

*Speothos venaticus*. By Beatriz de Mello Beisiegel and Gerald L. Zuercher

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***Speothos* Lund, 1839**

- Speothos* Lund, 1839:224. Type species *Speothos pacivorus* Lund, 1839, by monotypy.  
*Cynogale* Lund, 1842:203. Type species *Cynogale venatica* Lund, 1842, by monotypy; preoccupied by *Cynogale* Gray, 1837.  
*Icticyon* Lund, 1842(1843):80. Replacement name for *Cynogale* Lund, 1842.  
*Abathmodon* Lund, 1843:74. Type species not given.  
*Cynalicus* Gray, 1846:293. Type species *Cynalicus melanogaster* Gray, 1846, by monotypy.  
*Cynalius* Gray, 1847:18. Incorrect subsequent spelling of *Cynalicus* Gray, 1846.  
*Melictis* Schinz, 1848:177. Type species *Melictis beskii* Schinz, 1848, by monotypy.  
*Melictes* Gray, 1868:498. Incorrect subsequent spelling of *Melictis* Schinz, 1848.  
*Cynalycus* Gray, 1869:183. Incorrect subsequent spelling of *Cynalicus* Gray, 1846.

**CONTEXT AND CONTENT.** Order Carnivora, suborder Caniformia, family Canidae, subfamily Caninae (Stains 1984). The genus *Speothos* is monotypic. *Speothos* was previously placed in the subfamily Simocyoninae (Simpson 1945) with *Cuon* and *Lycyaon*.

***Speothos venaticus* (Lund, 1842)**

Bush Dog

- Cynogale venatica* Lund, 1842:203. Type locality “Lagoa Santa, Minas Gerais, Brazil.”  
*Icticyon venaticus*: Lund, 1842(1843):80. Name combination.  
*Cynalicus melanogaster* Gray, 1846:293. Type locality “Brazils.”  
*Melictis beskii* Schinz, 1848:177. Type locality “Nova Friburgo, Estado do Rio de Janeiro, Brazil.”  
*Speothos venaticus*: Thomas, 1903:236. First use of current name combination.  
*Speothos wingei* Ihering, 1911:222. Type locality “Estado de Santa Catarina, Colônia Hansa, Brazil.”  
*Icticyon panamensis* Goldman, 1912:14. Type locality “Cerro Pierre, Panama.”

**CONTEXT AND CONTENT.** Context as above. Three subspecies are recognized:

- S. v. panamensis* (Goldman, 1912:14); see above.  
*S. v. venaticus* (Lund, 1842:203); see above; *baskii* (Shinz) and *melanogaster* (Gray) are synonyms.  
*S. v. wingei* Ihering 1911:222; see above.

**DIAGNOSIS.** *Atelocynus microtis* and *Speothos venaticus* overlap geographically in the Amazonian regions of Brazil, Colombia, Ecuador, and Peru. *S. venaticus* is distinguished from *A. microtis* by absence of M3 and absence of metaconid and entoconid on M1 and M2. *S. venaticus* has interdigital webbing and a carnassial ridge that *A. microtis* lacks. *S. venaticus* has shorter legs and tail than *A. microtis* and has paler pelage around head and neck. Head of *S. venaticus* is mustelid like, whereas head of *A. microtis* is fox-like (Vieira 1946).

**GENERAL CHARACTERS.** *Speothos venaticus* (Fig. 1) is a small canid (body mass, 4–7 kg) with short legs and tail, interdental membranes, elongated body, and small rounded ears (Vieira 1946). Color ranges from uniform dark brown to yellowish red, with lighter color on neck, nape of neck, and ears (Sheldon 1992) and darker color on limbs, tail, and ventrum (Coimbra-Filho 1972). Young animals are uniformly black (Darling and Whitehead 1991).

Bush dogs lack facial markings. Skull is short (Fig. 2; Vieira 1946). *S. v. panamensis* is smaller than *S. v. venaticus* and *S. v. wingei*, which are similar in size (Linares 1967). *S. v. panamensis* and *S. v. wingei* are light-colored compared with *S. v. venaticus* (Linares 1967).

