

SOCIAL BEHAVIOR OF THE MANED WOLF (*CHRYSOCYON
BRACHYURUS*) AND BUSH DOG (*SPEOTHOS VENATICUS*):
A STUDY IN CONTRAST

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ABSTRACT.—Social behavior of the maned wolf, *Chrysocyon brachyurus*, and bush dog, *Speothos venaticus*, was compared. Differences in communication mechanisms between these two South American canids could be correlated with their social organization and ecology. *Chrysocyon*, inhabiting the savannahs of South America and feeding primarily on small vertebrates, invertebrates, and fruit, exhibits a dispersed social system, that is, it is essentially solitary in habit. The maned wolf relies primarily on signals that carry well over long distances and tend to promote the spacing of individuals through avoidance (for example, the bark), a conspicuous visual threat display, and locus-specific defecation. By contrast, *Speothos* is a cooperative hunter of the Neotropical rainforest, feeding mainly on rodents that are large relative to its own size. It is social and mainly employs short-distance signals, which promote approach behavior (tail-wagging), reduce intraspecific aggression (displays of active submission), and allow the maintenance of constant contact in the forest (the squeak vocalization). Quantitative observations on urine-marking suggest that the frequency of marking in *Chrysocyon* is partly dependent on the amount of available space, whereas in *Speothos*, marking may be influenced by social factors.

The maned wolf (*Chrysocyon brachyurus*) and the bush dog (*Speothos venaticus*) of South America are two of the rarest and least well known members of the Canidae. The external morphology of the two species is dramatically different. The bush dog is short-legged and stocky, with a short tail, small and rounded ears, and a thick muzzle. The short thin pelage is dark brown, the neck and hackles being more golden in hue. Unlike most canid species there is reverse coloration, the undersides being darker than the dorsum, and there are no distinctive body markings. By contrast, the maned wolf is thin and long-legged, with large pointed ears and a long tail. The thick long pelage is bright, reddish brown, with the inner ear, throat and tail being white, and the mane, muzzle, and limbs being black.

In addition to these striking external differences, there are other anatomical features distinguishing the two species. The maned wolf, like most members of the Canidae, has 42 teeth, whereas the bush dog, in common only with the Cape hunting dog (*Lycan pictus*) and dhole (*Cuon* sp.), has a smaller number of teeth due to a reduction of the last molars. The similarities in the dentition of *Speothos*, *Lycan*, and *Cuon* resulted in their being assigned to a separate subfamily of the Canidae, the Simocyoninae. In a recent study (Langguth, 1969), *Speothos* was considered a true member of the Caninae (containing the majority of dogs and foxes), and it was suggested that *Chrysocyon* and *Speothos* belong to two different lineages within the South American Canidae, a group which has undergone extensive adaptive radiation. Presumably, the

similarities in the dentition of *Speothos*, *Lycan*, and *Cuon* are due to convergence, because these three species, in contrast with most of the Canidae, subsist almost entirely on flesh.

A comparison of the ecology of *Speothos* and *Chrysocyon* in part explains the striking differences in the external morphology. Bush dogs inhabit the tropical forests of Central and South America where they hunt in packs and feed on large rodents (for example, the paca, *Cuniculus paca*, and the agouti, *Dasyprocta* sp.), birds, and other small prey. They are said to be excellent swimmers (Bates, 1944) and to live along river banks; thus, they may feed also on aquatic vertebrates and invertebrates. Presumably their short legs are an adaptation for moving through thick undergrowth and their stocky frames and thick necks allow them to tackle prey that are large relative to their own size. By contrast, the maned wolf inhabits savannahs, with mixed open forest and swamp areas. Its long legs have been considered an adaptation for seeing over long grass (Krieg, 1940). The prey species, in terms of absolute size, are smaller than those of the bush dog (for example, rodents such as guinea pigs, *Cavia*). The maned wolf also feeds on small reptiles and amphibians, insects, eggs, fruits, and roots (Da Silveira, 1968; Krieg, 1940). Thus, it is probably more omnivorous than *Speothos*. It is solitary in habit and rarely seen in the wild. Despite its long legs, the maned wolf is not a fast runner and does not pursue prey over long distances; instead, it will stalk and pounce much like a fox (Krieg, 1940).

Chrysocyon and *Speothos* present an interesting contrast, both in morphology and ecology. This study attempts to illuminate the degree to which these animals differ in their behavior, especially social behavior.

ANIMALS AND METHODS

The observations on which this paper is based were mainly conducted at the Zoological Society of London from 1964 to 1966 where there were four bush dogs (three males, one female) and three maned wolves (two males, one female). For the bush dog, data were recorded on the behavior of a male-female pair, a male-male pair, and a trio consisting of two males and a single female. Maned wolves were kept singly for part of the study period but a male-male and a male-female pair were later observed. In both species, encounters between both familiar and unfamiliar animals were staged when possible. Since the London study, further observations have also been made on the behavior of *Speothos* and *Chrysocyon* at other zoos.

