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Hyaena brunnea.

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Hyaena brunnea Thunberg, 1820

Brown Hyaena

Hyaena brunnea Thunberg, 1820:59. Type locality Cape of Good Hope.
Hyaena fusca Geoffroy St.-Hilaire, 1825:444. No type locality given.
Hyaena striata Smith, 1826:14. No type locality given.
Hyaena villosa Smith, 1827:461. Type locality South Africa.

CONTEXT AND CONTENT. Order Carnivora, Family Hyaenidae, Genus *Hyaena*, in which there are two allopatric species, *H. brunnea* and *H. hyaena* (Rieger, 1981). No subspecies of *H. brunnea* are here recognized (Coetzee, 1977).

DIAGNOSIS. The brown hyaena is larger than the striped hyaena (Skinner and Ilani, 1979), is unstriped except for the legs, and has long hair over most of the body, not just along the mane as is the case with the striped hyaena. The posterior choanae of the skull are wider in the brown hyaena than in the striped hyaena, and the height of the choanae at the end of the palate is about one-third of the interpterygoid width at the suture between the palatine and pterygoids, whereas in the striped hyaena this height is about half the interpterygoid width (Coetzee, 1977).

In the field, the brown hyaena is easily differentiated from the other two Hyaenidae with which it is sympatric, the spotted hyaena (*Crocuta crocuta*) and the aardwolf (*Proteles cristatus*) (Dorst and Dandelot, 1970). Differentiation of tracks of brown and spotted hyaenas is, however, difficult. The tracks of spotted hyaenas are typically larger than those of brown hyaenas and the difference in size between the front and back feet is more marked in brown hyaenas than in spotted hyaenas. The skulls of these two species are also similar, but in the brown hyaena the first upper molar is fairly large whereas in the spotted hyaena it is minute or absent, and the third upper premolar is less massive in the brown hyaena than in the spotted hyaena (Ewer, 1954). Furthermore, the lower border of the foramen magnum forms a narrow "V" in the brown hyaena, whereas it forms a rounded "U" in the spotted hyaena (Roberts, 1954). The auditory bulla and braincase are larger in the spotted than they are in the brown hyaena.

The sexual organs of *Hyaena* are not specialized as are those of *Crocuta*, in which the female has evolved a highly erectile clitoris and a false scrotum.

GENERAL CHARACTERS. The brown hyaena is a medium-sized, long legged carnivore with well-developed forequarters, weak hindquarters, and a sloping back. The pelage is shaggy and dark brown to black, except around the neck and shoulders, which are white, and along the underparts, which are light-colored. The ears are long and pointed (Fig. 1). On the lower forefeet and hindfeet are a series of white stripes.

With a few exceptions brown hyaenas do not vary greatly in size at different localities. The mean mass of 37 adults from the southern Kalahari (Mills, 1981), the southern and northern Transvaal (Skinner, 1976), the northern Cape Province (Liversidge, pers. comm.), the Orange Free State (Lynch, pers. comm.), Zimbabwe (Smithers and Wilson, 1978), and Botswana (Smithers, 1971), is 40.7 kg (range 28.0 to 47.5 kg). However, a female brown hyaena from the eastern Cape weighed 67.6 kg (Swanepoel, pers. comm.) and Roberts (1954) gave the mass of two unsexed animals from the eastern Transvaal lowveld as 72.6 kg and 59.9 kg. The mean total length of 22 brown hyaenas from the southern Kalahari was 1,440 mm (1,260 to 1,610 mm) and the mean height at shoulder was 787 mm (715 to 879) (Mills, 1981).

DISTRIBUTION. Brown hyaenas are mainly inhabitants of the southwest arid and adjacent drier parts of the southern savanna biotic zones of Africa (Von Richter, 1972). The nocturnal and secretive habits of brown hyaenas make it extremely difficult to accurately document their distribution. Although they are apparently now extinct in the extreme southern Cape, records collected over the last 20 years reveal that they still occur over large parts of southern Africa (Coetzee, 1977; Eaton, 1976; Skinner, 1976; Smithers, 1971; Smithers and Labao Tello, 1976; Smithers and Wilson, 1978; Stuart, 1981; Von Richter, 1972; pers. observ.) (Fig. 2). The southern and central regions of the Kalahari and the coastal areas along the west coast of Southwest Africa appear to harbour the largest populations.

