with small birds, lizards, snakes, frogs, and large insects (beetles, grasshoppers, winged termites, centipedes, spiders) taken as opportunity affords. The springhare and the African hare are normally the largest prey of this species.

SOCIAL ORGANIZATION: solitary, territorial.

Since the African wildcat and the housecat are one and the same species, interbreeding as readily as wolf and domestic dog, it should be one of the most familiar of Africa's wild animals. But no proper study of a wild population has been made, so in this case knowledge of a wild animal rests on studies of the domesticated form, and on observations of the closely related (if not conspecific) European wildcat. The variability in social organization found in

feral housecats, notably the formation of clans and the cooperative care of offspring where there is a food surplus (see family introduction), has yet to be seen in African wildcats. They appear to be quite strictly solitary and territorial (8). Yet a tendency toward cooperative care can be seen in the behavior of 2 hand-reared wild females. After littering, each became territorial, marking and fighting over the same range. The only way to keep the dominant one from attacking and driving the other away was to let them out by turns. However, despite their unrelenting antagonism, each brought back and left food offerings (mice, birds) for the other's kittens.

Since the African wildcat is dispersed in much the same way as its European and rural domestic counterparts, it probably has a similar social organization [see family introduction]. The following information on the dispersion pattern of wild and feral cats in Europe gives some indication of what to expect of *F. lybica*. Home ranges in good habitat may be 50–100 ha [4, 5]. A tomcat's territory encompasses the ranges of up to 3 females, reaching maximum extent in the mating season. Females are more intolerant of one another than are males, but only actively defend a core area within the home range. Here cats that are subordinate elsewhere (normally) become dominant and may fiercely attack even much larger individuals. The rest of the range is shared and all members of the local community have the right to use it on a first-come, first-served basis, regardless of rank [4]. Cats entering a common hunting range check carefully to see and smell whether another cat is already on the scene, often going to a vantage point to scan, sniffing vegetation where others have sprayed urine, scraped, or scratched, and leaving their own marks in turn. If another cat is spotted, the latecomer waits for it to move off, although occasionally 2 cats may hunt in the same field while completely ignoring each other. African wildcats have been seen hunting in pairs or family groups, the members moving in the same general direction and spaced 3–30 m apart [3].

ACTIVITY: nocturnal.

POSTURES AND LOCOMOTION. As in domestic cat.

PREDATORY BEHAVIOR. Described in family introduction.

SOCIAL BEHAVIOR

COMMUNICATION. Discussed and illustrated in family introduction.

Olfactory Communication: urine-spraying by both sexes, also chin- and cheek-rubbing and claw-sharpening. The feces are buried as in housecats.

AGONISTIC BEHAVIOR. Described in family introduction.

REPRODUCTION. Housecats remain in estrus about 4 days and ovulation occurs a day after copulation [1]. Several males have been seen accompanying a *F. lybica* female in estrus [8]. (More in family introduction.)

PARENT/OFFSPRING BEHAVIOR. Both in southern Africa and East Africa young tend to be born during the rains, the time when most prey species are at peak abundance. There is no evidence of more than 1 litter being born in a year in the wild state, whereas a hand-reared, free-ranging female littered 8 times in 3½ years, twice producing 2 and once 3 litters in 1 year, for a total of 20 offspring [8]. Gestation is 56–60 days and typically 3 kittens (2–5) are born in a hollow tree, hole in the ground, rocky crevice, or nest in dense grass. Their eyes open at 10–14 days, and they become mobile within a month, accompany the mother when less than 3 months, and are independent by 5 months. They are fully grown and begin breeding at 1 year, but males probably rarely have a chance until fully mature at 2–3 years [3, 4].

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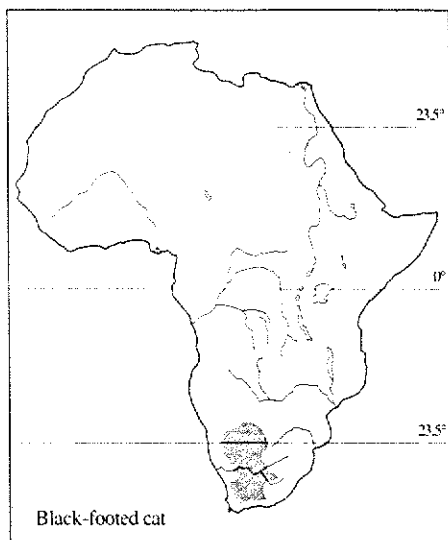


Fig. 21.11. Black-footed cat in defensive threat (from a photo by A. Bannister).

Black-footed Cat

Felis nigripes

TRAITS. The smallest cat, distinguished from the wildcat by size, bold markings, and ears the color of the body (never reddish) [4]. **Weight and length** (head and body): males 1.6 kg (1.5–1.7) and 40 cm (38–43),



females 1.1 kg (1–1.4) and 27–36 cm, tail less than ½ head and body (13–20 cm) [4]. Legs relatively long, wide head with large, rounded ears. **Coloration:** from cinnamon-buff (southern) to tawny (northern population), heavily spotted and barred: 3 broad transverse bars on upper limbs and narrow, shorter bars on lower limbs, undersides of feet black (hence *nigripes*), 4 black bands from head or nape extending onto the back and flanks, tail spotted with black tip, underparts pale with white chin, chest, and insides of thighs. **Scent glands:** undescribed, presumably as in other *Felis* species [see family introduction]. **Mammæ:** 6.

DISTRIBUTION. Restricted to the arid central parts of the South West Arid Zone in Botswana, Namibia, and the Karoo south of the Orange River [4]. Though it is often considered rare and endangered, its nocturnal habits and extreme shyness make its exact status hard to determine.

ECOLOGY. This cat inhabits open country with some cover in the form of scrub, bushes, and clumps of grass. By day it lies up in disused burrows (springhare, jackal, fox, etc.) or in termite-mound ventilation shafts. The arid country it inhabits, with rainfall of 100–500 mm, is mostly waterless, but it will drink occasionally when rainwater pools are present. Its food consists of small rodents such as gerbils and mice (present in 4 of 7 collected stomachs), spiders and solifugids (present in 3 stomachs), beetles and other insects, plus small ground



Fig. 21.12. Black-footed cat in skulking attitude (from a photo by A. Bannister).

birds (coursers) and lizards (each present in one stomach) (4).

SOCIAL ORGANIZATION: solitary, territorial.

Virtually nothing is known about the social behavior of the black-footed cat, which is not only nocturnal but so shy that it hides at the slightest disturbance (fig. 21.12) (3). These and other aspects of its biology, such as the abbreviated mating period, prolonged gestation, and relatively precocious young (see below), may be adaptations that enable a very small cat to live in a treeless environment. In the Kalahari, they become active only 2–3 hours after sunset (4). Black-footed cats have the reputation of being more intractable and antisocial in captivity than any other cat (2, 4). Even kittens taken before their eyes open and hand-reared make defensive threats (fig. 21.11) and retreat to dark corners, or attempt to attack their owners (4).

ACTIVITY: nocturnal.

POSTURES AND LOCOMOTION.

See Predatory Behavior.

PREDATORY BEHAVIOR. It seems likely that black-footed cats forage widely, since captives habitually walk and trot around for hours during nightly activity periods (2). Captives go off their food unless provided with plenty of grass. Skill and persistence in digging suggest that they dig for insects, spiders, and other small subterranean prey. To secure wriggling prey, one cat was seen to straddle and clamp it with its forearms, anchoring with the dewclaws while waiting, with head back, for the right moment to deliver a killing bite to the nape (1).

REPRODUCTION: gestation 63–68 days, 1–3 young, born mainly during the summer.

SEXUAL BEHAVIOR. Estrous behavior lasts no longer than 36 hours in this species, compared to at least 6 days in the

housecat and some other small felines. A female will actually accept copulation for a period of only 5–10 hours, during which a pair mates c. half-a-dozen times at intervals of 20–50 minutes, the intervals being longest near the beginning and end (2). The male's readiness to copulate may match the female's period of receptiveness, as one that mated with 2 domestic cats lost interest long before they did. The same male would no longer mate with housecats once he was provided with a female of his own species; since these 2 species overlap in southern Africa without interbreeding, there clearly is some sort of reproductive barrier. Hybrids produced in captivity have not been successfully back-crossed (2).

PARENT/OFFSPRING BEHAVIOR.

With a gestation period nearly a week longer than in the considerably larger domestic cat (2), black-footed kittens are more mature at birth and at first develop faster, perfecting coordinated movements a whole week earlier than domestic kittens. Their eyes open at 6–8 days; they leave the nest at 4 weeks, start eating solid food at 5 weeks, and capture prey [mice] at 6 weeks. A captive mother kept her kittens from leaving the nest until they were 3 weeks old, but later actually hauled kittens reluctant to leave out by the nape. She tried to move the nest site every 6–10 days. Once the kittens could run well, the nest ceased to be a refuge from danger, and the mother made no effort to drive them toward it, unlike housecats and a tame wildcat (cf. wildcat account). Instead, the kittens scattered and took cover, lying motionless until the mother sounded the "all clear": a peculiar, staccato but almost inaudible "ah-ah-ah," accompanied by synchronous up-and-down movements of the half-flattened ears (2). No similar sound has been heard in other cats. The kittens responded by relaxing and typically ran toward the mother.

Some days before her offspring were ready to eat meat, the mother began bringing dead prey back to the nest, and brought live prey when the kittens were c. 5 weeks. She neither stimulated the kittens' interest by coaxing or competing with them nor disabled the prey. She simply released it near them, sat back, and watched. If the prey was on the point of escaping, she skillfully drove it back toward the kittens with her paw rather than catching it. Consequently the kittens never saw how prey was killed before they did it themselves (1).

After about the fifth week, the growth and development of black-footed cats slows

was seen only on the border of the study area (but see next paragraph). Probably at least some of the adult females were related, for female offspring are tolerated much more than males, which the mother and the resident male force to emigrate during adolescence.

Most of the individually known servals in the study disappeared for up to 3 months at a time, but whether they stayed in the neighborhood or dispersed was never determined. In the acacia woodland around Lake Ndutu, bordering the Serengeti Plain, 2 known males changed their ranges from one year to the next but moved no more than $2\frac{1}{2}$ km (1). These 2 had overlapping hunting ranges of 1–2 km² which they shared amicably; once they were seen hunting 300 m apart. However, each male had an exclusive though not sharply defined core area.

ACTIVITY. Servals are more diurnal than most cats. They are very active in early morning, often up to 1000 or 1100 h, and again after 1600–1700. On cool and overcast days they stay active longer. At night servals spend 3–4 hours resting and, as usual, have 2 activity peaks, beginning at 2200–2300 and 0400–0500, the latter often carrying through into the morning (2). The average distance covered in a day by Ngorongoro servals was c. 2 km; one traveled 6.7 km. During the heat of the day, servals doze and groom themselves in the shade of a bush or grass clump, sitting up frequently to look around. They are less alert when there are no larger predators or game concentrations around.

POSTURES AND LOCOMOTION.

See Ecology and Predatory Behavior.