RESULTS

General Behavior in Captivity

In captivity both *Speothos* and *Chrysocyon* are typically fed on small rodents, birds, and lagomorphs, as well as chunks of horsemeat. *Chrysocyon* is usually given fruits, eggs, and insects as an addition to its diet (Encke *et al.*, 1970; Faust and Scherpner, 1967; Da Silveira, 1968). Both species will kill and eat live prey; for example, *Speothos* has killed live pigeons, chicks, rats, and mice in captivity (Kitchener, 1971). The predatory patterns of both species are

similar. As soon as the prey is grabbed in the mouth (a neck or head bite is typical), there is a rapid low amplitude lateral head-shaking, which usually either immobilizes or kills the victim immediately. The prey may be dropped to the ground and then picked up and shaken again. *Chrysocyon* often uses its forepaws for striking at or manipulating small prey and may also pounce on a prey object by rearing up and simultaneously dropping both forepaws onto it. Before or after feeding, or both, maned wolves also will rub and roll on their prey, as well as urinate over it. Both *Speothos* and *Chrysocyon* usually eat in seclusion within the den. Fighting over food has never been observed in *Speothos*.

Chrysocyon caches food using the typical canid patterns of digging a hole with alternate scratching of the forefeet, dropping the food into it, and covering the food by sweeping soil or other materials over the hole with the muzzle. *Speothos* has only been observed caching food in water; digging movements of the forepaws as well as pushing the food with the tip of the muzzle were seen. This may indicate that the bush dog, which has been reported to frequent river banks, typically hides food in the water.

Neither *Speothos* nor *Chrysocyon* dug a burrow in captivity, although individuals of both species had specific sleeping sites and individual *Speothos* did dig extensively in their enclosures. There are reports of *Speothos* using burrows in the wild for shelter (Goldman, 1920) and of a captive female digging a burrow (Bates, 1944). It is not known whether the maned wolf ever digs a burrow in the wild, or instead uses the abandoned burrows of other species. However, the long legs of *Chrysocyon* would make maneuvering within a burrow difficult.

Chrysocyon appears to be crepuscular in habit. Individuals tend to sleep during midday and to be active at dawn, dusk, and during the night. One of the main vocalizations, the bark (to be discussed below), is heard primarily after dusk (see also Encke *et al.*, 1970). The bush dog, however, is active during the day but retires to its den after dark. These differences in activity rhythms, although possibly reflecting the natural tendencies of the two species, may result from their responses to humans. The maned wolf tends to be much more timid and fearful in the presence of humans than does the bush dog, and thus may restrict its active period to those hours when there are few people about.

Chrysocyon has an annual cycle of estrus followed by a gestation period of 60 to 65 days. In South America, births occur from June to August (Da Silveira, 1968); however, in the Northern Hemisphere most births have been recorded in the months of January and February (Faust and Scherpner, 1967; Encke, 1971). Bush dogs have bred only rarely in captivity, and there is evidence that they may be unique among wild canids in having two estrous cycles per year (Kleiman, 1968). In the Northern Hemisphere, births have occurred in December and February (Kitchener, 1971; 112th Report of the Frankfurt Zoological Gardens, 1970).

The gestation period of the bush dog is not known. Crandall (1964) reported a gestation period of 65 days, but Kitchener (1971) suggested that gestation exceeded 80 days.

The *Speothos* female shows dramatic changes in behavior and morphology as she comes into estrus. Both Kitchener (1971) and I have recorded the swelling of the vulva before and during heat, and there is a great increase in the frequency of urine marking. The male and female sniff and lick each other's urine, and both sexes exhibit a characteristic flehman-like response to urine testing. The mouth is opened, the lips are horizontally retracted, and there is quivering of the upper and lower jaw. The tongue may be rapidly moved in and out of the mouth. A similar response was observed in *Chrysocyon*, but not during an estrous period.

The lordosis posture of *Speothos* resembles that of a cat and may be assumed by a female when she is not being mounted.

During estrus, *Chrysocyon* females also show a swelling of the vulva, and they exhibit increased activity, such as rubbing against the male, running around the enclosure, and dropping down on their forelegs in front of the male (Da Silveira, 1968). Reports of copulation indicate some similarities in the two species that differ from the remainder of the Canidae. Da Silveira (1968) reported that maned wolves have a 10 to 12 minute tie during copulation; Scherpner (personal communication) agrees but observed that they do not assume the back-to-back position. Kleiman (1968) observed a similar form of mating in the bush dog, but Kitchener (1971) never observed a copulatory lock. He did not, however, indicate the length of the copulations that he observed.