FOSSIL RECORD. Hyaenids are direct descendents of the Viverridae. The ancestors of *Hyaena* and *Crocuta* have existed separately since the Miocene, with *Hyaena* first appearing in the Pliocene (Thenius, 1966; Von Koenigswald, 1965). The early Pleistocene was a period of hyaenid abundance, but during the middle Pleistocene the hyaenid fauna shrank, leaving those few species which have managed to survive until the present (Ewer, 1967). The two *Hyaena* species probably have a common origin in southern Africa during the late Pliocene. *Hyaena brunnea*, however, has not been found in any east or north African deposits, nor is it known in European or Asiatic deposits. It appears to be a species which evolved in southern Africa, but was never sufficiently successful to spread to other areas, possibly because of competition with *C. crocuta* (Ewer, 1967).

FORM AND FUNCTION. The pelage is generally coarse, with the length of individual hairs averaging 112 ± 60.0 (SD) mm. The color of individual hairs is dark brown, dark brown merging into tawny then into white, and tawny banded with white. In cross section, guard hairs are normally circular with a small medulla; a few others, circular or oval, have large medullas. Hairs of the

FIGURE 1. Above: subadult (left) and cub (right) brown hyaenas in the southern Kalahri. Below: subadult and cub muzzle-wrestling. Photos by the author.

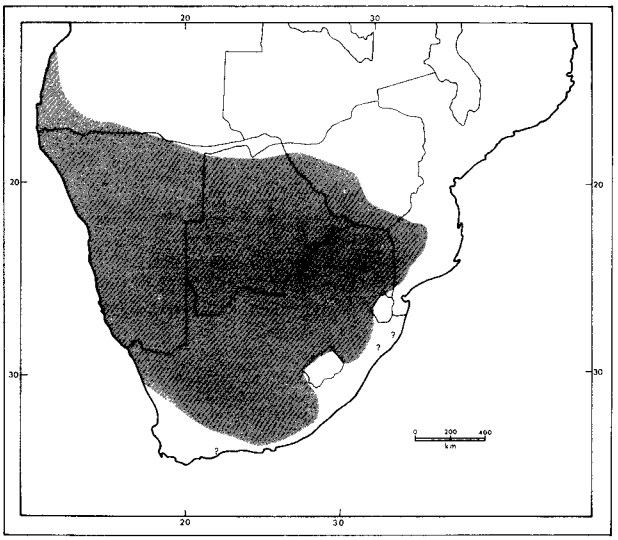

FIGURE 2. Recent distribution of the brown hyaena. Shaded area indicates approximate extent of range; question marks signify possible recent sightings.

underfur are round or oval with medium-sized medullas. Cuticular scale patterns are waved mosaics, with one or two scales across the width of the hair. The scale margins are crenate (Keogh, 1979).

The summer pelage is thin with little underfur, but in winter the pelage is thicker. These are adaptations to the large fluctuations in seasonal temperature that occur over most of the range of brown hyaenas. As in the striped hyaena (Rieger, 1981), teat numbers seem to vary individually. Murie (1871) recorded six pairs of mammae from a single specimen, but normally only two pairs are functional. Both front and back feet have four toes with non-retractile claws. The stance is digitigrade. The dental formula is i 3/3, c 1/1, p 4/3, m 1/1, total 34. Premolars are extremely robust. The sagittal crest forms a keel-like ridge sloping down to the cranium (Fig. 3). The heavy musculature associated with the skull and neck and the robust premolars form an efficient mechanism for crushing bone. Ewer (1954) presented a detailed discussion on the dentition of hyaenas.

When foraging, brown hyaenas travel at a walk of approximately 4 km/h (Mills, 1978*b*), but are capable of running at a speed of 40 to 50 km/h. They rely mainly on scent in locating food, but also act on visual and auditory cues and all these senses are well developed.

Defecation is used as a form of marking, but urination has no known marking function. The most important organ in scent marking is the anal scent pouch which lies between the rectum and the base of the tail. This structure secretes two distinct, strong smelling substances. The anal pouch consists of two distinct regions. The large central area has a groove running down it (into which grass stalks fit) and is composed of numerous enlarged sebaceous glands which are rich in lipid and produce a white paste. On each side of the central area, and separated from it by non-secretory epithelium, are two circular areas consisting almost entirely of apocrine sudoriferous tissue with accumulations of lipo-fuschin. These produce a black paste (Mills et al., 1980).