Measurements (ranges, in mm) of *S. v. wingei* are: length of head and body, 730–740 ( $n = 3$ ); length of tail, 110–150 ( $n = 3$ ); total length of skull, 132–133 ( $n = 2$ ); palatal length, 61–63 ( $n = 2$ ); zygomatic width, 80–81 ( $n = 2$ ); braincase width, 46–47 ( $n = 2$ ); interorbital width, 24 ( $n = 2$ ); length of mandible, 102–102.5 ( $n = 2$ —Vieira 1946). Measurements (in mm) of 1 adult male *S. v. panamensis* are length of head and body, 730; length of tail, 105; length of hind foot, 110; length of ear, 35; length of skull, 120; condylobasal length, 124; palatal length, 61.5; basal length, 116.5; nasal length, 29.5; interorbital width, 31.6; supraorbital width, 39.8; postorbital width, 26.5; zygomatic width, 75.8; length of mandible, 91 (Linares 1967).

**DISTRIBUTION.** *Speothos venaticus* occurs from Panamá to southern Brazil, Paraguay, and northern Argentina, extending west to Bolivia, Peru, and Ecuador (Fig. 3; Cabot et al. 1986; Cabrera and Yepes 1940; Linares 1967; Yahnke et al. 1998). *S. venaticus* is widely distributed in northern South America (Eisenberg 1989), with fewer reports from southeastern (São Miguel Arcanjo-Beisiegel 1999; São João da Boa Vista and Lorena—Carvalho 1980) and southern Brazil (Cimardi 1996; Ihering 1911). *S. v. panamensis* occurs in northwestern South America; *S. v. venaticus* occurs in the Amazon River basin, central Brazil, eastern Bolivia, northern Paraguay, northeastern Peru, eastern Ecuador and the Guyanas; and *S. v. wingei* occurs in southeastern Brazil (Linares 1967). Bush dogs occur from low elevations (Eisenberg 1989) to 1,900 m altitude (R. Wallace, pers. comm.).

**FOSSIL RECORD.** *Speothos* originated from canids that evolved in the Brazilian highlands (Berta 1984; Langguth 1975). *Speothos pacivorus* (extinct species) and *Speothos venaticus* occur in the late Pleistocene (300,000 years ago)—Recent deposits from Lagoa Santa Caves, Brazil (Berta 1984, 1987).

**FORM AND FUNCTION.** Bush dogs are a highly specialized lineage of South American canids that evolved for dwelling in forests (Langguth 1975). They have partially webbed feet (Macdonald 1996) adapted for walking on soft soil near streams. Bush dog tracks and stride in the field are as follows: forefeet, 5.7 by 5.4 cm; hind feet, 5.0 by 4.4 cm; stride, 28 cm (Villalba and Yanosky 2000). Bush dog dentition, specifically the reduced number of molars, indicates a highly carnivorous diet (Flower 1880). Dental for-



FIG. 1. A captive adult male *Speothos venaticus* at Parque Estoril, São Bernardo do Campo, SP, Brazil, 1999. Photograph by B. M. Beisiegel.