Most zoos have had little success in rearing the young of *Speothos* and *Chrysocyon* except when a litter is removed from the mother and hand-raised. Thus, there are few descriptions of the maternal behavior of these two species; however, Encke (1971) reported that a maned wolf mother became extremely aggressive after giving birth, spending most of her time in a den with the young. In the bush dog, it has been suggested that the presence of the male is necessary for the female to exhibit the appropriate maternal responses (112th Report of the Frankfurt Zoological Garden, 1970). Some observations on the growth of the maned wolf can be found in Encke (1971) and of the bush dog in Kitchener (1971).

Social Behavior

The bush dog appears to be a highly social species. In captivity, *Speothos* can be easily maintained in pairs of the opposite or same sex without fighting. The trio of two males and a female in the London Zoo lived together amicably for months as did a pair of males. In the pair of males, one individual was dominant over the other, but threat behavior was only seen when the female was in estrus. At other times, status was mainly determined by the submissive behavior of the subordinate animal. In the two males (before the introduction

of the female), play, consisting of mounting as well as nipping the legs and hind quarters, was observed, with the submissive male always initiating the encounter. Introductions of two unfamiliar *Speothos* males resulted in a fight, but no fighting occurred if an unfamiliar female was introduced to a male. Apparently the sociality of bush dogs is developed to the point that the male is necessary for the successful rearing of the young (see above).

The maned wolf, on the other hand, shows less social tolerance. A male-female pair can be compatible, except when a female is rearing a litter; but two males or two females may be difficult to maintain in the same quarters without fights breaking out (Da Silveira, 1968). During the first few introductions of the London male and female, both animals were aggressive and fought.

The differences in social tolerance in the two species is also evident from the amount of body contact seen between individuals; for example, bush dogs usually will sleep compatibly in the same den together whereas separate dens are necessary for a pair of maned wolves. In both species, dominant-subordinate relationships develop among individuals of the same sex that are housed together.

As mentioned above, maned wolves show less tendency to maintain body contact with a conspecific than do bush dogs. During investigation of a conspecific, however, an interchange of tactile information occurs in individuals of both species. During sniffing of the ano-genital region, bush dogs and maned wolves make contact with the tail and genital area, and during sniffing of the facial region, the cheeks, muzzle, and ear often are touched. Social grooming, as a means of tactile communication, occurs rarely in members of either species, although other members of the Canidae, for example, the bat-eared fox (*Otocyon megalotis*) and the raccoon dog (*Nyctereutes procyonoides*) often engage in social grooming (Kleiman, 1967).

Three main vocalizations have been heard in maned wolves. The first is a deep-throated single bark, heard mainly after dusk, and often produced in alternation by individuals. During a bout of barking, 20 to 30 barks with an interval of 5 to 8 seconds between each one would occur. The bark appears to be a long-distance contact call that in the wild may aid in spacing individuals, somewhat like the roar of the big cats. The second vocalization is a whine, of variable intensity, heard from submissive individuals. Some members of a partly tame litter at the Los Angeles Zoo produced a high-pitched, intense whine while lying in the submissive posture during interactions with familiar persons. The third maned wolf vocalization is a growl heard during food defense and occasionally accompanying the visual threat display during an agonistic encounter.

Four vocalizations have been heard from the bush dog; one a high-pitched squeak, heard commonly, and the other three, a loud drawn-out shriek or scream, a buzzing guttural growl, and a squeal, heard rarely. The high-pitched squeak, which is produced repetitively by individuals during regular patrolling

of their quarters and which does not carry well over long distances, appears to be a close-contact call serving to establish the relative position of pack members within the forest undergrowth. The buzzing growl was heard from the dominant male while he consorted with the receptive female. This threat was directed to the subordinate animal. The intense shriek or scream of the bush dog was only heard during and after a fight. The function of this vocalization is unclear, but it may act as a threat, if the outcome of an agonistic encounter between two individuals is not yet established. The squeal was heard from the subordinate male when threatened; Bates (1944) also described this vocalization for a tame *Speothos* during play with humans.

As in other canids, olfactory communication plays an important role in the social interactions of *Chrysocyon* and *Speothos*. There are both close-contact and long distance means of communication. During close-contact interactions, primary attention is paid to the ano-genital region; in the maned wolf (but rarely in the bush dog) the dorsal surface of the tail near the base also may be investigated if the tail covers the anus. In many canids, this area contains a gland (see Hildebrand, 1952), but, no glands were found in the specimens of *Chrysocyon* and *Speothos* that I examined. The absence of a caudal gland in these two species is unexpected, especially considering that *Chrysocyon* does investigate the area where the gland usually is located. Both species have paired anal glands.

The other main area of olfactory interest is the face, but both *Speothos* and *Chrysocyon* pay less attention to sniffing the ear and muzzle region than the ano-genital area.