ONTOGENY AND REPRODUCTION. Brown hyaena females are polyestrous with anestrous occurring during lactation. Matings do not always result in conceptions in either wild (Mills, 1982) or captive animals (Lang, 1958; Shoemaker, 1978). In captivity, a female whose cubs are removed or die immediately after birth can conceive again shortly afterwards (Anderson, pers. comm.; Schultz, 1966; Shoemaker, 1978). The gestation period is approximately 97 days (Asdell, 1946; Lang, 1958; Shoemaker, 1978). The mean size of 61 litters both from captivity and the wild is 2.3 (1 to 5) (Mills, 1981; Schultz, 1966; Shoemaker, pers. comm.; Skinner, 1976; Smithers, 1971). Females usually produce their first litter late in their second year (Mills, 1981; Shoemaker, 1978). In the wild, the interval between the birth of a successfully-raised litter and the next one varied between 12 and 41 months (Mills, 1982). The age at sexual maturity of males is unknown.

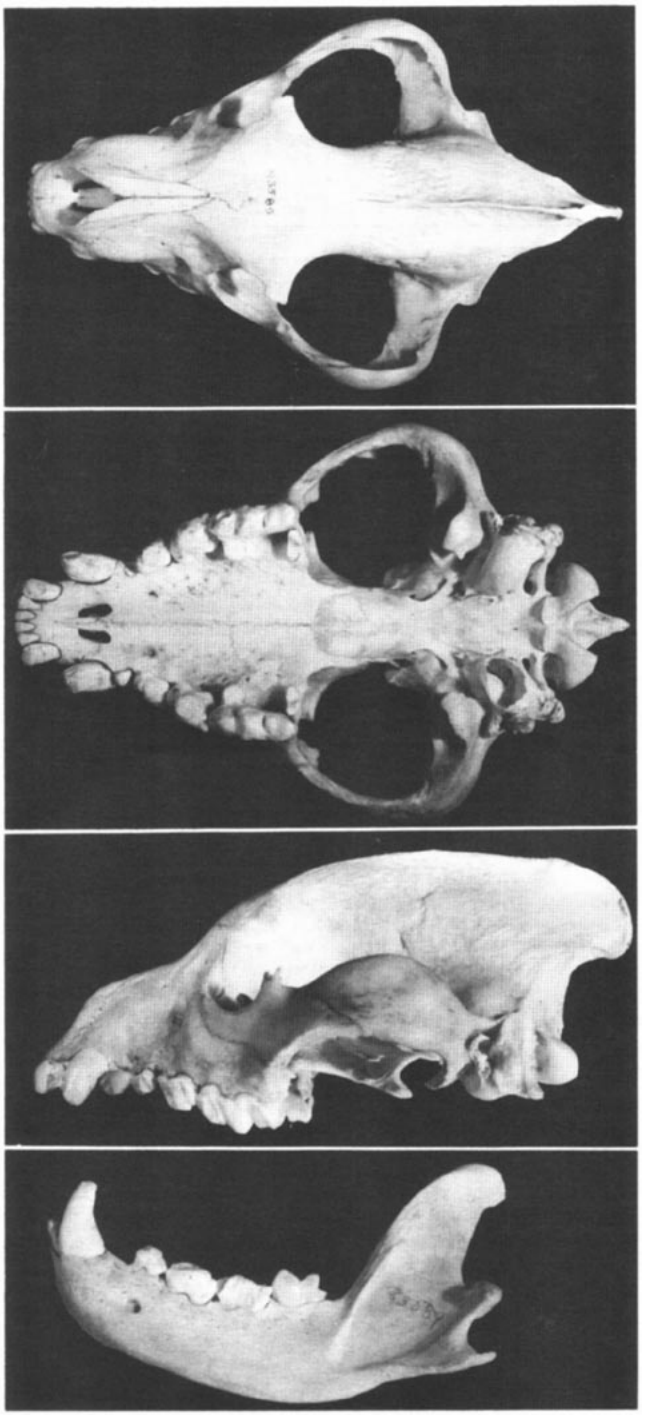

FIGURE 3. Skull of *Hyaena brunnea*, AMNH 83589, from Nkate, Botswana. Zygomatic breadth is 165 mm.

Brown hyaenas are born with their eyes closed, their ears bent sharply forward and with the same body color as an adult, but with shorter hair (Schultz, 1966). The mean birth mass of 13 brown hyaenas from captivity was 693.2 g (630 to 812 g) (Anderson, pers. comm.; Lang, 1958; Schultz, 1966). Data on growth of cubs in captivity can be found in the above references. Teeth are fully erupted at approximately 15 months of age and full growth is achieved at approximately 30 months (Mills, 1981).