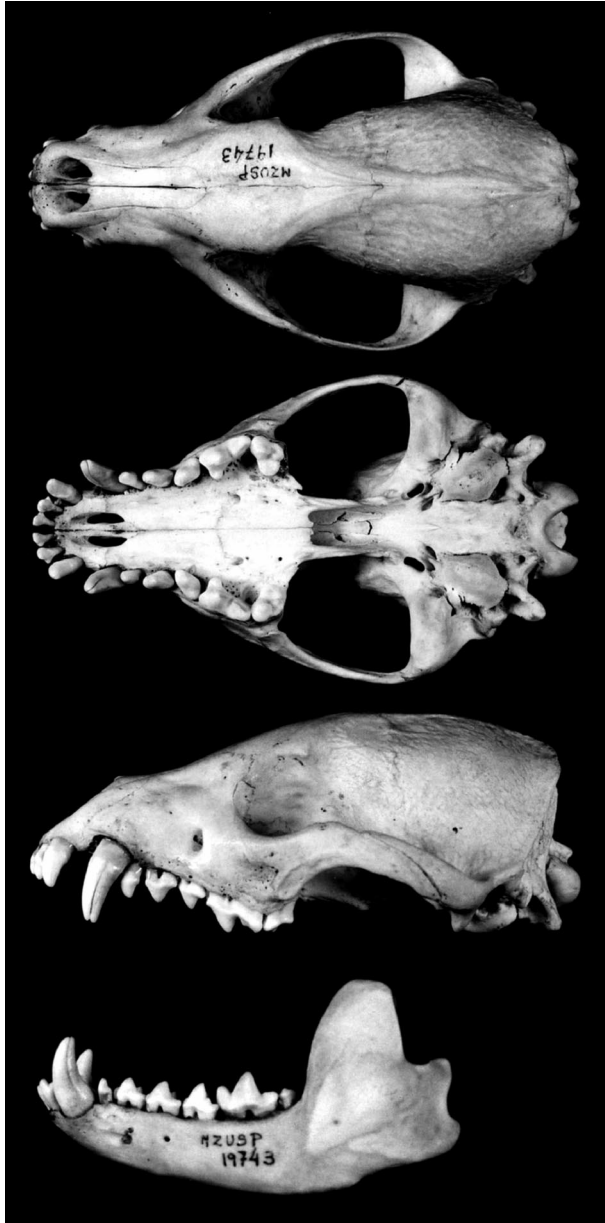


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Speothos venaticus* (specimen 19743 from Museu de Zoologia da Universidade de São Paulo, Brazil). Greatest length of skull is 130 mm.

mula is  $i\ 3/3$ ,  $c\ 1/1$ ,  $p\ 4/4$ ,  $m\ 1/2$ , total 38 (Vieira 1946). Lower carnassial differs from canid pattern: inner cusp of talonid is missing, resulting in this part of the tooth forming a subsidiary blade and not a basin. M1 is modified to form a basin into which fits the single hypoconid cusp of lower carnassial.

Bush dogs have 4 paired mammae (over the ribs ca. 5 cm behind elbows, on abdomen, opposite knee joints, 4.9 cm in front of vulva—Flower 1880). Stomach has a subglobular cardiac portion and a narrower pyloric portion, separated by a constriction. Digestive canal has a reduced caecum (ca. 3.2 cm—Berta 1984, 1988). Anal glands are large (2.3 cm long and 1.8 cm wide), oval, and open with a single orifice at lateral margin of anal aperture (Flower 1880). *Speothos venaticus* has a massive frontal pole of brain (Lyra and van der Geer 2003). A complete sulcus does not separate the upper curve of the gyrus immediately surrounding the Sylvian fissure on left side from the sulcus above it (Flower 1880).

**ONTOGENY AND REPRODUCTION.** Captive bush dogs do not reproduce seasonally (Porton et al. 1987). Aseasonality of bush dog reproduction in the wild has been largely confirmed by