In both species, scent marking with urine is an important means of communication. The scent-marking patterns already have been described (Kleiman, 1966), but will be briefly reviewed with some additional observations. Male maned wolves and bush dogs both cock a leg for urinating on vertical objects, and in both species this pattern occurs throughout the annual cycle. Certain objects in the environment are marked with urine regularly, that is, an individual may return to specific sites again and again. In the bush dog, all adult males of whatever status show leg-lifting; this differs from the wolf (*Canis lupus*) where, at least in captivity, the dominant male is often the only male to exhibit leg-lifting (unpublished observations). The urination pattern of the male bush dog is unique among the canids because the penis is slightly extruded, and there is a rapid lateral movement; the urine is emitted as a spray instead of a stream. *Chrysocyon* males, as well as showing leg-lifting, will urinate directly on the ground with the limbs slightly spread, often digging a hole before they do so. Food or feces are often marked with urine. *Speothos* males have never been observed to urinate using a standing posture.

Some quantitative data on frequency of urine-marking in two *Chrysocyon* males are shown in Table 1. Initially, the two males lived together, but they were eventually separated when the older male needed veterinary treatment. In mid-January 1965, they were reintroduced, but fought. The older male (male

TABLE 1.—Mean frequency of urine-marking for a 30-minute period by two *Chrysocyon brachyurus* males in adjacent enclosures (A) and during introductions (B).

Month	Mean frequency of marking		
	Male 1	Male 2	No. of 30-minute periods
(A) January 1965	10.6	7.1	N = 11
February 1965	7.1	7.4	N = 14
March 1965	5.5	9.0	N = 14
April 1965	5.5	11.3	N = 4
Average	7.3	8.2	N = 43
(B) May 1965	14.2	1.1	N = 10

1) was clearly dominant. The data in Table 1 were collected during the 5 months following this encounter. Male 1 exhibited an initially high level of urine-marking, but during the following months, there was a reversal, with male 2 eventually showing higher levels of marking than male 1.

During the encounters in May, male 1 was again dominant, and his marking level increased dramatically. This was partly a result of male 2 remaining inactive in his den during the introductions, thus giving male 1 free access to both enclosures. However, during the May encounter series, male 2 was occasionally given access to both enclosures in the absence of the dominant male, and his marking frequency averaged 14 to 15 for a 30-minute period.

By considering the marking behavior of male 2 when alone in both enclosures and the data in Table 1, it can be seen that the total marking frequency for the two males (for each condition) ranged between 14 and 18 per 30-minute period. This implies that the frequency of marking in the maned wolf is dependent on the amount of space available to the individual and, not necessarily, social status. Of course, one would expect that home range size in the wild would itself be dependent on social status.

Some quantitative data on the marking frequencies of the two *Speothos* males that lived together also was collected. During nine 30-minute observation periods (October 1964 to March 1965), male 1 averaged 2.1 urine marks and male 2 averaged 3.0. Male 1 was dominant. However, during the first 30 minutes of an encounter after a 4-day separation period, the males marked 11 and 12 times, respectively.

A third male, which was housed with a female for several months, varied in marking frequency. When he and the female were introduced to a new cage, he urine-marked 12 times in an hour or once every 5 minutes. On two occasions when the feces of a strange male were presented to him, he averaged one mark per minute for the observation period (15 and 7 minutes). During the female's period of estrus, the male marked approximately once every 3 minutes.

Although the data are less complete than for the maned wolf, they do suggest that subordinate *Speothos* males are not inhibited in their marking behavior, but marking frequency is somewhat dependent on social factors.