Observations in the southern Kalahari (Mills, 1981) revealed that cubs spent approximately 15 months in the den. For the first 3 months of their lives, the cubs were normally nursed by their mother at sunrise and sunset. After 3 months of age, they were brought meat, but were still regularly suckled. They were weaned at approximately 1 year of age. Occasionally a female

will allow a cub which is not her own to suckle from her (see also Owens and Owens, 1979*a*), but she shows a clear preference for her own cubs. Meat is carried back whole to the den for the cubs by all of the group members and is never regurgitated. From about their tenth month, the cubs begin to forage a little on their own, gradually increasing the extent of their foraging trips. Between the age of 15 and 30 months brown hyaenas are regarded as subadults and although they are capable of fending for themselves they still may on occasions get some food at the den.

Mills (1981) found that the survival rate of cubs up to 15 months of age in two adjoining national parks in the southern Kalahari was 86%. Mortality amongst subadults and young adults was often caused by dispersing animals trespassing onto neighboring agricultural areas where they were killed. After that, mortality was low until the animals reached old age. The most common form of natural mortality was brought about by violence on the part of other large carnivores. In old animals, hunger caused by worn and non-functional, bone-crushing premolars appeared to be the main cause of mortality. Longevity of over 13 years has been recorded for brown hyaenas in captivity, although maximum longevity records for this species are less than those for other hyaenas (20 to 25 years), probably because it is uncommon in captivity (Crandall, 1964). In the southern Kalahari, a living animal was known to be at least 12 years old (Mills, 1981).

ECOLOGY. The brown hyaena is predominantly a scavenger of all kinds of vertebrate remains, supplementing its diet with wild fruits, insects, eggs of birds, and the occasional small animal that it kills. In the southern Kalahari, the more common ungulates (gemsbok, wildebeest, hartebeest, springbok, and steenbok), springhare, bat-eared fox, and black-backed jackal are the most commonly eaten mammals. They, together with wild fruits such as the tsama melon (*Citrullus lanatus*) and gemsbok cucumber (*Acanthosicyos naudianus*), and Coleoptera and Isoptera, make up the bulk of the diet of the brown hyaena (Mills and Mills, 1978). Vertebrate prey killed by brown hyaenas contributed only 4.2% of the food items directly observed to be eaten, and comprised small mammals (springhare, springbok lamb, bat-eared fox, striped polecat) and ground nesting birds (mainly korhaan species) (Mills 1978*b*). The average daily rate of consumption of two lactating brown hyaenas was calculated as 2.8 kg (Mills, 1977). In the central Kalahari, the diet is similar to that in the southern Kalahari, except that giraffe occur there and are also sometimes scavenged by brown hyaenas (Owens and Owens, 1978). Along the west coast of southern Africa, the brown hyaena is reported to subsist on marine animals such as crabs, fish, birds, and mammals which have been cast up on the seashore (Roberts, 1954; Shaughnessy, pers. comm.; Shortridge, 1934). In several agricultural areas of the Transvaal, Republic of South Africa, cattle (as carrion) and medium-sized and small indigenous animals were found to be most commonly eaten (Skinner, 1976). Mills (1978*b*) showed that brown hyaenas were inefficient hunters. All hunting was orientated towards small animals. Of 88 observed attempts at hunting mammals, only five were successful. The success rate for hunting birds was higher, with five of 16 observed attempts being successful. Available evidence suggests that killing of domestic stock is usually confined to certain individual hyaenas and that once the culprit has been removed the problem is alleviated (Skinner, 1976).

Brown hyaenas do not require surface water, although they will drink when it is available (Mills, 1977). The tsama melon and gemsbok cucumber, which comprise over 90% water, are important sources of water for them (Mills and Mills, 1978). They conserve water by being nocturnal, selecting the coolest place to rest during the day at the hottest time of the year, and by kicking cool sand with their hindfeet onto their bellies. Furthermore, the thin coat in summer, which, when a breeze is blowing provides good ventilation, is adaptive in this regard (Mills, 1977).

Home-range sizes vary under different conditions depending on the distribution of the food (Mills, 1981). In different parts of the southern Kalahari, home-range sizes varied from approximately 235 km^2 to 480 km^2 (Mills, 1976, 1981). Each home range was shared by a varying number of mainly closely-related individuals. The number of individuals sharing a home range ranged from a single adult female and her cubs to nine adults and subadults plus cubs (Mills, 1978*a*, 1982). In the central Kalahari, Owens and Owens (1978) studied a group of nine individuals. The number of animals inhabiting the home range was dependent on the quality of food in the area (Mills, 1981).