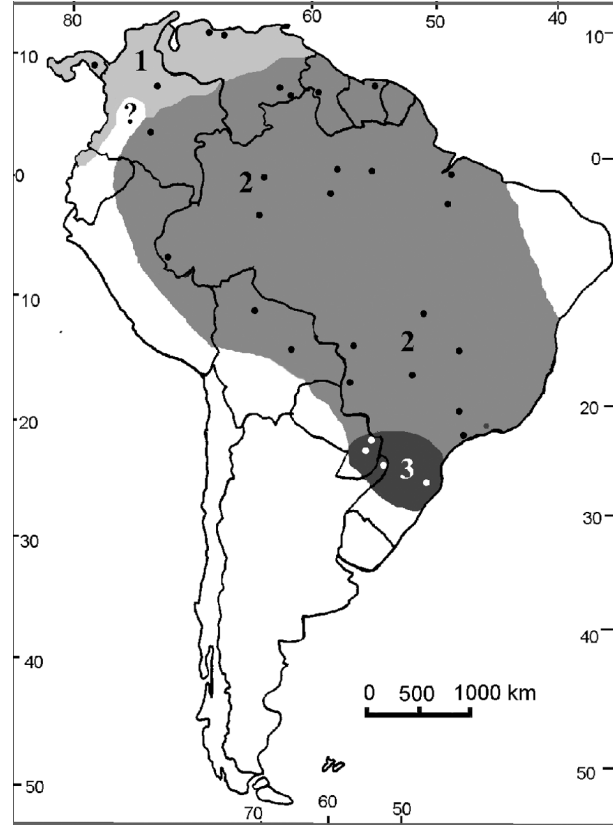


FIG. 3. Geographic distribution of *Speothos venaticus*. Subspecies are 1, *S. v. panamensis*; 2, *S. v. venaticus*; 3, *S. v. wingei*. Subspecies boundaries follow Cabrera (1957), Carvalho 1980, Ihering (1911), Linares (1967), and Massoia et al. (1987). Circles (open and solid) show sites of occurrence for which precise locations are reported in the literature. Sources are Barnett et al. (2001), Beisiegel (1999), Calouro (1999), Carvalho (1980), Cimardi (1996), Dalponte (1995), Eisenberg (1989), Massoia et al. (1987), Peres (1991), Redford and Eisenberg (1992), Vieira (1946), Wallace et al. (2002). Distribution map modified from Eisenberg (1989), Eisenberg and Redford (1999), Emmons (1997), Redford and Eisenberg (1992), and Zuercher et al. (2004).

survey respondents from 7 range countries (DeMatteo 2004). Births typically occur during the rainy season in Suriname (Husson 1978).

Estrus in captivity lasts 1–12 days (Porton et al. 1987). Two primiparous females had interestrous intervals of 15–44 days. One female had 4 and the other 7 estrous periods in 1 year. Earliest age at conception was 10 months (Porton et al. 1987) and earliest age of reproduction in males was 12 months (Bekoff et al. 1981). Bush dogs have copulatory lock, but not back-to-back posture (Drüwa 1982, 1983; Kleiman 1972). In captive bush dogs, copulatory locks occurred 1–3 times per day during estrus (DeMatteo 2004; Drüwa 1983; Kitchener 1971; Kleiman 1968; Porton et al. 1987). Pseudopregnancy occurred in captive bush dogs after an infertile mating or after an ovulation without mating (DeMatteo 2004).

In captivity, mean ( $\pm SE$ , in days) interestrous interval is 238 days  $\pm$  39.6 (range, 179–301;  $n = 11$ ), but may be shorter if the litter is lost (Dmoch 1995; Porton et al. 1987). Gestation averages 67 days (Porton et al. 1987), ranging from 65 to 83 days (Moehlman 1986). Bush dog litters typically have 3–6 pups, although litters of at least 10 occur (Dmoch 1995). Neonatal mass ranges from 125 to 190 g. Sex ratio at birth (males:females) is 1:1.4 (Moehlman 1986). Eyes of young open in 14–19 days (Collier and Emerson 1973; Darling and Whitehead 1991). Pups 1st emerge from den at 2.2 weeks and weaning occurs at 4 weeks (Bekoff et al. 1981).

A litter of 6 bush dogs (3 males and 3 females) was born in 1971 at the Los Angeles Zoo (Collier and Emerson 1973). One female was dead when the pups were retrieved from the mother and 1 died of bacterial septicemia 10 days later. Three males and 1 female were successfully hand raised. These surviving pups

weighed 170 g at birth, lost weight during the 1st week, but regularly gained weight afterward, weighing 476–546 g at 40 days of age.

Females raised by 1 or both parents, alone or with their sisters, do not cycle, but do so when paired with a male (Porton et al. 1987). Presence of a male was not required for ovulation but shortened interestrus intervals and increased frequency of estrous cycles (DeMatteo 2004).