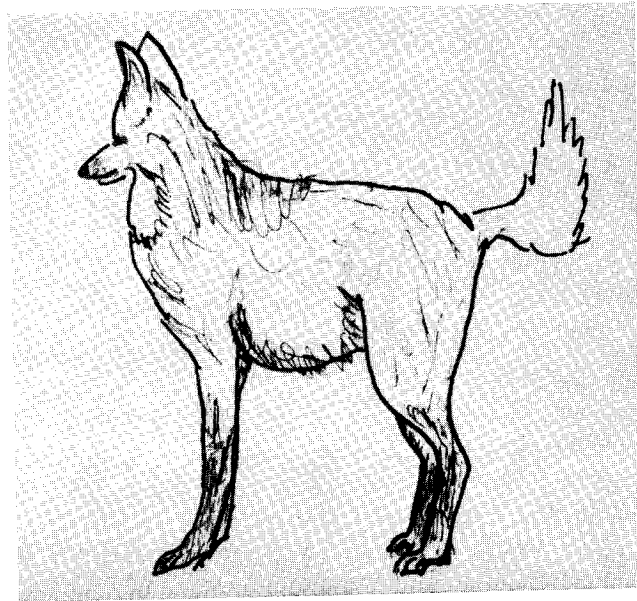


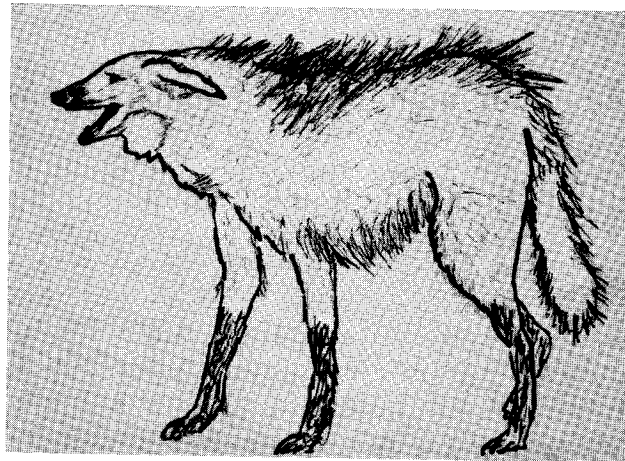
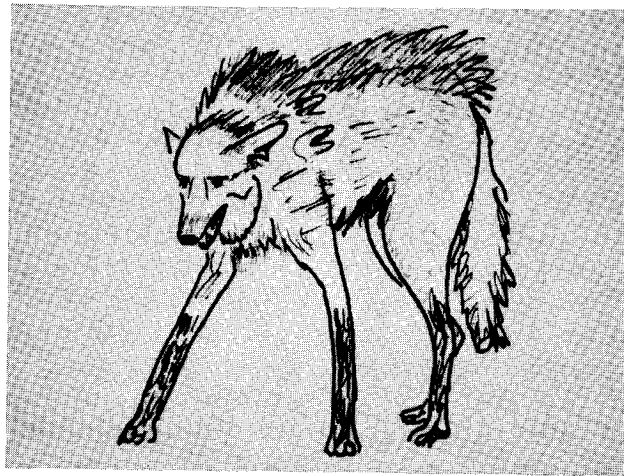
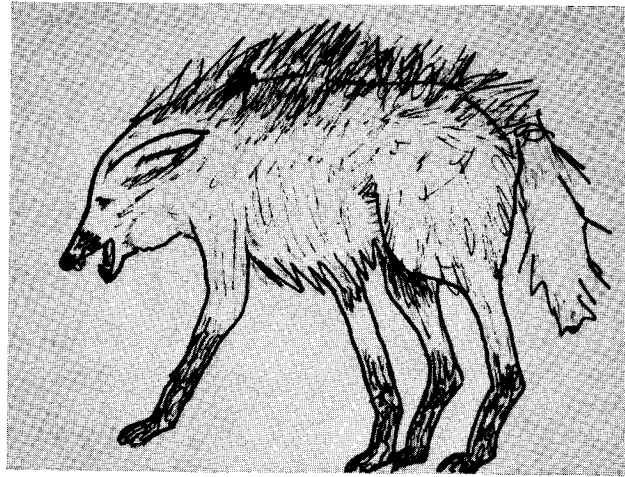
FIG. 1.—A confident *Chrysocyon* greeting a conspecific.

In the females of the two species, the typical urine marking pattern is different although the orientation of the mark is similar. The maned wolf female will approach a vertical object, turn away from it, avert the tail to one side, raise a hind leg vertically off the ground, and urinate while almost touching the object with the ano-genital region. Although the bush dog female was seen employing a similar posture once (she urinated onto some feces using a vertical leg lift), typically she climbs up backward onto a hand-stand posture to urinate, then drags the ano-genital region along the surface as she slides down. The main postures employed by *Speothos* and *Chrysocyon*, although different in performance, are undoubtedly related as both begin with a similar backward orientation. The urination pattern of the bush dog female may have evolved as a means of raising the site of the scent to a level where it can be detected more easily by other individuals. However, the urine of the male bush dog is typically deposited at least 6 inches below that of the female.

Although no data are available for the maned wolf, the bush dog female shows a dramatic increase in marking frequency during the proestrous and estrous period. The female specifically urinates on all sites previously marked by males and may even climb into the hand-stand posture and push a male

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FIG. 2.—The threat display of *Chrysocyon*: (top) from a lateral position; (center) from a frontal position; (bottom) a defensive threat display. Note that the line of the muzzle is nearly parallel with the back.



away while the latter is sniffing or marking a post. The frequency of urine marking was approximately 5 per 30-minute period when the receptive female was housed with one male, but during the first hour after her introduction to the pair of males, she marked 81 times. It was not clear whether she urinated every time she moved into the hand-stand posture.

Neither species has a special posture for defecating, but there is one important difference in the defecation patterns of *Chrysocyon* and *Speothos*. Bush dogs deposit their feces anywhere in their environment, whereas maned wolves defecate only at specific sites and then often urinate over the feces pile. The maintenance of specific sites for the deposition of feces in the maned wolf may be related to their dispersed social system; more olfactory information can be provided for conspecifics if the feces are localized rather than scattered throughout the home range.