In the southern Kalahari, the home ranges of neighboring groups overlapped little (Mills, 1976, 1981), members of neighboring groups were often aggressive toward one another (Mills, 1978*a*, 1981), and home ranges were scent-marked (Mills et al., 1980). Their home ranges can therefore be regarded as territories. Apart from hyaenas living in groups, the population of the southern Kalahari contained a number of dispersing subadults and a number of adult males which were nomadic, not belonging to any group for any length of time (Mills, in press).

Over much of their range, brown hyaenas live in association with other large carnivores and benefit from their presence by scavenging from their kills. Brown hyaenas are dominated by lions and spotted hyaenas and are sometimes killed by them (Mills, 1981). They are usually dominant to leopards, cheetahs, caracals, and black-backed jackals. Competition for food between brown hyaenas and black-backed jackals can at times be severe (Mills, 1977, 1978*b*; Owens and Owens, 1978; Shaughnessy, pers. comm.), and vultures too can deprive brown hyaenas of food (Mills, 1977). In areas where spotted hyaenas are present in high densities, brown hyaenas are usually absent or rare (Mills, 1981).

Little information is available on parasites carried by brown hyaenas. Of ectoparasites, Mills (1981) recorded fleas to be most often found on cubs, which sometimes spent long periods grooming themselves. The flea, *Echidnophada larina*, was identified from a brown hyaena (Peek, pers. comm.). Ticks (Acarina) are rarely found on brown hyaenas in the southern Kalahari. The most commonly found ectoparasite observed on adults was an as yet unidentified species of biting fly (Hippoboscidae). Twice, small patches of sarcoptic mange were observed on animals, but these soon cleared up. Internal parasites recorded were a tapeworm, *Taenia hyaenae*, and a nematode, *Spirocerca lupi* (Mills, 1981). A brown hyaena which died in captivity had nymphs of *Armillifer armillatus*, a wide-ranging pentastomid, and had developed a cataract in one eye (Greve and Russel, 1974). A 2-week-old cub which died in captivity had underdeveloped lungs with the centers being soft and macerated (Schultz, 1966).

A brown hyaena that was blind in one eye and another whose left hindfoot had been caught in a wire snare causing it to become crippled, survived for many years in the southern Kalahari (pers. observ.).

In undisturbed areas, brown hyaenas show little fear of vehicles and it is possible to follow them in a vehicle in open habitat. Radio transmitters and beta lights (sealed glass capsules which emit a green glow) attached to hyaenas greatly facilitated observations at night (Mills, 1978*b*; Mills and Mills, 1978). Capture by means of a baited drop-door trap (Mills, 1977) and drugging of free-ranging animals (Mills, 1977, 1981) with projectile syringes were successful in undisturbed populations. In agricultural areas, capture was accomplished by putting out drugged carcasses (Skinner, 1976). A dosage of 10 to 20 mg/kg of ketamine hydrochloride or 0.7 mg/kg of phencyclidine hydrochloride, both administered together with 0.5 mg of a suitable tranquilizer such as Combellem, injected intramuscularly, are suitable to anesthetize brown hyaenas (Mills, 1977). Food habits have been studied by direct observations, fecal analysis, and the collection of food items from dens.

BEHAVIOR. Brown hyaenas are almost exclusively nocturnal. In the southern Kalahari they were active 42.6% of the 24-hour period and covered an average of 32 km (2 to 54 km) per night in their search for food (Mills, 1978*b*). They forage alone, although several may come together at a carcass (Mills, 1978*a*, 1981; Owens and Owens, 1978). When a brown hyaena finds a large amount of food, the excess is often stored, typically under a bush or in a clump of grass (Mills, 1978*b*).

The members of a social group do not cooperate in foraging, although they do in feeding young (Mills, 1982). Overt defense of the territory is shared by all members of the group and involves neck-biting (Owens and Owen, 1978, 1979*b*), normally only between members of the same sex from neighboring groups (Mills, 1978*a*, 1981).