PREDATORY BEHAVIOR. Servals hunt in typical cat fashion [see family introduction]. Having located and stalked a rat concealed in the grass, a serval leaps into the air and comes down with both front feet on its victim, in the manner of a pouncing jackal or fox (fig 21.14). Sometimes one will make a whole series of spectacular jumps and pounces, but it usually moves on after a miss. A serval not only can jump high and far but has a wonderful ability to swerve and change direction at full speed. Its actions and reactions are so quick that it can pluck birds from the air, sometimes jumping high and batting with powerful downward paw strokes (caracals bat sideways) (4). One male, while stalking something in a bush, suddenly looked

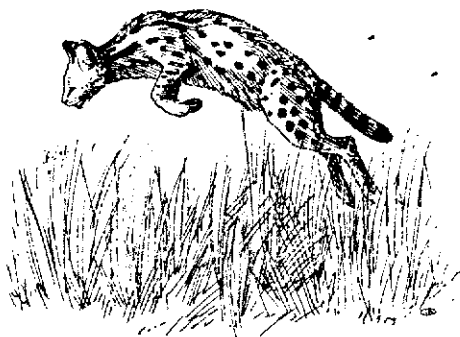


Fig. 21.14. Serval jumping to pounce on concealed prey (from a photo in Van Lawick and Van Lawick-Goodall 1970).

back at a tree 18 m away, turned and ran to it, jumped 2 m high, and snagged an agama lizard (1). Servals also reach deep into holes to catch mole rats and hole-nesting birds, aided by their elongated forearms. They readily enter water in pursuit of wading birds and waterfowl, and one spent $1\frac{1}{2}$ hours in a pool after a heavy storm stalking frogs and toads (2).

Having caught a rat or other quarry, a serval may play with it for up to 10 minutes, throwing it 2–3 m in the air, catching it as it falls, and so on. The cat may eat its prey in the open or carry it to a protected spot. It eats in the same manner as a housecat, crouching down and beginning at the head end, bolting small rodents whole after a little chewing, but often leaves the viscera (1). Judging by the hunting-success rate of Ngorongoro servals, this feline is an efficient predator: 40% of its pounces by day and 59% by night were successful. One big male caught 20 rodents in 31 pounces (2).

SOCIAL BEHAVIOR

COMMUNICATION

Olfactory Communication: *urine-spray-
ing, rubbing face on objects.*

Both sexes mark by spraying (males) and squirting (females) urine on the grass and sometimes against conspicuous clumps, bushes, or reeds. They also rub their faces against grass stems or on the ground, meanwhile salivating freely. In the Ngorongoro study area, the male spent much more time than the female in patrolling, visiting different parts of his range and pausing to urinate frequently: 556 times in one 12-hour period (2). Although the cats seemed to take certain preferred routes, for example, along the edge of the swamp, no individual was seen marking the same bush twice. Scats are deposited at random along paths or roads,

preferably in a depression or patch of short grass. Beyond a few cursory scrapes with the hindfeet, no effort is made to cover the feces [6].

AGONISTIC BEHAVIOR. See family introduction. The aggressive displays of servals differ from other cats' in 2 respects: during offensive threat the head is thrown up and down instead of sideways, and an aggressor may prod its opponent with an outstretched foreleg [4]. An encounter between 2 male neighbors began when A intruded into B's core area [1]. B was just becoming active after a rest when he noticed A approaching. He sat down and watched as A paused to spray a bush. When he was within about 30 m of B, A suddenly started racing and bounding around, tail arched over his back and with all 4 feet sometimes off the ground. B ran toward him and joined in this activity until suddenly they stopped and stood facing only 30 cm apart. With tails raised, hair bristling, and backs somewhat arched, they threw their heads up and down while yowling in a low key and showing their teeth. One and then the other raised a forepaw only to lower it again. This went on for 5 minutes, when the intruder backed away and around B, then slowly moved off, glaring back with tail still fluffed. When he got back to his own valley, he sniffed and sprayed bushes (fig. 21.13).

REPRODUCTION: gestation 65-75 days, 2-3 young/litter (1-5).

SEXUAL BEHAVIOR: unrecorded.

During estrus a male and female may consort for several days during which they hunt and rest together [1].

PARENT/OFFSPRING BEHAVIOR.

Kittens are hidden in dense vegetation and subject to frequent moves. A Ngorongoro female that had 2 litters in 2½ years hid hers in tall sedges bordering the marsh. Her daily routine was altered radically while they were young: she spent most of the day hunting and bringing food back to the kittens, only resting in late afternoon. Returning over a kilometer with a mouse she had caught, she began calling as she came within 50 m of the marsh, stopped, listened, then called again. Three pairs of ears appeared behind a clump of reeds. When the mother called again, 1 kitten galloped to her, followed by the others, all meowing. One kitten picked up the mouse, while the mother licked, then suckled the others, meanwhile purring loudly [2].

When the kittens were older, she had

trouble making them go into hiding so that she could resume hunting; it took up to ½ hour, with increasingly severe growling and spitting on her part, to get rid of them. The males are driven away soon after becoming competent at hunting for themselves, whereas daughters are tolerated much longer [2].

ANTIPREDATOR BEHAVIOR. Ngorongoro servals behave very fearfully when they encounter spotted hyenas, immediately crouching or ducking into cover and waiting. If a hyena comes close, the cat flees with tail raised in leaps and bounds with sudden changes of direction. Without high grass for cover, servals would be highly vulnerable, in particular to this predator and to wild dogs.

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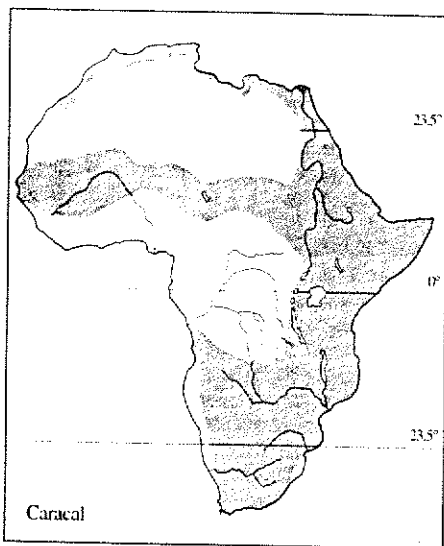


Fig. 21.15. Caracal carrying prey.

Caracal

Felis caracal

TRAITS. The African version of a lynx. **Weight:** up to 20 kg [6], heaviest of Africa's small cats; Botswana series: males 14 kg (12-18), females 10 kg (8-13). **Length** (head and body): males 78 cm (62-91), females 73 cm (61-81), tail 26-34 cm. **Height:** 40-45 cm [8]. Long legs with hindquarters higher and more developed than forequarters, and big feet; short face with powerful jaws and long, tufted ears. **Coloration:** plain tawny to rufous coat with spots faintly indicated in whitish underparts; lips, ear backs and tufts black, dark facial markings on cheeks and over the eyes, bordered by white fur; newborn light yellow with relatively distinct spots and markings already formed. **Scent glands:** anal sacs, other glands undescribed [see family introduction].



DISTRIBUTION. Arid zones and dry savannas of Africa and North Africa, through the Near East to India and Russia's Karakum Desert.

ECOLOGY. Though equally at home on plains, rocky hills, and mountains, probably most caracals live in arid bush country. They may venture into open grassland at night to hunt but seem to require woody vegetation for cover, while avoiding dense evergreen forest [8]. This cat is replaced by the serval in better-watered areas where grass is dominant for much of the year [5].

In South Africa's Mountain Zebra N.P., where the caracal is the largest predator, mammals made up 94% of the prey species identified in collected scats [4], with rock hyraxes predominating (53% of the kills). In terms of biomass, however, adult mountain redbucks (average weight c. 30 kg) accounted for 70% of the prey harvest. Other prey included springboks, steenboks, gray duikers, hares, rabbits, springhares, small rodents [5%], and Cape gray mongooses. Birds represented 5% and reptiles 1% of the identified remains. The caracal also preys on sheep in South Africa. Like jackals, perhaps it tends to take bigger animals in areas where larger carnivores have been eliminated or where the choice of prey is limited. Records of caracals taking adult impalas, a sitting ostrich, and young kudus attest its predatory prowess, but the mainstay appears to be hyraxes and other mammals in that size range, including jackals, monkeys, and game and other birds

in addition to the kinds already listed. The caracal's predatory niche is thus very different from that of the serval, a specialist on rodents.

SOCIAL ORGANIZATION: solitary, territorial.

During the aforementioned study of caracal food habits, the cats were sighted a total of 57 times, mainly early and late in the day [4]. Forty-one of the sightings were of single adults, large juveniles and adult pairs were seen 11 times, and the rest were family groups consisting of a female with 1-4 kittens. The estimated population in the 6536 ha park was 15 adult and 10 juvenile caracals, giving a density of 1 caracal/261 ha.

ACTIVITY: mainly nocturnal [9] but may be active at twilight and also by day.

POSTURES AND LOCOMOTION

The caracal is fast over a short distance, propelled in long bounds by its powerful hindquarters, which also give it remarkable jumping powers: a housepet, startled as it lay asleep, bounded against a wall, its front feet reaching the height of 3.4 m [9]. It is also an agile climber, using its strong dewclaws to scale smooth tree trunks [9]. The combination of speed, strength, and agility makes this a very formidable predator for its size.

PREDATORY BEHAVIOR (fig. 21.15).

The caracal kills medium-sized antelopes over twice its own weight by employing the same technique as the big cats: suffocation with a throat bite. It uses its jumping and climbing ability to catch hyraxes in the rocks. It also takes sleeping birds from their perches, including martial and tawny eagles, and ground birds up to the size of a kori bustard. Sandgrouse, doves, pigeons, and the like are vulnerable to caracals when they come to drink at waterholes with nearby cover [5]. A caracal is so quick that it sometimes gets 2 birds from a flying flock by leaping high and batting sideways with its paws, but more often it uses both paws together to snag a bird from the air. The dewclaws also serve to hold prey (or an opponent) securely. A pet female killed hares with a bite to the nape. If the hare continued thrashing, she would throw herself on the ground and hold the hare while raking it with her hindfeet.

The caracals studied in Mountain Zebra N.P. ate small birds completely except for a few feathers, and partially plucked larger

birds [4]. The viscera, primaries with attached flesh, portions of skull, and occasionally a lower leg were left uneaten. The viscera of all mammal prey were left untouched, and the fur of mammals of hyrax size and up was partially plucked with the incisors. Caracals also avoided eating hair by shearing meat neatly away from the skin. Access to carcass kills was gained through the anus. The meat on the hindquarters was consumed first, then the forequarters. They rarely ate more of the larger antelopes before the meat became putrid, though they returned to all but 2 of 21 kills. Grass and leaves were raked over 1 carcass; in other areas, small kills may be cached in tree forks [5].

A tame but free-ranging subadult caracal weighing 11 kg ate 796 grams of meat a day. Assuming that an adult would eat 1 kg a day (up to 2 kg at a time), the 25 caracals in Mountain Zebra N.P. consume about 7200 kg of meat a year, thereby accounting for 2995 hyraxes and about 190 mountain reedbucks [4].

SOCIAL BEHAVIOR COMMUNICATION

Visual Communication. Caracals are cryptically colored except for the head, which is boldly marked and surmounted by remarkably conspicuous ears, white on the inside and black on the outside, with black tufts, so that every twist, turn, and flick is clear to see [5]. White fur bordering the black lips repeats the same basic pattern, emphasizing facial expressions and bared teeth. Taken together, these markings make an effective semaphore system. Thus, when 2 caracals spot each other and, in typical cat fashion, sit and *look around*, the movement is exaggerated and ritualized as a side-to-side head-flagging, during which the ears flicker rapidly [5]. But slightly flattening and pulling back the ears causes a narrow wedge of sandy fur along the leading edge to mask the contrasting black and white pattern from the prey of a stalking caracal. Thick fur over the eyelids also masks the eyes (possibly against glaring sunlight), except when a caracal opens them wide [5].

Vocal Communication: meowing, growling, spitting, hissing, purring, screaming, loud coughing calls (in mating season) [5].

Olfactory Communication. Caracals have been seen urine-marking grass tufts, rocks, and trees [2]. A free-ranging pet sometimes buried its dung but at other times left it exposed [4].

REPRODUCTION. Though births have been recorded through the year, there is an extended birth peak during the summer, at least in South Africa [1]. The average litter numbers 2.2 kittens [1-4] and gestation varies from 62 to 81 days. Both sexes reach puberty at 7-10 months. Apparently females do not reenter estrus until after lactation ceases at c. 4 months.