Another behavior pattern that plays a part in olfactory communication is rubbing the side of the body and rolling onto the back, a typical canid behavior. *Speothos* occasionally rubbed the chin, throat, cheeks, and neck on the ground after a bout of feeding and dragged the ano-genital region along the ground after defecating, but was never seen rubbing its side along an object or rolling onto its back. The maned wolf exhibits rubbing of the side of the body and the neck against vertical objects as well as objects on the ground with a conspicuous odor, such as meat. It also often rubs its whole side along vertical posts with previous urine marks; this may not only cover the urine with extra body odor, but also may cover the maned wolf with its own urine scent.

Because of the nature of its size and the presence of striking body markings, postures and movements in the maned wolf are much more conspicuous than in the bush dog. Thus, like its bark vocalization, *Chrysocyon* visual displays are probably perceived over greater distances than would be the same display in *Speothos*. In fact, *Chrysocyon* tends to assume and maintain a threat posture at a greater distance than does *Speothos*, even in conditions of captivity where space is limited.

In the maned wolf, a self-confident individual will greet a conspecific by standing erect with the head nearly perpendicular to the back, thus exposing the white throat patch (Fig. 1). The ears are erect and the openings directed toward the partner; the tail may be raised vertically to a J-position. The mouth is closed, and the mouth corners shortened. A self-assured bush dog exhibits a similar posture, although the size of the ears and tail (the tail is held slightly above the horizontal line of the back) reduce the effectiveness of the display (at least for the human observer). A self-confident individual moves slowly, and in both species there is a jerky stilted quality to the movement.

There is little visible difference in the dominance and threat postures of *Speothos* except for pilo-erection of the tail, an opening of the mouth, and the production of the buzzing growl. *Chrysocyon*, on the other hand, exhibits a distinct visual threat posture while positioned in front of or lateral to a conspecific. The head is lowered with the ears flattened back against the head,

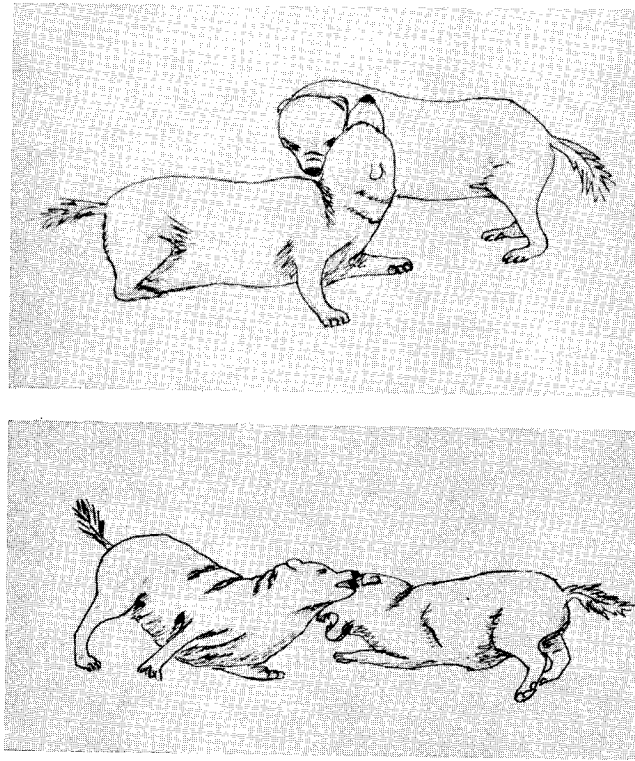


FIG. 3.—Neck-oriented fighting in *Speothos*: (top) both animals have a grip; (bottom) one animal has a grip.

thus exposing the white fur of the inner ear. There is extensive pilo-erection of the back, tail, and throat patch, which emphasizes the blackness of the mane and the whiteness of the tail and throat patch. The tail may be held down, but it is not tucked between the legs. In this posture, the maned wolf will stand or move slowly, often maintaining a distance of about 4 to 8 feet between itself and its opponent (Fig. 2, top and center). The mouth is usually closed. When more highly aroused, the maned wolf will thrust forward toward its opponent with the mouth open in a gape. The forward thrusting may then alternate with the lateral display, with little or no body contact occurring for much of the agonistic encounter. More defensive individuals raise the head so that the muzzle is held parallel with the back instead of directed downward. The mouth corners are pulled back during the gape (Fig. 2, bottom). If a full fight breaks out, bites usually occur at the throat, neck, and on the back; head-shaking occurs as soon as there is a successful bite.