**ECOLOGY.** Bush dogs are extremely rare over most of their distribution, but are common at some sites in Suriname (Husson 1978). *S. venaticus* typically occurs in lowland habitats including gallery forests, forest edge, wet savannas, and riparian areas (Aquino and Puertas 1997; Deffler 1986; Eisenberg 1989; Emmons 1997; Strahl et al. 1992; Zuercher et al. 2005). Bush dogs also occur in open habitats such as cerrado (savanna—Silveira et al. 1998; Zuercher and Villalba 2002), ranchlands (T. Oliveira, pers. comm; L. Silveira, pers. comm.), and altered habitats (da Fonseca and Redford 1984). Home range estimates are 3.8–10.0 km<sup>2</sup> (minimum convex polygon—Beisiegel 1999). Bush dogs have semi-aquatic habits (Langguth 1975), and most sightings occurred near rivers, streams, and watercourses (Aquino and Puertas 1997; Barnett et al. 2001; Deutsch 1983; Linares 1967; Peres 1991; Wallace et al. 2002). A female swam across the Negro River with 2 pups (Coimbra-Filho 1972), and a pair swam in the Caura River in Venezuela (Strahl et al. 1992). Bush dogs pursue and kill pacas (*Agouti paca*) in water (Strahl et al. 1992; Tate 1931). At Emas National Park, a cerrado (savanna) area of central Brazil, 3 of 9 sightings occurred at sites within 200 m of water; the other 6 were from 2,600 to 5,700 m from water (Silveira et al. 1998). At the Mbaracayú Reserve in eastern Paraguay, most bush dog feces, tracks, and sightings (>70%) were detected <1,000 m from water (Zuercher 2001). A captive female spent a great deal of time in a water pond where she dived and swam with ease (Bates 1944).

Bush dogs use dens dug by large armadillos (Coimbra-Filho 1972) and sometimes tamanduas (Sanderson 1949). Other den sites are fallen tree trunks (Aquino and Puertas 1997) and rock shelters (Linares 1967). Den sites occur with scattered dry and fresh feces (Aquino and Puertas 1997) or free of fecal material (Linares 1967).

Agouti (*Dasyprocta*), capybara (*Hydrochoerus hydrochaeris*), and paca are the main prey of bush dogs (Aquino and Puertas 1997; Cabrera and Yepes 1940; Deutsch 1983; Peres 1991; Silveira et al. 1998; Strahl et al. 1992; Tate 1931; Zuercher et al. 2005). One group of 6 bush dogs hunted a tapir (*Tapirus terrestris*) that weighed 250 kg (Wallace et al. 2002). Near Serra das Araras, State of Mato Grosso, Brazil, bush dogs also hunt armadillos (Dasypodidae), collared peccaries (*Tayassu tajacu*), and deer (*Mazama*—Beisiegel 1999). Indigenous groups from Ecuador and Peru report that *S. venaticus* successfully hunts collared peccaries and tapirs (Descola 1994). Bush dogs also hunt rheas (*Rhea americana*—Santos 1945). In Paraguay, bush dog feces contained remains of agouti, paca, tinamou (Tinamidae), an unidentified snake, several unidentified small rodents, and seeds from *Cecropia* (Zuercher et al. 2005). In the Peruvian Amazon, a single bush dog's feces contained hair of agouti (*Dasyprocta fuliginosa*), coati (*Nasua nasua*), smaller rodents (*Myoprocta pratti* or *Proechimys*), and feathers similar to those of tinamous (Aquino and Puertas 1997). Captive bush dogs readily accepted 9-banded armadillos (*Dasypus novemcinctus*), opossums (*Didelphis*), and rabbits (*Sylvilagus brasiliensis*—Van Humbeck and Perez 1998). Bush dogs individually hunt small prey (Silveira et al. 1998). In Paraguay, *S. venaticus* and other carnivores have minimal dietary overlap (Zuercher 2001).

Only indirect evidence of predation exists on bush dogs. In Peruvian Amazonia, the carcass of an adult bush dog was surrounded by tracks of jaguar (*Panthera onca*) or puma (*Puma concolor*—Aquino and Puertas 1997). *Speothos venaticus* is hunted for human consumption in some areas of Amazonia (Calouro 1999).