SEXUAL BEHAVIOR. Estrus lasts 3 to 6 days and recurs every 2 weeks until conception occurs. Copulation occurs during a period of 1 to 3 days, initiated by the female assuming the *copulatory crouch*, and averages 3.8 minutes [1, 5-8]. Immediately afterward both partners groom themselves [1].

PARENT/OFFSPRING BEHAVIOR.

In zoo observations, the expectant mother prepared a nest of hair and feathers, and stopped eating a day before littering [6]. In the wild, caracals may litter in burrows; for instance, 2 kittens were found in an old aardvark hole [9]. In one observed birth, the mother behaved restlessly, licking her genitals and teats and scratching at the earth floor for 35 minutes before visible labor contractions of the abdominal muscles began. The emergence 110 minutes later of the kitten was followed shortly by the placenta, which the mother ate after licking the baby.

A rich rufous color like the adults, with the black facial markings already pronounced, the offspring of a pet caracal opened their eyes at about 9 days, but avoided the light the first 2 weeks and were very sensitive to noise [9]. The ears remained folded back on the head, only becoming fully erect after 30 days. Kittens stop crawling and begin walking at 9-17 days, and begin cleaning themselves at 11 days, licking their front paws and legs. At 12 days a hand-reared pair began uttering twittering food calls. Kittens may only begin eating meat at 1-1½ months and are weaned at 4 to 6 months [1]. Caracals as young as 3 weeks may leave the nest and begin to chase moving prey [3, 6, 9].

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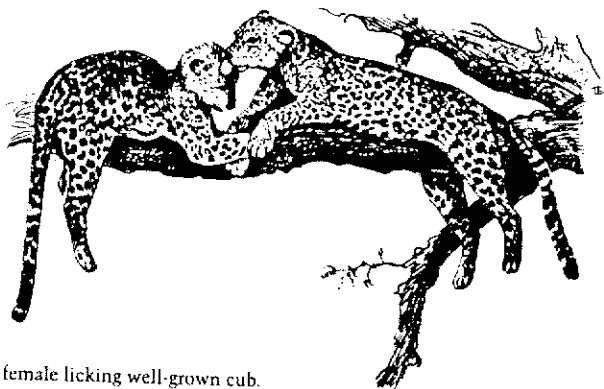


Fig. 21.16. Leopards: female licking well-grown cub.

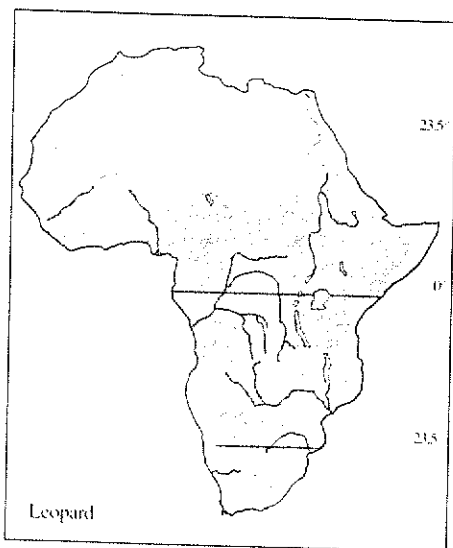
Leopard

Panthera pardus

TRAITS. A long, low, spotted (sometimes black) big cat. *Height and weight:* males 60–70 cm and 35–65 kg, females 57–64 cm and 28–58 kg (12, 15, 16). Limbs short and massive, head wide with short, powerful jaws and long canines. *Coloration:* ground color tan, highly variable, generally darker and more closely spotted in forests, spots grouped in rosettes on torso and upper limbs. Cubs woolly and dark with close-set, indistinct spots. *Scent glands:* anal and probably other glands (see family Traits). *Mammæ:* 4.

DISTRIBUTION. The most ubiquitous of all cats [except the domestic cat], the leopard occurs throughout Africa wherever there is sufficient cover for concealment, and from the Arabian Peninsula through Asia to Manchuria and Korea. Though eliminated in many densely settled areas and heavily poached for its valuable pelt, this cat is so stealthy and so bold and versatile as a predator that it manages to survive in places other, smaller cats cannot. Where its natural prey has been eliminated, it may subsist largely or entirely on domestic animals and sometimes (in Southeast Asia, very rarely in Africa) becomes a man-eater. It is the only large predator in Africa's rain forests, and it also ranges the montane forests and moors of the highest mountains; on Kilimanjaro a leopard carcass was found frozen in the ice at 5692 m (9). Despite dire predictions of extermination, it turns out that leopards are far commoner over much of Africa than conservationists had supposed (10). The least specialized of the big cats, the leopard is successful wherever diversified habitats afford a variety of small to medium-sized mammals.

ECOLOGY. A leopard will consume protein in almost any form, from beetles up to antelopes twice its own weight. It readily eats carrion, and often caches sizeable kills in trees, returning nightly to feed on them. In Serengeti N.P. a sample of 150 leopard kills included over 30 different species, compared to about 12 regularly taken by lions. Medium-sized antelopes (impala, Thomson's gazelle, reedbuck) and the young of larger species (topi, hartebeest, wildebeest, zebra) predominated, with hares, birds, and several small carnivores rounding out the list (2, 3, 14). In Zimbabwe's Matopos N.P., an area with a variety of mammals and no great preponderance of ungulates, 72% of 200 leopard scats contained the remains of small mammals (< 5 kg) and 19%, mammals of medium size (5–45 kg) (7). Birds, reptiles, and invertebrates (in-



sects, etc.) accounted for 10% of the animal remains. Although leopards prey on baboons in some areas (e.g., Kruger N.P. [11]), the common notion that this primate is a mainstay of their diet is false [2]; clever leopards don't risk their own hides by attacking baboon troops on the ground, and clever baboons sleep in safe roosts at night. Unclever ones may indeed turn up missing in the morning—as do even large, savage dogs a prowling leopard finds sleeping.

SOCIAL ORGANIZATION: solitary, territorial.

The leopard is a typical cat. Adults associate only long enough to mate and the young become independent as subadults, at around 22 months. The ranges of females often overlap (see below), but authorities differ about whether male ranges also overlap. The practice may well vary in this highly adaptable cat, just as home-range size is widely variable.

In Sri Lanka's Wilpattu N.P., home ranges are as small as $8\text{--}10\frac{1}{2}\text{ km}^2$ and males apparently defend territories, by calling and by demarcating the boundaries with urine, dung, and tree-scratching [5]. In Tsavo N.P. the home ranges of 10 leopards that were radio-tracked for 3 years varied from 9 to 63 km^2 [3]. Density was estimated at 1 leopard/ 13 km^2 . Each leopard used only about half its range at a time and overlapped with others by as much as 70%. The core areas of 2 males were only about 0.8 km apart, and 1 female had sporadic contact with at least 4 different males. Female ranges in Serengeti and Kruger N.P. were estimated at $10\text{--}25\text{ km}^2$ [3, 11]. Several may be included within a male's range. One adult male and no less than 3 females have been known to hunt independently along the same 5 km stretch of river [14].

The maternal bond is strong and enduring [fig. 21.16]. Mother and offspring often have reunions after separating, and the mother may continue to share kills until her offspring become fully self-sufficient. For instance, a radio-collared $2\frac{1}{2}$ -year male who stayed within a 5 km^2 range during the 4 months he was observed often joined and went hunting with his presumed mother at night [2]. A similar association is described under Predatory Behavior. Continuing tolerance of adult female offspring probably explains overlapping female ranges (cf. cheetah). A $1\frac{1}{2}$ -year female, hunting alone, spent her time stalking hyraxes, hares, and small birds, and was unsuccessful at capturing larger prey. Her mother killed an impala or Thom-

son's gazelle every few days, stashed it in a tree, then went to fetch her daughter. They would feed 1–2 days together intermittently until it was gone, then separate again. Six weeks later the mother came into heat and spent several days consorting with a male. The 2 females, both radio-collared, were never found together again; however the daughter stayed in the same range [2].

ACTIVITY. See also under Parent/Offspring Behavior. Leopards spend the day and part of the night inactive, draped over a tree limb or lying up in a dense thicket. Beginning perhaps $\frac{1}{2}$ hour before dark, they move around intermittently all night and for a couple of hours after dawn. The radio-tracked Tsavo leopards regularly wandered 25 km a night, covering much of the used part of the range within a few days. They seldom rested in the same spot 2 nights in a row [8].

POSTURES AND LOCOMOTION. See Predatory Behavior.

PREDATORY BEHAVIOR. The leopard is the quintessential ambush and stalking predator. A lion rushes upon its quarry as it is trying to escape; a leopard seeks to pounce *before* its quarry can react [2], stealing to within at most 20 m and preferably within 5 m before pouncing. It seldom chases if it misses and then for no further than 50 m, although its estimated top speed is a respectable 60 kph (fig. 21.17) [3]. Hunting by day is hardly worth a leopard's while: 61 of 64 daylight attempts by Serengeti leopards failed. Even at night its success rate per attempted stalk is thought to be comparatively low [2].

Some individuals develop a particular fondness for dogmeat and are bold enough to come onto a veranda or even through open windows to carry off sleeping pets. And yet a barking terrier can easily tree a leopard by daylight, and one even gave way to a yapping jackal [2]. But another leopard, which visited my camp in Ngorongoro Crater almost nightly for several weeks, brought

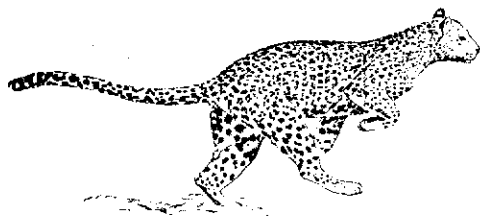


Fig. 21.17. Leopard running gait.

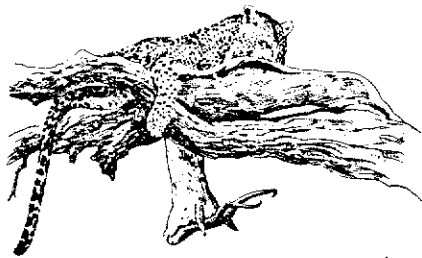


Fig. 21.18. Leopard eating springbok it carried up a tree (from a photo by J. Dominis, *Life* magazine).

back 11 jackals in that time and proceeded to eat them on a tree platform beside my cabin, sometimes after cat-and-mouse play with them (6). She also caught 2 large male Grant's gazelles, members of a bachelor herd that often ventured dangerously close to tall streamside vegetation to feed at night. At 70–75 kg apiece, they were too heavy for her to carry up a tree, so she left each in turn on the ground after feeding on the carcass, first scratching leaves and a little dirt over it.

Once in the Serengeti I witnessed apparently deliberate teamwork between a female and a subadult male in capturing a bush hyrax, shortly before dusk. The male ran swiftly up the trunk and into the crown of a 10-m umbrella acacia, while the female waited below. A hyrax jumped out and the female caught it as it landed. After playing with it briefly (tossing it in the air and catching it), she surrendered it to her son, who carried it onto a nearby rock outcrop. He laid it down, then ignored it to survey his surroundings. The hyrax suddenly came to life and jumped into a patch of *sansevieria* (Spanish bayonet). The leopard jumped after it, but too late; he landed right on the stiletto-tipped plants, yet showed no pain.

RELATIONS WITH OTHER PREDATORS.

Of the 7 large African carnivores, the leopard only outranks the cheetah. Not only the lion but all 3 hyenas outweigh a leopard, and wild dogs, though smaller, operate in packs. But that an animal as well armed and powerful as a leopard would surrender its own kills to a single hyena is somewhat puzzling (see brown hyena account). Not that the outcome of an encounter is invariable: a leopard with young cubs is far more likely to take the offensive than to run from a hyena, for instance. However, the practice of eating and caching kills in trees (fig. 21.18), so common in Africa, is not observed where leopards are the only large predator (5).