By contrast, *Speothos* exhibits no prolonged visual threat display before an attack and the fighting posture consists of attempts by both individuals to obtain and maintain a good hold on the throat or neck of the opponent. At

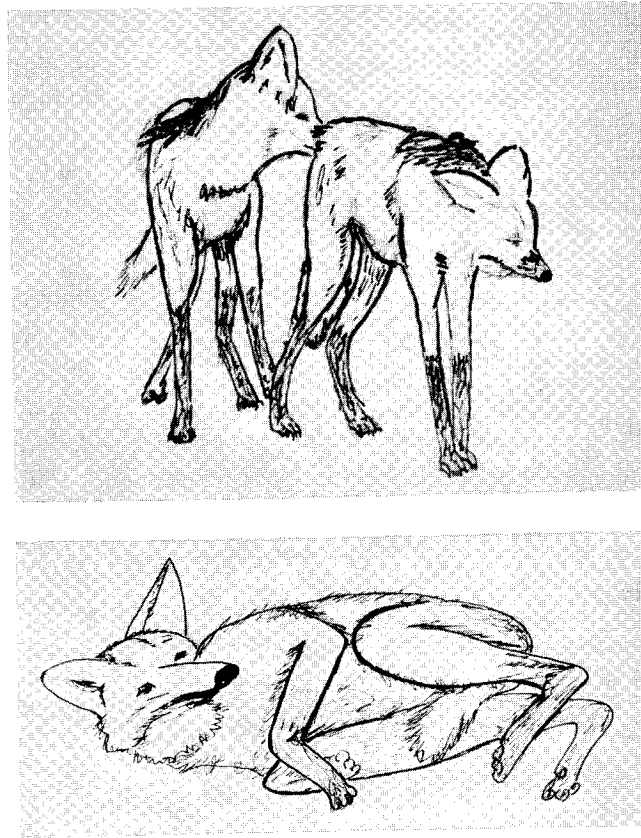


FIG. 4.—Submission in *Chrysocyon*: (top) low intensity submission; (bottom) the recumbent submissive posture.

the initiation of a fight, bush dogs use a frontal or lateral approach as does the maned wolf. The neck bite is typically combined with vigorous lateral head-shaking movements, which resemble the head-shaking observed during the capture of small prey. Both individuals can and do maintain a neck grip simultaneously (Fig. 3). Despite the continued neck biting that occurs during a *Speothos* fight, severe damage does not occur as the neck of the bush dog is extremely thick relative to its size (Hildebrand, 1954). This is certainly in contrast with *Chrysocyon* fights where serious wounding easily occurs.

Maned wolves possess postures of subordination that vary according to the level of arousal of the individual during an encounter. Animals exhibiting subordination to a superior may lower the head and tail, spread the ears so that the openings are pointed downward, and occasionally tuck the tail between the legs or around the side of the body. The mouth corners are pulled back into the submissive grin and the animal stands immobile (Fig. 4, top). Tail wagging occasionally occurs and resembles the high amplitude tail lashing seen in other

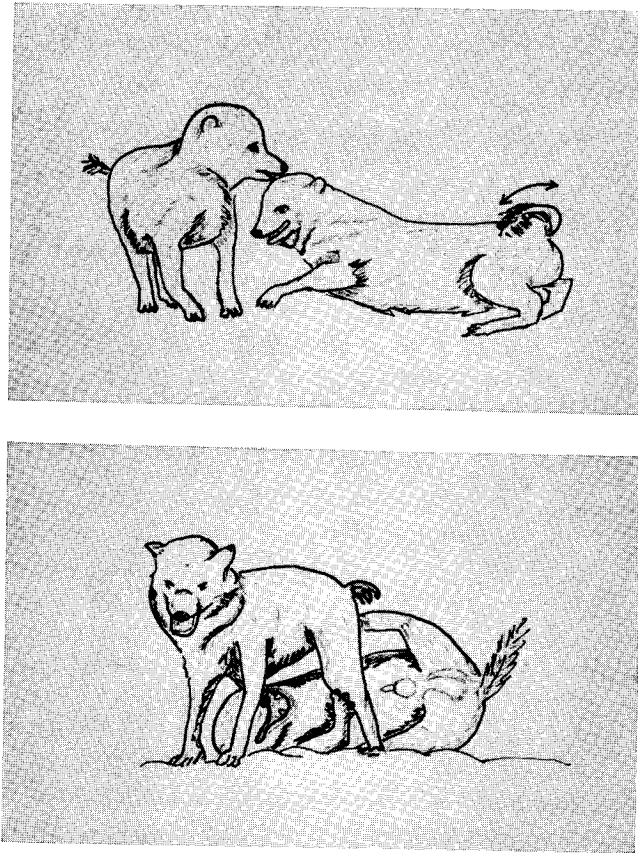


FIG. 5.—Submission in *Speothos*: (top) low intensity submission, the tail is lowered and wagging; (bottom) the recumbent submissive posture, also with tail wagging. Note the posture of the dominant animal.

long-tailed canids, for example, the red fox, *Vulpes*. More highly aroused individuals may lie down on the side or back in response to the dominant animal. Several tame maned wolves observed at the Los Angeles Zoo combined this immobile submissive posture with a high intensity whine in response to humans (Fig. 4, bottom).