*Speothos venaticus* hosts *Echinococcus vogeli*, a cestode with pacas as the intermediate host (D'Alessandro et al. 1979; Rausch and Bernstein 1972). In Venezuela, bush dogs host *Lagochilascaris*, an ascariid nematode with rodents, such as *Dasyprocta leporina*, as intermediate hosts (Volcán and Medrano 1991). Captive bush dogs have succumbed to canine parvovirus (Janssen et al. 1982; Montali and Kelly 1989). Captive animals may have succumbed to a vaccine-induced canine distemper virus (McInnes et al. 1982). Other pathogens from captive bush dogs include bacteria (*Escherichia coli*, *Klebsiella*, *Proteus vulgaris*, *Shigella*, *Staphy-*

*lococcus aureus*, and *S. epidermis*), fungi (*Candida*—Van Humbeck and Perez 1998), and protozoans (*Giardia*).

**HUSBANDRY.** One captive bush dog lived for 10 years and 4 months (Jones 1982). At the Los Angeles Zoo, a suckling response was difficult to elicit from pups during the first 8 days. Pups were fed a formula of 1 part Esbilac and 2 parts boiled distilled water; concentration was increased until full Esbilac by day 19, and bottle feeding continued until day 39. From day 7 to day 25, a vitamin supplement was added and, from day 40 on, the young were given Esbilac in a shallow dish and puppy chow in small fragments (Collier and Emerson 1973). At Twycross Zoo, United Kingdom, bush dogs are fed raw meat, live rats, and bone meal with vitamin supplements. A more varied diet of commercial dog food, fruit, and eggs caused vomiting, dehydration, and loss of appetite, mainly due to the commercial dog food (Darling and Whitehead 1991). Other zoos feed only carcasses and live animals (Macdonald 1996).

Bush dogs can be immobilized with 10 mg/kg Telazol supplemented, if necessary, with 10 mg/kg ketamine, or with 20 mg/kg ketamine plus 0.2 mg/kg acepromazine (Kreeger et al. 2002). Bush dogs at the St. Louis Zoo were immobilized with 50 mcg/kg medetomidine combined with 5–6 mg/kg ketamine (DeMatteo and Kochanny 2004).

**BEHAVIOR.** A summary of behavior of *S. venaticus* is available (Beisiegel and Ades 2002). *S. venaticus* is diurnal/crepuscular (Dalponte 1995; Deffler 1986; Deutsch 1983; Linares 1967; Peres 1991; Silveira et al. 1998; Strahl et al. 1992; Zuercher and Villalba 2002), although individuals have been observed at night between 0100 and 0400 h (Wallace et al. 2002). In captivity, bush dogs are active during the day and retire to dens at night (Kleiman 1972). Play behavior has been described for young *S. venaticus* (Biben 1983). Seventy-one percent of object play by a captive group occurred in water (Macdonald 1996).

The basic social unit of *S. venaticus* is a monogamous pair and extended family. In captivity, bush dogs form pair bonds (Druwa 1983; Macdonald 1996; Porton et al. 1987) and parents are dominant over all group members (Macdonald 1996). Only the alpha female reproduces and other group members display alloparental behaviors, such as guarding, carrying, and licking pups (Macdonald 1996). Fathers help during parturition by grooming their mate's anogenital region and removing the afterbirth (Porton 1983). Group living occurs in the field (Aquino and Puertas 1997; Barnett et al. 2001; Deffler 1986; Strahl et al. 1992). In the Peruvian Amazon, 2 adult bush dogs explored an area of ca. 60 m diameter around a pile of branches. Fifteen minutes later, a young bush dog, followed by a pup, emerged from the pile (Aquino and Puertas 1997). Although most sightings of bush dogs are of groups, sightings in the cerrado of Emas National Park were mostly of single individuals (Silveira et al. 1998).

Members of bush dog groups hunt cooperatively (Aquino and Puertas 1997; Barnett et al. 2001; Dalponte 1995; Deffler 1986; Linares 1967; Peres 1991; Strahl et al. 1992). When a bush dog group is hunting a paca, part of the group chases it on land and part waits for the paca in the water (Cabrera and Yepes 1940). Communal hunting occurs in captivity (Macdonald 1996). Captive pups are fearful when they individually encounter prey, but attack prey when near their parents. During ingestion of large prey, parents position themselves at the extremes of the carcass, thus facilitating dismemberment of prey by pups (Biben 1982b).