SOCIAL BEHAVIOR COMMUNICATION

Olfactory Communication. Leopards use all the usual feline scent-marks plus feces to communicate with one another (14). Large trees with inclined trunks or big branches 2–3 m from the ground are preferred scent posts. Here a leopard pauses to sniff at previous scratch marks, stretches out along the branch or trunk, and "sharpens" its own foreclaws. (Sometimes it scratches with its hindclaws.) The marking ritual is completed by spraying urine at the base of the tree. Leopards [especially males] also spray bushes and other objects at frequent intervals during their nightly wanderings, after rubbing the head and cheeks on the spot (5, 14). In addition, feces are deposited along paths and roads, where other leopards are likely to encounter them.

Vocal Communication: "sawing," grunting, growling, snarling, hissing, caterwauling, purring; cubs: meowing, *urr-urr*, *wa-wa-wa*.

The distance call of a leopard, given both while inhaling and exhaling, sounds a lot like someone sawing wood. A typical series has 13–16 "strokes" in a period of a dozen seconds. Sawing is repeated at intervals of 6 minutes or so during peak calling bouts, which tend to occur early in the evening and shortly before dawn, often while the leopard is moving (5). Occasionally 2 leopards duet, for instance when 2 males "shout" at each other from near their common territorial boundary. In addition, leopards grunt when alarmed, growl, snarl, and hiss in fear/rage, and sometimes caterwaul when treed by dogs (16). Small cubs give a soft *urr-urr* call to their mother, a *wa-wa-wa* when comfortable, and a high-pitched meow of distress (1, 14). A mother summons her cubs with loud, abrupt purrs (8).

Visual and Tactile Communication: as in other cats (see family introduction).

The white tail tip, which looks like a flitting moth when flicked in the darkness, no doubt functions as a follow-me signal between mother and cubs (8).

REPRODUCTION. Leopards are capable of breeding at two years. From 1 to 3 cubs are born at intervals of c. 25 months, after a 90–100 day gestation (4, 13). Estrus is known from zoo records to last about 7 days (4–12) and to recur every 46 days (25–58) until conception occurs (13).

SEXUAL BEHAVIOR. Behavior during estrus is typically feline (see family account). A precopulatory sequence involving wild leopards began when the female came up

to the male that had been following 10 m behind her and *rubbed cheeks* with him as he stopped to scent-mark a tree. She then *presented* in the *copulatory crouch*, whereupon he mounted, only to leap off the next moment as she whirled about with a snarl (15). Another time a female removed a gazelle kill that her male consort had cached in a tree that morning, and dragged it to a patch of bush where the 2 proceeded to share it. Such unwonted sociability was a sign that the female was nearing estrus.

Leopards may copulate as often as lions and the male emits harsh, growling cries (*copulation call*) (5, 17). One captive male broadcast every copulation by growling, snarling, and teeth-gnashing as he symbolically bit the female's nape. Judging by the calls, copulation recurred night and day at roughly 1/4-hour intervals (author's observation).

PARENT/OFFSPRING BEHAVIOR.

Weighing only 400–600 g at birth, cubs are concealed in dense thickets, hollow trees, or caves. Their eyes open at 6–10 days, but 6 weeks pass before they venture from hiding and make short excursions with their mother. At the same time they start to eat meat. Weaning may occur as early as 3 months, when cubs weigh about 3 kg, but more than a year passes before they are ready to fend for themselves. A radio-collared mother spent 44% of her time with and 56% of her time away from her 2 cubs when they were 3 weeks old (15). During 168 hours of continuous recording, she stayed with them 62% of the nighttime and 30% of the daytime. After spending up to 33 hours with them, she would leave them for up to 36 hours at a time, but went no farther than 3/4–2 km (average 1 1/2) from their hiding place (which she changed from time to time). When the cubs were 2 months old she spent about half her time with them, staying for up to 39 hours at a stretch, and left them for up to 25 hours while feeding on a sizeable kill and guarding it against vultures and jackals. During a further 127 hours of continuous monitoring, she spent 67% of the time with them and 33% away. Throughout this period the female used an 8 km² range. Her movements and activities were shaped by the time required to find and kill prey, and the need to protect it from scavengers and consume it before it decomposed in the tropical heat. Since leopard milk is not markedly richer than housecat milk, it is clear that leopards become adapted from the very beginning to long fasts relieved by intervals of gorging (15).

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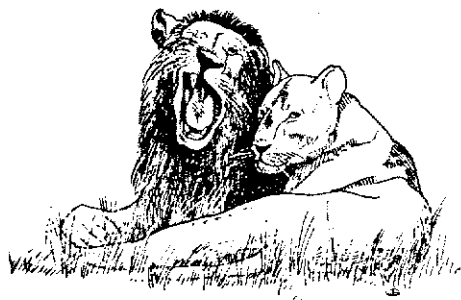


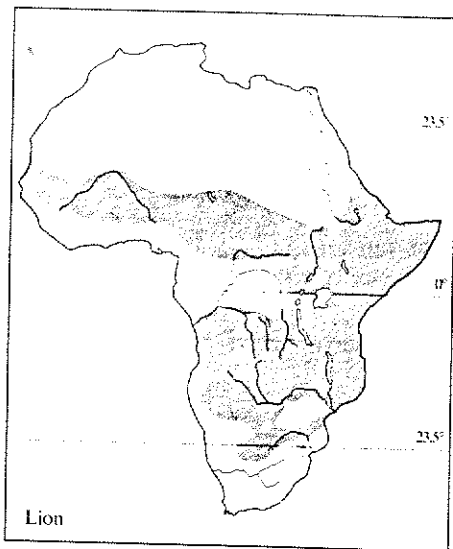
Fig. 21.19. Lion consort pair.

Lion

Panthera leo

TRAITS. The largest African carnivore. **Weight:** adult males 189 kg, females 126 kg (Serengeti N.P. sample) (12); up to 260 kg (1). **Average height:** males 120 cm, females 110 cm (19). Coat short; mane in males only, variable in length, extent, and color—just visible in 2-year-olds, maximum development in early prime, declining in late prime (16), but sometimes undeveloped. **Coloration:** tawny with white underparts; tail tuft, ear backs, and lips black; mane tawny to red-brown to black; cubs spotted with woolly, grayish coats, changing to adult color beginning at 3 months, but faint spotting may persist in adults (especially in East Africa). **Scent glands:** anal glands and possible foot glands. **Mammæ:** 4.

DISTRIBUTION. Formerly from the Cape to the Mediterranean wherever suitable prey existed, except in desert and rain forest, and in biblical times or later throughout the Near and Middle East as far west as Greece and as far east as India, where a few hundred lions still persist in the Gir Forest (19). Lions were eliminated from North and South Africa by the end of the nineteenth century, except for the area that is now Kruger N.P. Since then, this cat has



been shot out of or greatly reduced over much of Africa along with other big game. But in savanna and plains habitats where large herbivores still abound, it is the most numerous large carnivore next to the spotted hyena, reaching a density of c. 38 lions/100 km² in Ngorongoro Crater, 26/100 km² in Nairobi N.P., 12.7 in Kruger N.P., and 12 in Serengeti N.P. [13, 14, 17].

ECOLOGY. Lions eat a great variety of animal food, and will scavenge a meal sooner than hunt for one. But their size and gregarious habits are specifically adapted to predation on the larger ungulates. In most areas of abundant wildlife, only around 5 of the most numerous ungulates weighing between 50 and 300 kg make up ¼ of their prey [14]. Lions that hunt cooperatively often succeed and they feed communally on large kills, whereas smaller and weaker individuals often lose out when the carcass is small. Single lions readily bring down animals up to twice their own weight, wildebeests and zebras being particular favorites, and some lions regularly kill buffaloes 4 times their weight; even animals weighing well over 1000 kilos (e.g., bull giraffe) are sometimes killed. Usually a cooperative effort is used to overcome such large prey; males, being much bigger and stronger, though slower, tackle large prey more readily than do females.

SOCIAL ORGANIZATION: gregarious, territorial, matriarchal society, communal care, male coalitions.

Most lions live in resident prides that

occupy hunting ranges large enough to support a certain number of animals during occasional periods of game scarcity. The home range may be as small as 20 km² in the best habitat, and over 400 km² where prey density is low. The average area of 9 Serengeti prides was c. 200 km² [14]. There may be as many as 40 lions in a pride, including from 2 to 18 adult females and up to 7 adult males, but it is rare that all assemble in one spot. Pride members are usually scattered singly and in small groups that change from day to day as individuals come and go on their own initiative. Groups typically number 3–5 lions, and any given pair of females may only be found together 25%–50% of the time [10]. Mere presence in a pride's territory is no proof of membership, as some lions are transients or "lodgers" (squatters). Pride membership can only be determined by observing which individuals interact amicably over a period of time; that is, one has to recognize the lions individually. Both in the Serengeti and Kruger N.P. the typical pride numbers about 13 lions. In Kruger, the average composition of 14 prides totaling 181 lions was 1.7 adult males (1–4), 4.5 adult females (2–9), 3.8 subadults, and 2.8 cubs (including yearlings). In another sample of 60 Kruger prides, the mean number of pride males was 2.1 (15).

The part of the range currently used by the pride is defended against outsiders of the same sex. Adult females are normally all related, descending from females that have lived generation after generation in the same range. However, if the number of lionesses should fall below the capacity for the range and there are no female offspring to fill the gap, subadult immigrants may be permitted to join [16, 17]. Conversely, when the roster is filled female cubs have to emigrate as 2-year-olds. The existence of a "female capacity" for each territory is illustrated by the fact that the number of lionesses in 6 neighboring Kruger prides remained constant for 2½ years, despite a turnover in membership [17].

Because of the clumping of females in discrete territories, male lions can monopolize mating opportunities to an unusual degree: in the Kruger sample, there were 2.6 adult females per pride male. The degree of male competition in this species has led to innovations in social behavior unlike those of any other carnivore, but similar in some ways to baboon society. The development of greater sexual dimorphism than in other carnivores is only the most obvious outcome of this competition

(14). The advantages of size and a showier mane have caused males to become so beefy and conspicuous that their hunting ability is actually impaired. It takes them 5 years to mature and they only reach puberty at 2½ years [range 26–34 months] (16). By 3 years at the latest, male offspring are forced to emigrate, at least partly because of the intolerance of adult males (5). From then until they mature and succeed in taking over a pride range, these males and also emigrant females lead an unsettled existence, either as nomads following migratory game, as in the Serengeti ecosystem, or within the ranges of established prides as unwelcome lodgers which have to avoid the proprietors (16).

Being sociable, outcasts associate, preferably with members of the same sex. This is just the reverse of the primarily intrasexual aggressiveness displayed between resident and nonresident lions. Within prides, too, females associate and behave much more affectionately with one another than with males, and vice versa for males. Companionships may last a lifetime. In fact this social bonding, usually between closely related individuals that have grown up together, and particularly between mothers and daughters, is the very foundation of lion society.

Male littermates often stay together after leaving their pride, and when ready to compete for a territory they operate as a team. A single territorial male that finds himself confronting 2 challengers is clearly at a disadvantage. Two established males are at a disadvantage against 3 challengers, and so on. But the advantage of an additional male decreases as coalition size increases and 9 is the largest number I have heard about. A Serengeti septet dubbed the Seven Samurai took over and divided their time among 3 or 4 different prides. But this arrangement did not work well, for other males invaded territories left unguarded and kept most of the females from rearing cubs (6).

Wherever lions are plentiful, single males can rarely take over or keep a territory. Their mating opportunities are accordingly limited to nomadic females, which seldom manage to rear young, or to pride females in estrus left unattended by the resident males. The reproductive advantage enjoyed by coalitions forces even unrelated males to band together (2, 6, 12). In the Serengeti population, 42% of the coalitions composed of known individuals included 1 or more nonrelatives (7). However, out of 40 sightings of transient males seen passing through Serengeti territories, all but 3

were pairs and singles, indicating that most coalitions are small and that some males fail to team up at all (8).