Speothos also has a highly stereotyped submissive posture, which (to the human observer) is much more conspicuous than their postures of dominance and threat. Low ranking animals will approach a dominant with a lowering of the body, a spreading and then flattening of the ears against the head, and vigorous tail wagging (Fig. 5, top). The mouth corners are pulled tightly back and the molars exposed in an exaggerated form of the submissive grin. At times, a bush dog also will turn over onto its side or back. In this position, it does not assume immobility as do many other canids (for example, *Chrysocyon*) when in a submissive posture, but will rapidly tail-wag and writhe on the

ground with the dominant animal standing over it (Fig. 5, bottom). In its tendency to seek out the dominant actively and assume a submissive posture, it resembles Schenkel's (1967) descriptions of *Canis lupus*.

DISCUSSION

A comparative account of canid social behavior has already been presented elsewhere (Kleiman, 1967) and it appears as though *Chrysocyon* and *Speothos* both possess the main elements of social communication found in other canids. However, there are some special features as well as a few exceptions. In the sphere of olfactory communication, both sexes of *Speothos* possess specialized postures, the male showing the extrusion of the penis and emission of urine in a spray rather than a stream, and the female exhibiting the hand-stand posture.

The vocalizations also show some variations. The production of a short distance contact call during routine activities in *Speothos* appears to be unique among the canids, although many species including the maned wolf and wolf (*Canis lupus*) have long distance contact vocalizations, such as barks and howls.

With respect to visual displays, the vertically raised tail of the self-assured maned wolf differs from the horizontally raised tail seen in other canids during dominance displays; whether the derivation of tail-raising is the same in all canids is unclear. The lack of a conspicuous visual threat display in the bush dog is also notable since most canids do communicate threat through body posture and facial expression; however, the size, shape and hair-length of *Speothos* are undoubtedly a limiting factor. Also, neither *Speothos* nor *Chrysocyon* have been observed using the snarl (exposure of the teeth through vertical retraction of the lips), although it is likely that both species have the musculature to do so. This clearly differentiates them from the genus *Canis* where the snarl is a common feature of threat and aggressive behavior (Kleiman, 1967). In the postures of submission, *Chrysocyon* resembles *Vulpes* more closely than *Canis* in its low frequency of tail-wagging and its tendency to exhibit a passive immobile submissive display. *Speothos*, however, shows a higher frequency of active submission, with approaches to the dominant and vigorous tail-wagging and writhing on the ground. Although both species employ the submissive grin, a universal feature of canid behavior, *Speothos* has evolved an exaggerated form of this display in that the back molars are exposed.

Some comment must be made about the urine-marking behavior of the two species. Ralls (1971) recently has suggested that high frequencies of scent-marking are found primarily in dominant individuals who are aggressively motivated. In fact, based on studies of male hamsters, *Mesocricetus auratus*, and gerbils, *Meriones unguiculatus*, to which she referred, it is suggested that one can determine the status of a male from his marking levels even in the absence of conspecifics. Neither *Speothos* nor *Chrysocyon* conform to this

hypothesis. In the two bush dog males that lived together, marking levels were equivalent, regardless of dominance. The maned wolf males also showed similar frequencies of marking with only tactile communication being prevented. The subordinate maned wolf male was only inhibited in his marking during encounters, when all his activity was inhibited. Thus, marking behavior does not seem to be related to either dominance or aggression in these two canids.

In order to make some sense of the differences one finds in the social behavior of *Speothos* and *Chrysocyon*, it is necessary to reconsider their behavior in light of their ecology, morphology, and probable social organization. Most of the differences in behavior can be explained as specific adaptations to a particular ecological niche. The maned wolf is a large predator that mainly hunts small game in a relatively open region with long grass. Since this species exploits prey of limited size, pack hunting is unnecessary and individuals can exist at a thin density and remain solitary or paired. One would expect their social behavior to emphasize patterns involved in long distance communication, such as we have found—for example, specialized olfactory (locus specific defecation and high levels of urine marking), auditory (the bark), and visual signals (the threat display). By contrast, the bush dog is a small predator feeding on prey that are large relative to its own size. Thus, pack-hunting has evolved as a more efficient method of hunting, and with it, increased sociality. Its communication system is geared to close contact information transfer (for example, the squeak vocalization) with an emphasis on socially positive displays, such as the posture of active submission and tail wagging. Although several authors (for example, Fox, 1969) have emphasized the importance of a pale ventral surface in the canids as an additional sign of submission while an individual is lying on its back, the opposite is true of the bush dog where the ventral surface is darker than the dorsum. The reason for this discrepancy is not apparent.

It is clear from the previous paragraphs that *Speothos* and *Chrysocyon* have both evolved specialized postures and vocalizations for communicating with conspecifics, even though they are at opposite ends of the spectrum of social organization. The differences in social behavior are reflected, not in the numbers (if one attempted to count the total number of social displays, it is unlikely that *Chrysocyon* and *Speothos* would differ by much) or complexity of social displays, but in the types of social displays, the context in which they are used, their frequency and function. Thus, the maned wolf relies on communication mechanisms tending to space individuals or produce avoidance (or both), whereas the bush dog depends on submissive or appeasement displays which reduce intraspecific aggression.

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