Greeting between two brown hyaenas involves mutual sniffing at the head, neck, back, and anus (Mills, 1978*a*). One of the participants often presents its anal region to the other by cutting in front of it on its carpals; concurrently, its lips are drawn back ("grinning") and its ears are flattened out sideways (Mills, 1981; Owens and Owens, 1978). When hyaenas of different ages meet, the younger animal invariably displays to the older one (Mills, 1981). Apart from this, no suggestion of a dominance hierarchy was found between members of a social group intensively studied in the southern Kalahari (Mills, 1981), although Owens and Owens (1978, 1979*b*) alleged that a stable rank order between group members existed in the central Kalahari and that this was maintained by ritualized fighting.

When several hyaenas collect at a large carcass, they typi-

cally feed in turn; often each individual breaks off a piece which it carries off for consumption away from the carcass (Mills, 1978*b*, 1981; Owens and Owens, 1978). Muzzle-wrestling (Owens and Owens, 1978), which involves mutual neck and jowl biting, is common between members of a group, particularly cubs and subadults (Fig. 1) (Mills, 1981).

In the southern Kalahari, the task of finding a mate falls to the far-ranging, nomadic males (Mills, 1982). During the initial stages of courtship there is a period of approach-avoidance behavior between the male and female, the duration of which has not been established (Mills, 1981). Mating takes the form of numerous short mountings by the male (Mills, 1982; Yost, 1980). Estrous lasts several days, but the female is not accompanied by a male all the time, and it is possible that more than one male may mate with a female during any one estrous period (Mills, 1982).

The young are raised in a den, which is usually a single hole in the ground. This opens into a narrow, oval-shaped tunnel approximately 30 cm high and 50 cm wide, which is only large enough for the cubs to move through. This tunnel in turn opens into a larger chamber (Mills, 1981). In some areas caves are used as maternal dens (Skinner, 1976). Brown hyaena dens are characterized by accumulations of bones in and around them (Mills and Mills, 1977; Owens and Owens, 1979*a*; Stevenson-Hamilton, 1947). In the southern Kalahari brown hyaena cubs use several dens during the course of their development. Reasons for moving dens included the den caving in, a build up of ectoparasites at the den, and disturbance by man; in most cases no obvious reason could be found for moving. It is unusual for the same den to be used more than once, although females often choose the same area in which to den over a number of years (Mills, 1981). Normally only one litter of cubs is raised at a den, although communal denning has been recorded (Mills, 1978*a*, 1981; Owens and Owens, 1979*a*).

The most striking visual display of a brown hyaena is extensive pilo-erection along the neck, back, and tail (Mills, 1978*a*). This is a threat posture, either aggressive or defensive. An aggressive or confident hyaena stands erect with its head held up, accentuating the white ruff, its ears cocked, its mouth closed, and often with its tail curled over its back. The defensive posture is characterized by the body being held low, the ears flattened backwards, and the mouth open wide. Tactile communication through occasional grooming has also been observed (Mills, 1981; Owens and Owens, 1979*a*).

The brown hyaena is generally silent. It has a relatively simple vocal repertoire and no long-distance call. Vocalizations are graded. Owens and Owens (1978) recognized five distinct vocalizations. On the basis of spectrographic analysis, Mills (1981) recognized four categories: a yell, a hoot, and an assortment of whines and growls. The loudest sound it makes is a high-pitched yell, which has a fundamental frequency around 1.0 kHz; most of the energy lies under 2.2 kHz and overtones typically rise and fall at frequencies up to 4kHz (Mills, 1981).

Scent marking is accomplished by defecating at latrines (Mills, 1973, 1981) and pasting (Mills et al., 1980). In the southern Kalahari, brown hyaenas pasted on average 2.6 times per km. The pasting frequency was highest around territorial boundaries, but most pastings were deposited in the internal part of the territory where the hyaenas spent most of their time. Both chemical and behavoral evidence for brown hyaenas producing pastes with individual smells was found. Mills et al. (1980) concluded that pasting served to inform other group members of movements as well as to inform outsiders that a territory was occupied.

GENETICS. The diploid chromosomes number is 40; there are 70 autosomal arms. The X chromosome is submetacentric and the Y chromosome is acrocentric (Wurster, 1973).

REMARKS. The brown hyaena is listed in the Red Data Book of the International Union for the Conservation of Nature and Natural Resources, where its status as an endangered species is given as vulnerable. Its quiet and retiring nature makes it difficult to observe and it is probably more common than usually believed.

One of the Afrikaans and German names for the brown hyaena is "strandwolf" meaning beach wolf, which is testimony to its habit of foraging along the coast. Another German name is "Schabrackenhyaene" which refers to the long fur of this species (Rieger, pers. comm.).

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