Even males in coalitions have a remarkably brief reproductive career. Pride tenure for most lasts no more than 2 years, 4 at the outside, and very few ever get a second chance (2, 16). The prime years are between 5 and 9, and males are biggest and fittest between 5 and 6. After 8 they lose weight and mane hair. Only 2 of 25 known-age Kruger males were older than 9 and both were alone: a 10-year-old and a decrepit 16-year-old that had survived several years beyond the usual life span (16, 17). Large coalitions are likelier to have a longer tenure than small ones: Serengeti coalitions of 1–2 reigned for less and coalitions of 3 reigned for more than 25 months, whereas coalitions of 4–6 often lasted longer than 46½ months (8). As we shall see, the effect of these differences in tenure on reproduction is the difference between success and failure for both sexes.

Often one of the first acts of males after taking over a pride is to kill any cubs under a year old which they can catch. Older juveniles may escape with their lives but cannot survive unless their mothers leave with them—as sometimes happens (9). Lionesses often attack males in defense of their cubs and may be wounded and sometimes killed. They are most effective when they gang up on the infanticidal males. Females with very young, concealed cubs may be kept from going to them until the cubs starve, or they may simply abandon them. The more males in the coalition, the likelier it is that they will do in all the cubs, including any born in the months following the takeover (16). Such behavior used to be considered aberrant, but it has now become apparent that lions are one of a number of highly social mammals in which infanticide is a vital part of male reproductive strategy (2, 11). Normally, lionesses produce cubs at intervals of no less than 2 years, and only come into estrus when their offspring are c. 1½ years old. The average interval between birth and the next estrus is 530 days. However, the loss of a litter causes a lioness to reenter estrus and mate within a few days or weeks (5). With an average tenure of only about 2 years in which to propagate their genes, males that delay breeding will leave few progeny and their cubs will be liable to fall victim to their successors.

And what about the females? Is there no way they can prevent this waste of their far greater maternal investment? Lionesses

mate without becoming pregnant for an average of 134 days after losing their cubs in a takeover (9). During this interval they engage in an unusual amount of mating activity and display heightened sexuality, initiating more copulations and seeking more partners than in normal times. Even pregnant females may go through apparent estrus (16). Other lionesses come into heat every few weeks but apparently fail to ovulate. The period of infertility may well be an adaptation that (a) protects the females against the consequences of desertion by the new males, (b) helps to bond the new males to the pride and reduces the likelihood of their deserting, and (c) allows time for the strongest coalition around to come onto the scene and take over. Serengeti females often mated with males of more than 1 coalition during their infertile stage and in 5 observed cases the larger coalition ended up staying in the territory (9).

Although lions have no special breeding season, reproductive synchrony is very common within prides. Several adult females conceive and give birth at about the same time, then care for the cubs communally. It now appears that synchronization commonly follows a takeover: once the infertility period ends, the chances that pride females will ovulate and conceive at nearly the same time are greater than at any other time; there is no need for—and no evidence of—any more complicated synchronizing mechanism (8, 17).

Perhaps the most extraordinary aspect of lion social organization, considering the degree of male sexual competition, is the gentleman's agreement governing mating rights: it is a matter of first-come, first-served, literally. Instead of fighting over a lioness in heat, pride males race to be first at her side; the winner becomes her consort, and the losers keep their distance. Only if one male is clearly stronger and fitter than another will he preempt mating rights. Competition to be first leads to the practice of guarding a female some days before she comes into heat (7, 10). The extended period of estrus, marked by hundreds of copulations, and the frequent synchrony of female cycles help make the system work. Consort males often lose interest in females toward the end of their estrus period, giving another male a chance to mate, and more than 1 lioness was in heat during 43% of the times that Serengeti females were observed in estrus (7). As over a third of these matings were fertile, it would mean that second-ranking males could sire up to 20% of the offspring,

thus making it reproductively worthwhile to belong to a coalition (6). Half a loaf . . .

ACTIVITY. Lions typically spend 20–21 hours a day resting (14). To see lions doing anything other than conserving energy requires luck or persistence. The times when they are most likely to become active are late afternoon, when females often suckle their young followed by play and other social activities, early and late at night, when hunting activity shows slight peaks (14), and the early hours of daylight. However, lions will seize opportunities to capture prey at whatever time and even if they are too gorged to eat (see *Predatory Behavior*, family introduction). Prides living in woodland habitats with plenty of cover hunt in daylight more often than those living on open plains. Lions are obviously also well aware of the advantage of darkness for hunting: hungry animals will lounge on moonlight nights until the moon disappears, then suddenly become active (14).

POSTURES AND LOCOMOTION.

See *Predatory Behavior* and family introduction.

PREDATORY BEHAVIOR. With a maximum speed of 48–59 kph which they can maintain for hardly more than 100 m, lions need skill, patience, and judgment to capture such fleet animals as antelopes and zebras. An experienced lion will rarely charge unless it is within 30 m and/or the quarry is turned away so that the lion can start its rush before the victim becomes aware of the danger and can get up speed.

To get within range, lions rely primarily on stalking. They use cover with great skill and show a remarkable ability to anticipate and take advantage of opportunities to get close (even using moving vehicles to screen their approach). Lions frequently attempt a running approach toward an animal that is inattentive or distracted, freezing instantly and sinking to the ground when the quarry faces in their direction. Lions of the Serengeti Plain approached by stalking and running in 88% of over 1300 observed hunts, and seldom tried to ambush prey (3%) (14). But since ambushes commonly take place in daylight, typically at water holes with convenient cover, this is the kind of hunt park visitors are most likely to see.

Some 48% of the 1300 hunts involved 1 lion, 20% involved 2, and the rest were communal hunts, with 3–8 (occasionally up to 14) participants (14). Lionesses were

the hunters 85%–90% of the time. On group hunts, males usually trailed behind without taking part, and as soon as a quarry was caught ran up and claimed "the lion's share." The success rate of solitary hunters was only 17%–19%, compared to 30% when 2 or more lions hunted together. Schaller found that hunting lions respond to one another's postures and movements, not to facial expressions or sounds (they maintain silence). On communal hunts they usually move on a broad front. Sometimes prey is encircled by the wings while those in the center lie low, evidently expecting the game to flee in their direction. When game concentrates on strips of green grass beside streams or marshes in the dry season, lions may advance on a front quite openly, causing the animals to panic as they see their escape route blocked and giving the hunters chances to intercept animals as they dash through the line. There was no indication that lions deliberately roar to drive prey into an ambush (in my experience prey species normally ignore lion roars), and in 300 hunts where wind direction could be determined, the hunters approached downwind as often as upwind. Even though upwind stalking (of gazelles) was 3 times as successful, lions apparently do not learn to take this factor into account (14). But on the whole, African ungulates are not very reactive to the scent of predators, perhaps because their scent-marks are so pervasive and persist in their absence.

Killing Technique. Once within catching distance of its prey, a lion has to overpower and kill it without getting hurt in the process. Game the size of an impala or reedbuck is brought down with a slap on the haunch, tripped, or clutched with both paws and simply dragged down, then quickly killed with a bite to the neck or throat. To bring down large game, a lion usually comes in at an oblique angle, rears and throws 1 paw over the shoulder or rump, and using its full weight and strength pulls the quarry down backwards and sideways. To gain additional leverage a lion may grip the quarry's neck, shoulders, or back in its jaws (fig. 21.20). Once the victim is down, the lion lunges for its throat or nose and proceeds to kill it by strangulation, maintaining a firm grip until all movement ceases, for up to 13 minutes (see leopard, fig. 21.1). Assertions that lions kill big game by twisting the head so that the victim breaks its own neck in falling are largely anecdotal, although lions in the Kalahari Gemsbok N.P. may possibly

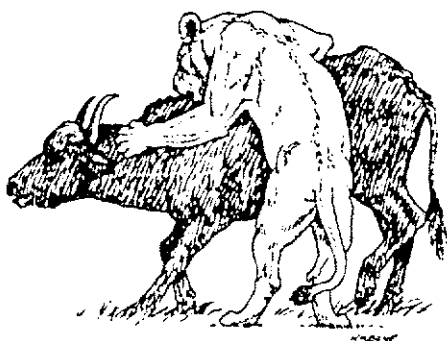


Fig. 21.20. Lioness pulling down buffalo (from Schaller 1972b, drawing by R. Keane).

have developed some such tactic for killing gemsboks (4). None of several hundred lions kills Schaller examined had broken necks (14). The stranglehold protects a lion from the horns and hooves of the struggling victim and makes it easy to hold it down. Very few victims ever get a chance to defend themselves before being overpowered.

Food Sharing. Lions share food but often grudgingly, depending on how hungry they are and the size of the prey. Pride males are the most irascible and piggish, regularly monopolizing small antelopes killed by the lionesses. When game is scarce, cubs are the first to suffer, even their own mothers will not share until they have eaten their fill (10). At best, feeding lions often growl, snarl, and slap at one another. Schaller attributes this scramble competition to the lack of an accepted rank hierarchy in lion society. If weaker lions simply deferred to stronger ones without putting up a fight, they would be far likelier to starve during periods of food scarcity, for lions may gorge until they have eaten $\frac{1}{4}$ of their own weight (up to 50 kg), whereas the average daily consumption is only 5–7 kg. In normal times there is more sound than fury among feeding lions and all members of a pride get enough to eat. Even crippled and old animals may survive on the leftovers. The best evidence that sharing is a lion trait is that nomadic strangers will feed on the same kill (14). If there is anything left over, lions stay and guard carcasses against other scavengers. They themselves scavenge kills whenever possible rather than hunt, keeping a watchful eye out for vultures and responding to the rallying calls of hyenas as readily as other hyenas. Large packs of hyenas can often intimidate lionesses into leaving kills before they are ready, but get nowhere with males in their prime.



Fig. 21.21. Lion roaring (from Schaller 1972b, drawing by R. Keanel).

SOCIAL BEHAVIOR COMMUNICATION

Vocal Communication: roaring, grunting, moaning, growling, snarling, hissing, spitting, meowing, purring, humming, puffing, woofing.

The lion's roar is rightly considered one of the most impressive natural sounds. Loud roaring typically begins with a few moans, followed by a series of 4–18 full-throated, thunderous roars, ending with a series of grunts (average c. 15, up to 57) [14]. Males begin roaring at 1 year, females a couple of months later [3]. The male's roar is deeper and louder, but sex and distance are both hard to judge because of a ventriloquial quality and gradations in volume: the same call grades from a soft "*huh*" or moan barely audible at 100 m to full-throated roars audible up to 8 km. Lions can roar from any position and even while running, but usually stand. The facial expression is distinctive (fig. 21.21). Active animals roar most frequently, hence night and shortly before dawn are peak times, but how often pride members call in a night is also highly variable. One pride monitored continuously for 16 days averaged 6.5 roaring episodes (range 0–16) a night. The stimulus is often indeterminate. Lions definitely respond to other lions' roars, especially when near, but they also roar spontaneously [14]. Probable functions of roaring, depending on who is sending and receiving, include (a) territorial advertising, (b) location of pride members, (c) intimidating rivals during aggressive interactions, and (d) strengthening social bonds (roaring in chorus).

Like roaring, meowing and growling/snarling are graded calls that enable lions to express a wide range of emotions by changes in the volume, intensity, tempo, and tone of the call. The meow of cubs, a signal

of light distress, varies from short and yippy when greeting an adult, being licked, and moving close to the group, to harsh and snarly when competing for a nipple with teeth bared; adults also meow while snarling. The cough is a short, explosive growl often given during a charge. The snarl is simply a slurred growl given with open mouth, and hissing is emitted with the mouth open as if to snarl. An abrupt hiss becomes spitting, given at sight of a strange lion (or when a vehicle approaches too closely).