Bush dogs have 10 distinct vocalizations: short whines, extended whines, repetitive whines, pulsed vocalizations, short screams, long screams, barks, growls, infant whines, and infant grunts (Brady 1981; Villa 2001). Frequency ranges for several vocalizations are short whines, 450–1,790 Hz; extended whines, 540–1,660 Hz; repetitive whines, 520–1,570 Hz; pulsed vocalizations, 1,140–1,590 Hz; short screams, 800–1,720 Hz; long screams, 690–1,550 Hz; barks, 410–1,720 Hz; growls, 450–1,590 Hz; infant whines, 670–880 Hz; infant grunts, 820–1,590 Hz (Villa 2001). Vocalizations facilitate communication among group members in an environment that obstructs visual contact (Brady 1981; Villa 2001). Recorded vocalizations and deposition of urine have attracted and elicited vocal responses from wild bush dogs (DeMatteo et al. 2004).

Female bush dogs have a specific urinary posture (the raised-hindquarters posture, or handstand) in which they climb a vertical

surface backward with their hindlegs and urinate while standing on their forelegs. They then slide their ano-genital region down the vertical surface (Biben 1982a; Kleiman 1966). Male bush dogs slightly extrude their penis and move laterally to create a spray when they urinate (Kleiman 1972).

**GENETICS.** *Speothos venaticus* has  $2n = 74$  chromosomes with 36 acrocentric chromosomes (Schreiber and Dmoch 1994; Wayne et al. 1987). Fundamental number is 76. X chromosome is a large metacentric and Y is a small subacrocentric (Chiarelli 1975; Schreiber and Dmoch 1994).

**CONSERVATION STATUS.** *Speothos venaticus* is considered vulnerable by the IUCN and appears in CITES, Appendix I. Studies of its distribution and abundance are considered a priority by the IUCN Canid Action Plan (Sillero-Zubiri et al. 2004).

**REMARKS.** *Speothos* means cave wolf, referring to location of 1st fossil specimens; living animals do not commonly frequent caves (Simpson 1980). The species name *venaticus* means hunter (Ihering 1968). Vernacular names include cachorro do mato vinagre, janaufr, and janaufr (Brazil); zorro vinagre, perro vinagre, and perro de monte (Bolivia, Ecuador, and Venezuela); perrito venadero (Colombia); perro de la selva, perro de agua, and guanfando (Ecuador); and jagua vygygu (Paraguay).

*Speothos* was originally placed in the subfamily Simocyoninae with *Cuon* and *Lycaon* based on the unicuspid lower carnassial (Simpson 1945; Stains 1975). However, this character evolved independently in other carnivore groups and convergence is possible for *Cuon*, *Lycaon*, and *Speothos*. Morphological characters suggest that *Speothos* is a sister taxon to *Atelocynus* (Berta 1988; Lyras and van der Geer 2003; Tedford et al. 1995). Based on molecular characters, *Speothos* forms a monophyletic clade with *Chrysocyon* (Wayne et al. 1997). The *Chrysocyon*-*Speothos* clade supports multiple canid invasions of South America from North America (Wayne et al. 1997). Phylogenetic placement of *Speothos*, based on combined analyses of 3 genes (cytochrome *b*, cytochrome *c* oxidase subunit I, and cytochrome *c* oxidase subunit II), behavioral, developmental, ecological, and morphological characters supports the monophyletic clade of *Speothos* and *Chrysocyon* (Zrzavy and Ríčníková 2004).

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BEATRIZ DE MELLO BEISIEGEL, DEPARTAMENTO DE ECOLOGIA, INSTITUTO DE BIOCÊNCIAS DA UNIVERSIDADE DE SÃO PAULO, RUA DO MATÃO, TRAVESSA 14, 321, CEP 05508-900, SÃO PAULO SP, BRAZIL; GERALD L. ZUERCHER, DEPARTMENT OF NATURAL AND APPLIED SCIENCES, UNIVERSITY OF DUBUQUE, 2000 UNIVERSITY AVENUE, DUBUQUE, IOWA 52001.