Purring and humming are sounds of contentment, heard during affectionate interactions and when cubs suckle. Puffing, a faint "*pfiff-pfiff*" through closed lips given repeatedly as lions approach each other, signifies peaceful intentions (comparable to *prusten* in tigers), and *woofing*, an abrupt sound given by a startled lion, expresses alarm.

Grunting (which grades into roaring) is used at low intensity by mothers to summon cubs and as a contact call between close-by adults. It may grade into moaning or soft roaring. Cubs also grunt and moan while trailing behind a moving group. In fact, starting with a hiss at 9–10 days, cubs acquire the full vocal repertoire in rudimentary form by the age of 1 month [14].

Olfactory Communication: *urine-spraying*, *scuffing*, *clawing*, *urine-testing*.

Lions may pay little attention to the odors of other species but display intense interest in the odors of other lions. Anal sniffing is common when lions meet, and males very often sniff females in heat and make a spectacular *grimace*. They can follow the scent trace left by another lion's feet, and pay close attention to one another's scent-marks. Pride males spend a lot of their time patrolling and marking the currently defended part of the range, stopping to spray bushes and other landmarks at frequent intervals. Although females occasionally squirt urine against vertical objects, urine-marking is mainly a male behavior. But both sexes perform the *scuffing ceremony*, beginning at about 2 years, raking the ground 2–30 times with the backfeet, with or without urinating (fig. 21.6). Prominent objects bordering roads, paths, kopjes, water holes, and solitary trees tend to become regular scent posts that reek of lion urine. Individuals and groups often scuff- and spray-mark after aggressive interactions with other lions and competitors such as hyenas, before leaving a kill, and (males) beside estrous females. It seems to be an assertion of the right to be at that

place, if not a claim to ownership. Lions of all ages also rake trees, and on treeless plains claw the earth like cats clawing a carpet (10).

Tactile Communication: *greeting ceremony, social licking, lying in contact.*

The kind of close, affectionate contact seen between mothers and young in other cats carries over to the adult stage in lions. Pride members have to go through the *greeting ceremony* whenever they meet, as a proof of membership in the pride and of peaceful intentions (fig. 21.7). Two lions approach each other, often moaning softly, rub heads then sides together, with tails raised and frequently draped over the partner's back. They lean against each other, so hard that a standing lion may roll over on top of a lying one, and when females roll on cubs in greeting, you wonder why the little ones are not crushed. But cubs more often rub lionesses than the other way around, and females greet each other more often than they greet cubs. Both females and cubs often seek to rub pride males, which may allow it but reserve their greetings for other males of their coalition. The fact that weaker animals tend to take the initiative indicates that greeting serves an appeasing function (14).

Social-licking is less prevalent than *head-rubbing* but also plays a part in reinforcing social bonds. Any pride member can initiate a licking session and it may be one-sided or reciprocal. Cubs are licked all over, whereas licking is otherwise largely confined to the head, neck, and shoulders.

Visual Communication. See family introduction. The black ear backs, lips, and tail tip accentuate the expressions and movements of these parts.

AGONISTIC BEHAVIOR

Dominance/Threat Displays: *strutting, head-low threat, accompanying vocalizations.*

Defensive Displays: ears flattened, teeth bared, head turned, eyes narrowed, crouching, lying on back, with accompanying vocalizations.

Fighting: slapping, grappling, biting, ganging up.

The *strutting display* is performed only by adult males (and by cubs in play), primarily to females, as a show of dominance (fig. 21.22). The lion makes himself as tall as possible and presents his side to or walks stiffly around the female with erected tail looped over his back.

The offensive threat is unconventional in that a lion stands with head low, forelegs straddled, and shoulders higher than nor-

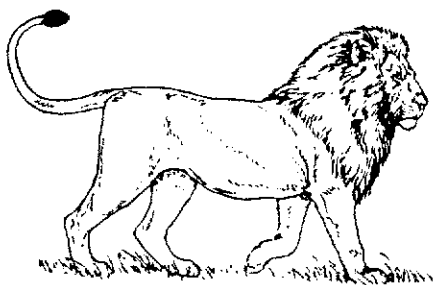


Fig. 21.22. Lion *strutting* [dominance] display (from Schaller 1972b, drawing by R. Keane).

mal, gazing steadily at its opponent. The tail is often lashed up and down—perhaps the only unambiguous tail movement in this species (14). If the other indicators of feline aggressive threat are also present (mouth slightly open with lips set in a straight line covering the teeth, eyes wide and pupils small, ears twisted so that the black marks face forward), accompanied by growls or coughs, a charge is imminent. The defensive threat is typically feline (see family introduction, Visual Communication and Agonistic Behavior).

The efficiency of the lion's scent and sound communication system enables nomads, lodgers, and trespassing neighbors to avoid encounters with territorial proprietors. For their part, pride lions show less inclination to rush upon outsiders in blind fury than to intimidate and drive them away without coming to blows. Once strangers have been put to flight, residents may escort them for miles at a fast walk or trot while staying at least 10 m behind (14).

Fighting is commonest between pride members competing over meat, but rarely goes beyond slapping, which is just as well since lions show little restraint when biting and may inadvertently administer the killing neck bite. However, severe, often fatal fights are usual during takeover attempts, females may fiercely attack infanticidal males in concert, and occasionally members of male coalitions fight over females in estrus. These battles are usually provoked by a female moving close to a male that has been keeping his distance, but sometimes 2 males get to a female at exactly the same time and neither is willing to defer (7, 10).

REPRODUCTION. Breeding is nonseasonal but often synchronized within prides (see Social Organization). Females begin breeding at four (43–54 months), only a year earlier than males (12). Gesta-

tion is $3\frac{1}{2}$ months (14–15 weeks), the typical litter numbers 3 cubs (1–4), and the birth interval is 20–30 months if cubs survive (as a rule half die in the first year). A preponderance of male cubs in synchronized births that occurred within 300 days of a pride takeover (129 males:96 females) in the Serengeti lion study suggests that mothers are somehow able to bias the sex ratio of their offspring (possibly through division of male zygotes to produce identical brothers) to take advantage of the higher lifetime reproductive success enjoyed by the members of larger male coalitions (6, 11).

SEXUAL BEHAVIOR. It has been estimated that lions copulate 3000 times for every cub that survives to the yearling stage (2). The discovery that females may cycle for months after a takeover without actually ovulating helps to explain why only 1 mating cycle in 5 results in progeny (9). However, even in normal times, many copulations are apparently necessary to induce ovulation. Once ovulation occurs, the fertility rate is very high: 95%.

Estrus typically lasts about 4 days (2–6), during which couples couple at the rate of 2.2 times per hour (8), each copulation lasting c. 21 seconds (8–68). One male copulated 157 times in 55 hours, with 2 different females (14). The male's rate increases to 3.5 copulations per hour when serving 2 females—evidence against the notion that females but not males are inexhaustible. Giving other males a chance late in the estrus cycle may be of more social than reproductive significance (8).

Mere proximity of a male and female is usually a reliable sign of a mating pair (fig. 21.19), and the way the male follows, practically tripping on the female's feet, is characteristic. The lioness rebuffs mounting attempts with snarls and slaps at first, but later often initiates mating by crouching and presenting before the lion. Instead of biting her nape during the climax, the male makes at most a few quick, light biting movements (fig. 21.9). The female keeps up an ominous rumbling the whole time, possibly from resentment at being straddled. The male may react by meowing in distress, leading into loud, harsh yowls at the climax. Immediately afterward he either dismounts or jumps aside, sometimes with a snarl or half-roar, as the lioness twists her head with an explosive snarl, prepared to cuff him. But once unburdened, she then languidly rolls onto her side or back (14). During estrus, a female will accept any adult male.

PARENT/OFFSPRING BEHAVIOR.

Lion cubs are born in a well-hidden lair, tiny (1–2 kg) and completely helpless. Their eyes open at 3–11 days; they can walk at 10–15 days and run at 25–30 days. They can scratch the first day but bite only after the milk teeth erupt at 21–30 days (3). At 4–8 weeks mothers begin leading their cubs to kills; they can keep up with the pride by 7 weeks and are weaned at 7–9 months (at latest by 10 months), but are unable to fend for themselves before 16 months. Cubs have the best chance of surviving when the births of several females are synchronized and there are no older cubs around to hog most of the milk of females suckling one another's cubs communally (fig. 21.23) (8). Suckling bouts last 1–10 minutes and at 4 months cubs suck about 15 minutes a day (14).

Cubs are often left alone for over 24 hours, while their mothers consort with other pride members. They stay closely hidden and if disturbed crawl into nooks and crannies to escape detection. They are quick to take cover even when grown-ups are present. Starvation and abandonment are most likely to occur when large prey is scarce. A mother will not slow her pace for cubs more than 5–7 months old; those too weak to keep up and single offspring are often abandoned. The risk of starvation recedes only when the young become capable of killing for themselves.

Already at $2\frac{1}{2}$ months cubs observe prey movements, and as usual play enacts the stalking, ambushing, grappling, and killing motor patterns used by adults to capture prey. Females never lose their playfulness, whereas males older than 3 rarely join in. Cubs as old as 7 months are still unresponsive to the stalking postures of their elders and often manage to spoil hunts by blithely running ahead, playing, meowing, and so on. A little later they stay back and observe intently, but become participants only when c. 11 months. Unlike various other cats, lionesses rarely school their young in killing by bringing them young animals

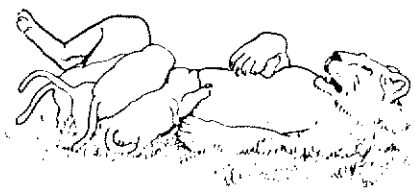


Fig. 21.23. Lioness suckling her own and other cubs (communal suckling).

to chase. But lion cubs stay in the maternal group much longer than any other cat.

ANTIPREDATOR BEHAVIOR.

Adults in good health have little to fear from any animal but man, who has been a major competitor from the days when our kind began eating meat. Small cubs left alone in hiding are very vulnerable to predation by spotted hyenas, which probably also prevent most starving, diseased, and old lions from dying of natural causes.

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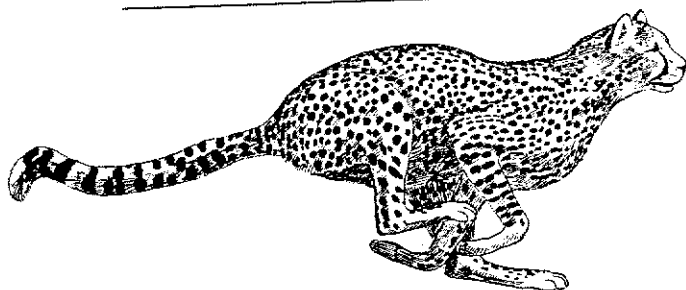


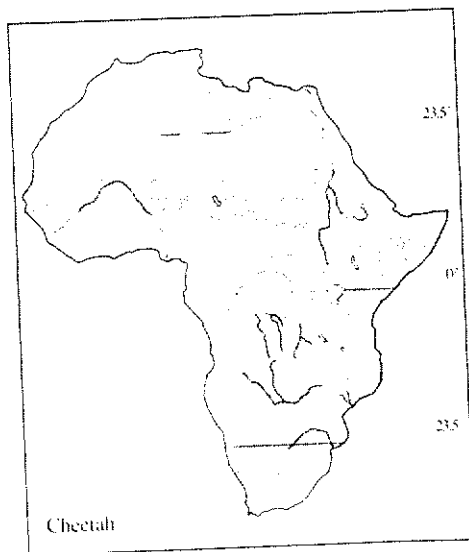
Fig. 21.24. Cheetah sprinting.

Cheetah

Acinonyx jubatus

TRAITS. The felid version of a greyhound, the most specialized cat. *Height and weight:* 78 cm (70–90), and 50 kg (35–65), males more robust and c. 10 kg heavier than females. Lightly built with long, comparatively thin legs and small feet with blunt (except dewclaw), unsheathed claws; swayback, short neck, small, rounded head with foreshortened face, broad but low ears, teeth relatively small, especially canines. *Coloration:* tawny, with white underparts, a short ruff, more developed in males, and fluffy hair on belly and chest; spots small and solid, outer tail ringed black and white, tip usually white; black ear backs, lips, nose, and "tear stains" from eyes to mouth; juvenile coat black with faint spots and a cape of long, blue-gray hair. *Scent glands:* presumably anal glands. *Mammæ:* 12.

and arid zones, but greatly reduced in range and numbers. This species is far less adaptable to man than the leopard, but in Namibia has benefited from the removal of lions and hyenas and the reintroduction of antelopes on ranches (13). However, an extraordinary degree of genetic uniformity in this species raises the possibility that a disease could devastate wild populations (15).



DISTRIBUTION. Similar to the lion's: the cheetah formerly ranged through the Near East to south India and throughout Africa except in equatorial forests and true desert. The cheetah became extinct in India in the early 1950s, and is now extremely rare elsewhere in Asia and North Africa (14). It is still widely but sparsely distributed south of the Sahara in the savannas

ECOLOGY. The cheetah is specialized to prey on the fleetest antelopes, especially the gazelles and their close relations, the blackbuck and springbok, which dominate the arid wastelands of Asia and Africa. That the cheetah is built for speed (fig. 21.24) is demonstrated by the fact that the fastest dogs—greyhound, whippet, Afghan hound—produced after centuries of selective breeding, have a similar conformation. No other mammal is as fast as a cheetah, which has a top speed of 90–112 kph (60–70 mph), but dogs have something the cheetah lacks: stamina [19] (more under *Predatory Behavior*). To capture its prey, the cheetah has to overtake it within 300 m. It has a hard time getting within sprinting range on plains with no cover; optimum cheetah habitat therefore includes cover in the form of bushes, medium-length (not tall) grass, trees, broken ground, and such. In the bush and savanna woodlands, the impala takes the place of gazelles as the cheetah's mainstay, accounting for 68% of 1092 cheetah kills in Kruger N.P., for instance [16]. This cat also occurs in the *Miombo* Woodland Zone, where its main prey is probably the bush duiker, reedbuck, lechwe, oribi, juvenile sable and roan, and warthog. Single cheetahs seldom kill antelopes heavier than themselves, and often take smaller game; in Serengeti N.P. hares are second (12%) in importance to Thomson's gazelles (62%), especially during times when gazelles are scarce [8]. Serengeti cheetahs regularly go 4 days between drinks, after which they will travel 5–10 km to water if necessary. In the Kalahari, where they eat melons, cheetahs easily go 10 days without drinking [8].

SOCIAL ORGANIZATION: diurnal, territorial, females solitary, males in colonies or alone.

Being an inhabitant of open country, diurnal, and often seen in groups, the cheetah could well be supposed to be a social carnivore. However, these groups almost always turn out to be mothers with subadult cubs, young adult siblings recently separated from their mother, or coalitions of males. Adult females are as solitary and shy as other cats (7, 17). In acquiring the speed to catch the fleetest antelopes, the cheetah sacrificed the strength and weapons needed to defend its kills and offspring against competitors (5, 7). Perhaps its delicate build is enough to explain the timidity that characterizes this cat. It is afraid of lions, surrenders its kills to hyenas, and can even be intimidated by vultures—maybe

because it realizes that vultures attract other predators. To avoid being victimized, it makes itself as inconspicuous as possible, aided by its cryptic coloration.

Home Range and Territory. Where their main prey is migratory, cheetahs cover a wide area: the annual range of Serengeti females that subsist largely on Thomson's gazelles is c. 1000 km² [7]. But several females whose histories were recorded for up to 11 years had narrow ranges 50–65 km long which included habitat utilized by gazelles both during wet and dry seasons. The cheetahs were able to move with the gazelles in a regular cycle that took them from end to end of their home ranges. When offspring reached 17–23 months and separated from their mother, daughters remained within the maternal home range but each stayed alone. Once a mother and daughter were seen only 20 m apart, but parted without coming any closer. However, despite minor adjustments of range during ensuing years, a broad overlap between the ranges of the mother and 2 daughters persisted. The daughters' ranges overlapped much less.

Male offspring emigrate and typically wander huge distances while maturing and seeking to establish territories. Nine males marked in Namibia were retrapped at distances of over 200 km from the marking site [13]. Among other dangers, transient males run the risk of injury, even death, if caught trespassing on the territories of established males (example under *Agonistic Behavior*); consequently females may be twice as numerous as males in the adult population [7]. Males compete for the best hunting grounds, and defend areas much smaller than the females' ranges—the reverse of the arrangement seen in most carnivores. However, males may range outside their territories [3]. The areas defended by Serengeti males were found to be 39–78 km²; they had no overlap and sharp boundaries. Territorial males did not trespass, whereas females passed through a number of territories during the circuit of their ranges.

In the Serengeti study, 41% of the adult males were solitary, 40% lived in pairs, and 19% lived in trios [3]. The benefits to male cheetahs of forming coalitions are far less obvious than in the case of lions. Female cheetahs are solitary, and as single males apparently meet as many as do males in coalitions, singletons would not have to share or compete for copulations with companions. However, there is evidence that single males have a harder time acquiring and keeping a territory. Only 4% of the



Fig. 21.25. A male coalition of 3 cheetahs, drinking.

observed single males ever held a territory, whereas all the single males that joined coalitions acquired territories. Furthermore, estimated territorial tenure increased with coalition size: the median tenure for singletons was 4 months ($3\frac{1}{2}$ –9), it was $7\frac{1}{2}$ months ($2\frac{3}{4}$ –16) for pairs, and 22 months ($18\frac{1}{2}$ –24 $\frac{1}{2}$) for trios. One trio held a territory for 6 years (3).

How Coalitions Are Formed. Littermates often stay together for several months after separating from their mother. One by one the females drop out before they reach 2 years of age, presumably at the onset of estrus. Some males also separate, whereas others stay together as permanent companions (fig. 21.25). Of 6 Serengeti litters containing more than 1 male, brothers of 4 litters went their separate ways (7). A single male joined a pair of brothers after separation while they were still living in their mothers' adjacent ranges. Then they moved 20 km and established a 36 km² territory on the Serengeti Plain. Fourteen months later they extended their range by 22 km² during a time when gazelles were scarce, but within a month were back in their usual area.

Social relations between cheetah males are more restrained and less affectionate than relations within lion coalitions. Cheetahs seldom lie in contact and their greeting ceremony proceeds no further than *cheek-rubbing*. During 38 hours of observation over a five-day period, males of the above trio exchanged cheek rubs only five times (7). The unrelated male, which proved to be dominant, administered 4 of the 5 cheek rubs, two to each brother, and he issued 5 of 9 play invitations, all declined (the 2 brothers played once for a minute). No cheek rubs were initiated by the lowest-ranking member of the trio. In addition to cooperative defense of their territory, the males jointly marked their property. They sniffed existing marks 55 times and urine-marked 59 times in 34 hours. Number 3 male

marked most (27 times) and number 2 marked least (13 times), although he sniffed as often as the alpha male (20 times).

The largest number of cheetahs seen in the Serengeti totaled 9 and consisted of 2 females with their offspring. Associations between adult females were seen about once in every 500 cheetah sightings and lasted only a few hours. Of 1260 cheetah sightings, 35% were lone adults, 40% were females with offspring, 7% were littermates on their own, 7% were male coalitions, and 3% were female-male consorts (7). In Namibia, however, groups numbering from 10 to 14 are not uncommon; 16% of 102 adult females were observed in groups of 2 or more, and 28% of all litters were accompanied by more than 1 adult. This population also kills bigger game than usual, including adult kudus and wildebeests (13). These differences may be explained by the fact that the cheetah has become the dominant predator on fenced range, where other large carnivores have been exterminated. The implication is that the cheetah's social organization and predatory role are shaped elsewhere by the presence of hyenas and lions (13).

ACTIVITY. The most diurnal cat, cheetahs do almost all of their hunting by daylight, but usually rest during the hottest hours. Rarely, cheetahs will engage in brief chases by moonlight or even on dark nights. In Nairobi N.P., females and cubs moved about 3.7 km per day, compared to 7 km for males (12).

POSTURES AND LOCOMOTION. See Predatory Behavior and family introduction.

PREDATORY BEHAVIOR. Of 493 observed hunts by Serengeti cheetahs, 203 were successful (41%) (7). Only 40% of the stalks of Thomson's gazelles, which made up nearly 60% of the kills, ended in chases (fig. 21.24), but half of those chased were caught. Male coalitions and females with subadult young use their combined might to pull down game the size of yearling and 2-year-old wildebeests. Four males in Nairobi Park even killed a zebra and a waterbuck (6).

An actively hunting cheetah walks along alertly, utilizing termite mounds and trees with low branches as vantage points from which to spot potential prey. To get within sprinting range (50 m or less), a cheetah uses several different techniques, depending on the terrain and the type, disper-

sion pattern, and behavior of the prey. It may simply wait at a vantage point if it sees that a group of gazelles is moving in its direction. Or it may approach slowly and openly an alert herd on the open plain, whose members stand and watch or even trot closer for a better look. If it can get within 60–70 meters before the animals take flight, the cheetah may gallop at them, but will accelerate to full speed only after selecting a particular quarry. Alternatively, if all the animals are grazing unsuspectingly, the cheetah may rush at them from over 100 m (rushing) and try to get close enough to select a quarry before being detected. But whenever cover is available cheetahs stalk as close as possible, walking semicrouched with head lowered to shoulder level, trotting, freezing in mid-stride when the game looks up, dropping to the ground, lying crouched, and sitting (8, 22). In a sample of 129 complete hunts, stalking was employed 85 times, taking anywhere from a few minutes to more than an hour. In $\frac{1}{2}$ of the hunts the cheetah first walked closer, and then began stalking or tried rushing. Forty-six of the hunts ended in failure, either because the prey spotted the hunter before it could get within range (28 times), the quarry wandered away during the stalk (5 times), or the cover ran out before the cheetah could get near enough. Five times cubs alerted the quarry. Lone animals at a little distance from a group and individuals near cover are most likely to be singled out (22), but the cheetah does not look for individuals in poor condition and takes no account of wind direction. However, it will single out and pursue small fawns that leave their hiding places, coming on the run from as far away as 500–600 m. Hunting success with fawns is 100%—a small but sure meal (17).

Once a cheetah gets within range, often flight seems to trigger pursuit. An antelope or warthog that stands its ground may well not be chased (11). Although a cheetah can accelerate to about 112 kph (70 mph), the average speed during a chase is less than 64 kph (40 mph). If it fails to overtake its quarry within 300 m the cheetah's breathing rate goes up to 150 a minute, its temperature soars, and it has to cool down for half an hour before trying again (11, 19). Having overtaken its quarry the cheetah may yet fail to catch it, for the tommy, in particular, reacts by turning sharply and the cheetah is hard put to follow closely, the more so the greater the difference in speed. A tommy seldom makes

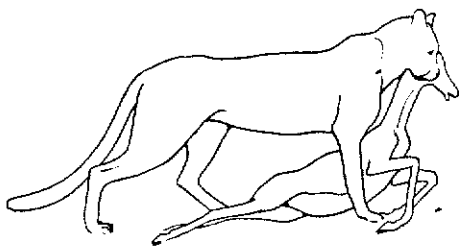


Fig. 21.26. Cheetah dragging prey to cover.

more than 3–4 such turns, but by then the cheetah is often winded (11).

The harder its quarry is running, the easier it is for a cheetah to unbalance it by striking rump, thigh, or hindleg with a sideward or downward stroke of a forepaw, or simply by tripping it. The victim crashes on its side or even flips end over end, sometimes breaking a leg (11). If the prey is going slower or standing, the cheetah rears, hooks into the flank or back with a dewclaw, and yanks backward, causing it to fall on its side. Using one or both legs and its chest to hold the struggling animal down, the cheetah lunges for the throat and secures a grip on the windpipe, usually from behind, out of the reach of flailing hooves. The canines are so small that they only penetrate a short distance, but the skull is designed to give the cheetah a viselike grip (11).

After the victim's struggles have ceased (typically within $4\frac{1}{2}$ minutes), the cheetah proceeds to drag it into nearby cover (fig. 21.26), if any, and there settles down to eat, while keeping a wary eye out for other predators and scavengers. It opens the carcass by shearing the belly skin with its cheek teeth, then eats the muscles of the limbs, back, and neck first. It may eat up to 14 kg at a sitting, then not kill again for 2–5 days (9). A female with cubs is kept much busier. One with youngsters 3–4 months old that was followed for 35 days captured 31 gazelles and a hare during that time (17). An estimated 4 kg of meat per day is available in a cheetah's kills. Most bones, the skin, and the digestive tract are left uneaten. Unlike other big cats, cheetahs do not hold their meat between their paws, but gnaw or tear off large chunks. They do not return to their kills, and only occasionally rake dirt over a carcass before leaving it (11).

Relations with Other Predators. Serengeti cheetahs lose about 10% of their kills to other predators, mainly spotted hyenas and lions, half the time before they

have begun feeding (9). Sometimes a cheetah, especially a mother with cubs, will resist giving up a kill to a hyena or wild dogs, growling, moaning, spitting, and even making mock charges, but will not hold its ground if a larger carnivore continues to advance. Lions catch and kill cheetahs whenever possible; cheetahs will often flee even from a lion's voice. Leopards and wild dogs have also been known to kill cheetahs. Man is another one of the predators which have long exploited the cheetah's hunting skill: a silver vase from the Caucasus dated to 2300 B.C. depicts a cheetah wearing a collar (11).

SOCIAL BEHAVIOR COMMUNICATION

Vocal Communication: *chirping* or *yelping*, *churring*, growling, snarling, moaning, *bleating*, purring. Maternal and juvenile: *whirring*, *nyam nyam*, *ihn ihn* [mother calling cubs], *pr* [maternal "follow me" call].

Many of the cheetah's calls are unlike the sounds of other cats, particularly the 2 discrete contact cries, *chirping* and *churring*, which are often given alternately and repeatedly, at varying intensity. The bird-like chirp, which sounds like a yelp or a dog's yip at high intensity and may be audible for 2 km, is the usual call given by females to summon hidden or lost cubs, by greeting or courting adults, and by cubs around a kill, the intensity reflecting the degree of excitement. *Churring* is a staccato, high-pitched growling sound that is less far-carrying. These 2 calls have been compared to the lion's loud and soft roars (11). Cheetahs also growl, snarl, hiss, and cough in anger or fright, but less frequently than other big cats. When forced to surrender its prey to another predator, a cheetah may hiss and sometimes moan loudly. *Bleating*, equivalent to meowing, is a sound of distress, as in the lion; for example, a female circling a lion that had stolen her kill uttered a growling bleat (11). Cubs squabbling at a kill made a whirring sound possibly equivalent to growling in other cats, which rose to a ferocious squeal at peak intensity and subsided to a rasp. A sound like *nyam, nyam, nyam* is also associated with eating, and captives anticipating food sometimes utter a curious humming (2, 11). Contented and friendly cheetahs purr like huge housecats, especially while greeting or licking each other. Other calls heard between mothers and young include *ihn, ihn, ihn*, which, like chirping, is used to

summon young; a sharp *pr*, *pr* which elicits close-following when the mother is moving; and a short, low-pitched sound that makes the young stay still. Small cubs disturbed in hiding sometimes make sounds like breaking sticks (11).

Olfactory Communication: scent-marking by *urine-spraying*, *scuffing* (\pm urination), defecating on landmarks, clawing [rare].

Scent is apparently the main communication channel among cheetahs. They spend much time searching for, smelling, and depositing their own scent on previously marked places. Elevations and other landmarks used as observation points are preferred marking places, thus serving as regular stations where virtually every cheetah receives and leaves olfactory information. When a cheetah comes to a marking place, it crouches on its forelegs and sniffs long and carefully. In a group, the posture stimulates other cheetahs to approach and do likewise. A male then sprays urine on the spot and (unlike lions) often sniffs his own mark before continuing on his way (17), which may zigzag between established scent posts (4). Females also urine-mark, with increasing frequency as they come into estrus, but less actively than males; in Botswana, ranchers have trapped up to 40 cheetahs in a decade—all males—at traditional marking trees situated at junctions between several territories (13). Both the urine and feces of estrous females also attract males from far and wide. It is not known whether feces have any territorial significance, but both sexes often defecate on the mounds, boulders, and trees they use as observation and scent posts.

Tactile Communication. The cheetah *greeting ceremony* features much mutual sniffing (oral and anogenital), face-licking, and cheek-rubbing, but no body-leaning or side-rubbing (11, 17).

Visual Communication. The "tear stains" and black lips edged with white fur direct attention to the face and clearly signal changes of expression at close range. A cheetah sitting and *looking away* (mildly intimidated) keeps its lips pursed so that the mouth line is concealed, whereas the lips and tear stripes merge in an emphatic geometric figure in cheetahs with confident and aggressive expressions (fig. 21.27) (11). But otherwise the cheetah's coloration and markings are cryptic except at close range. The continuation of spots onto the face makes the head as hard to see as the body from a distance. The black ear-

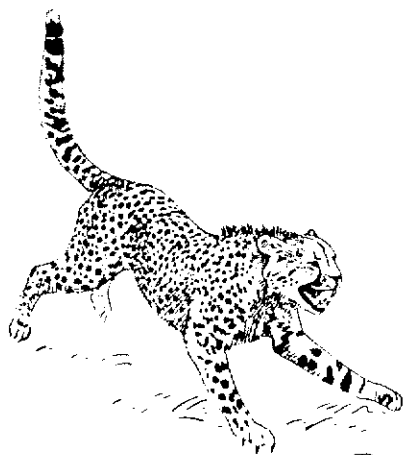


Fig. 21.27. Cheetah charging [offensive threat].
(From a photo in Eaton 1971.)

marks only show up well from behind or when a cheetah has its head lowered in threat. However, the tail with its black and white rings is conspicuous, functioning perhaps mainly as a follow-me signal for the young.

AGONISTIC BEHAVIOR

Dominance/Threat Displays: *stiff-legged approach with head below shoulder level, often in lateral presentation, charging [fig. 21.27], and aggressive facial expression [see fig. 21.3].*

Defensive/Submissive Displays: *looking away, lying on side, rolling on back, crouching with wide-mouthed snarl, lunge or mock charge, slapping and snapping.*

In defensive threat, a cheetah crouches low, snarling with mouth wide open and ears flattened, eyes glaring upward. At highest intensity the animal makes sudden lunges and thumps the ground sharply with downward strokes of its forepaws, meanwhile moaning and hissing, but rarely growling. Two cheetahs performed this display convincingly enough to discourage 8 hyenas from moving in on their kill (11).

Fighting. Rare as long as unassociated cheetahs avoid meeting, fights are most likely to occur when males collect around an estrous female or catch other males on their territory.

Fatal fights are occasionally reported, including one gruesome case in which the coalition of 3 Serengeti males mentioned earlier repeatedly attacked and finally killed a member of another trio of known males which intruded on their territory (7, 10). The territorial trio chased the intruders,

overtook and proceeded to attack one viciously while the others withdrew to a distance of several hundred meters and merely looked on. All 3 resident males participated, tearing out fur and biting the intruder hundreds of times, but the unrelated, alpha male was the most persistent and vicious. However, the number 2 male administered the coup de grace, by securing a throat grip and strangling the intruder like a gazelle. Strangely enough, the victim made almost no effort to defend himself, but just lay there and took it.

REPRODUCTION: minimum age at first conception 21–22 months; interval between birth and next conception 18 months; perennial breeding with possible mating peaks after short and/or long rains; gestation 90–95 days; average litter 3–4 (1–8) [8, 17].

SEXUAL BEHAVIOR. Courtship may be extended or brief, stormy or calm, depending on the female's receptiveness and individual temperament and the number of competing males.

A lone female that revealed she was nearing estrus by stopping to sniff virtually every tree, bush, and grass clump she came to, and urine-marked at the high rate of once every 10 minutes, was observed for 8 days (10). Early on the sixth day a male came across her tracks and broke into a fast walk, alternately *yelping* and *staccato-purring*. When the female heard him, she immediately turned and trotted toward him, then lay down as soon as she saw him. The male mated her practically without preliminary, while maintaining a hold on her nape. Afterward the female rolled, groomed her face and legs, and studiously ignored the male. He growled and hissed whenever she moved, then followed and sniffed the grass where she had lain. After resting the whole day, the pair mated again at dusk, and stayed together until the next afternoon. The female then stole away while the male was sleeping.

In another, more typically feline courtship sequence, the female alternately tempted and resisted her suitor (17). Both uttered *churring* and *chirping* calls (18).

PARENT/OFFSPRING BEHAVIOR.

Since females withdraw into cover to give birth and carefully hide their cubs, cheetahs less than a month old are rarely seen. A litter of 3 cubs born in captivity emerged at 20–25 minute intervals; the female broke the fetal membrane of each in turn with her teeth (18). Blind newborn cubs

weighing 150–300 g can crawl, turn their heads, give soft *churring* calls, and spit explosively. Four wild-born cubs only 3 days old were found in a patch of high grass when the mother was seen transporting them [by the back, once by a foreleg]. After depositing them in a thicket, she returned twice to the former site as if to make sure none had been overlooked (17). A mother with 10-day cubs moved them at least every other day. Another female kept her cubs within a 1 km² area and hunted a 10 km² area for the first month (8).

The zoo-born cubs' eyes opened at 10 days; they could walk on day 16 and got their first teeth at 20 days (18). A litter of wild cubs was first led to a kill at c. 5½ weeks and thereafter followed wherever the mother led, except when she chased prey. However, they often ignored her stalking movements and sometimes spoiled hunts by playing or trotting ahead of her. She countered this by sitting and patiently waiting until they came back. After 3 months, when the cubs were probably already weaned, they stayed behind, following slowly or waiting for the kill. They formed a close-knit family with remarkably little friction, even when feeding together on small prey. After eating, the mother would lick their faces clean, to the accompaniment of purring (17).

Cheetah cubs begin practicing catching and killing for themselves well before they become independent. The mother brings back gazelle fawns and the like and lets the cubs try catching them before they are ½ year old. Between 9 and 12 months, cubs may hunt and capture hares and fawns for themselves while the mother remains on the sidelines, but they are rarely able to make the kill. Even at 15 months, 3 cheetahs took turns swatting and bowling over a gazelle fawn they flushed 10 different times; finally the mother rushed in and bit it in the neck (17).

PLAY. Joy Adamson described the spirit-
ed, incredibly athletic games played by young cheetahs in great detail (1, 2): mainly stalking, pouncing, chasing, boxing, wrestling, and tug-of-war. Playing animals run with tail raised in typical cat fashion; they also climb trees and play king-of-the-mound. The commonest form of play, beginning at about 3 months, is chasing and swatting at one another's hindquarters, the typical way of bringing down prey (17).

ANTIPREDATOR BEHAVIOR. See Relations with Other Predators. Probably less than half of Serengeti cheetahs survive the first 3 months. They are fair game for a whole range of predators down to the size of the larger eagles. Whether the resemblance of the juvenile coat to a ratel's color pattern has any deterrent effect on predators [eagles, for instance?], a recurrent suggestion, remains to be tested. Mothers may courageously defend their offspring. One with 3 one-third grown cubs went out of her way to charge and tree a leopard, normally a dominant competitor which could kill a cheetah [author's observation].

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