# Ecology and Social Organization of the Maned Wolf (*Chrysocyon brachyurus*)

JAMES M. DIETZ

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 392

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## ABSTRACT

Dietz, James M. Ecology and Social Organization of the Maned Wolf (*Chrysocyon brachyurus*). *Smithsonian Contributions to Zoology*, number 392, 51 pages, 24 figures, 21 tables, 1984.—Although the maned wolf is prized by zoological gardens and is considered endangered throughout its range, little is known of the ecology and social behavior of the species. This monograph presents the results of a 2-year field study conducted in the Serra de Canastra National Park, Brazil, and of a 15-month behavioral study of maned wolves captive at the Conservation and Research Center of the National Zoological Park, Front Royal, Virginia, USA.

Results of the field study are based on radiotelemetric and visual observation of 11 individuals living in four discrete home ranges. Wolves are largely nocturnal, with the majority of circadian activity occurring from dusk to midnight. Males are active more often than females, and pair-members are usually found in close association only during the breeding season. *Solanum lycocarpum*, small mammals and miscellaneous fruits are the most important dietary components, as determined by examination of feces. Consumption of these food items is consistent with seasonal availability indicating that maned wolves are trophic generalists. Males and females are monogamous and share territories averaging 27 square kilometers. Vacancies created by the deaths of resident wolves are filled presumably by unlanded loners. The greatest source of recorded mortality was due to reprisals by ranchers for wolf depredation on domestic fowl. Six of eight wolves tested positive for cystinuria, a metabolic disease occasionally fatal in captivity.

Behavioral observations on eight captive pairs of maned wolves were conducted during two breeding seasons. Males scent mark, vocalize, and initiate activity more often than do females, suggesting a more prominent role by males in territorial defense. Anestrus is characterized by mutual avoidance and minimum levels of scent marking and vocalization. Proestrus is a period of social approximation culminating in estrus. Distance-decreasing behavior drops to a minimum during gestation. However, the continued high level of mutual use of space suggests that females regulate the extent to which males participate in parental care.



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# Contents

# Ecology and Social Organization of the Maned Wolf (*Chrysocyon brachyurus*)

*James M. Dietz*

## Introduction

Thousands of years before the advent of civilization, the highlands of central South America were covered with grass prairie and scrub forest. These habitats generally lacked the large and diverse herds of ungulates characterizing the African plains, but they abounded with smaller vertebrates—particularly rodents of the family Cricetidae. The maned wolf (Figure 1), largest and most distinct of the South American canids, must have hunted in this environment and been shaped morphologically and socially by it.

Since the arrival of modern man, the Brazilian Central Highlands have been changing dramatically. Grassland and cerrado forest are being converted at an unprecedented rate to cattle pasture and farmland. Because we knew little of the ecology of free-living maned wolves, it was impossible to predict the effects of these environmental changes on this species. Thus, the general objective of the present study is to document the ecology and social organization of the maned wolf so that rational decisions can be more effectively made concerning the managment and conservation of this endangered species.

This research project consists of two distinct studies: a 2-year field study of free-living maned wolves in the Serra da Canastra National Park, Brazil (July 1978–June 1980), and a 15-month study of captive maned wolves at the National Zoological Park's Conservation and Research Center (CRC) in Front Royal, Virginia (September 1981–December 1982). This monograph reports the methods and results of both studies, and the subsequent discussion deals largely with the social organization and conservation of this endangered species.

The specific objectives of my field study of the maned wolves of the Serra da Canastra include quantifying for the relative use of available habitat types, diurnal and seasonal activity patterns, social organization, seasonal food habits, reproduction, and mortality and relations with humans. The objectives of my research at CRC were suggested by results obtained in the Serra da Canastra (Dietz, 1981) and include an examination of the behavioral mechanisms maintaining the pair bond in maned wolves, and of the changes in these parameters that were related to stages of the reproductive cycle.

ACKNOWLEDGMENTS.—The field study partly satisfied the requirement for my doctoral degree at Michigan State University, and it is with pleasure that I acknowledge the contributions of the following individuals to that portion of the project: to R.H. Baker, chairman of my advisory

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FIGURE 1.—Adult maned wolf.

committee, I extend my warmest thanks for participation in every aspect of this research; similar thanks are also due advisory committee members S.C. Bromley, J.H. Fitch, L. Gysel, R.W. Hill, and G.A. Petrides.

Coordination of this research project at the federal level in Brazil was not an easy task, but it was handled smoothly and efficiently by Dra. Maria Tereza Pádua, Dr. Renato Petry Leal, José Carlos Duarte, Eduardo Kunze Bastos, and the other competent professionals at Instituto Brasileiro de Desenvolvimento Florestal (IBDF), Brasilia. The late Dr. Ivens P. Franqueira, past director of IBDF in Minas Gerais State, invited me to study maned wolves in the Serra da Canastra. Without his zeal and enthusiasm for conservation, that national park would not have been created. I am also indebted to park director Oliveiro A. Soares, and his administrative personnel, work crew, and guards.

Dra. Rosa Vieira, director of the Clinical Laboratory, School of Veterinary Medicine, Federal University of Minas Gerais, performed the laboratory analyses during the course of this research. I also thank J.O. Whitaker and N. Wilson for identification of ectoparasites; D.O. Straney, P. Myers, and R. Pine for identification of small mammals; R. Ramalho and J. Duarte for identification of botanical specimens.

The field study was partially funded by grants from the following agencies: World Wildlife Fund/International Union for Conservation of Nature and Natural Resources, Instituto Brasileiro para Desenvolvimento Florestal/Fundação Brasileira para Conservação de Natureza, New York Zoological Society, and Michigan State University.

Finally, I would like to acknowledge the par-

ticipation of my wife, Lou Ann, in this study. It was she who gave up two years of her career to help me chase maned wolves in the Serra da Canastra.

My research at the National Zoo's Conservation and Research Center was made possible by Devra Kleiman. She deserves special thanks for allowing me to conduct the behavioral observations largely absent in my field study. Thanks are also due Chris Wemmer and his staff for making the Conservation and Research Center an enjoyable and productive place to work. M. Ditton and the personnel who work with her in managing and caring for the canid collection contributed to several aspects of this study. L. Hayek advised on statistics. D. Kleiman, C. Wemmer and J. Horn read later drafts of this monograph and made suggestions for its improvement. My research at the Conservation and Research Center was supported by grants from the Friends of the National Zoo and from the Smithsonian Institution Scholarly Studies Program (to J. Eisenberg et al.). The use of brand names in this report is for descriptive purposes only and does not constitute endorsement by the Smithsonian Institution.

## The Study Area

"Serra da Canastra," loosely translated, means "mountain range shaped like a foot-locker," and is the regional name given to an area of hills and ridges located 300 km west of Belo Horizonte, capital of the state of Minas Gerais, Brazil (Figure 2). The hills rise abruptly from surrounding agricultural land to elevations of nearly 1500 m and descend into valleys of about 800 m elevation. The areas of higher elevation are characterized by poorly drained soils supporting seasonal grasslands. Subject to heavy grazing and to local pasture improvement techniques, these grasslands are composed of a variety of species of Gramineae, such as *Aristida* sp., *Tristachya* sp., and with the exotic *Melinis minutiflora*. Also present are occasional shrubs and small trees such as *Vellozia* sp. and *Arnica montana*. Grassland habitat comprises perhaps 50 percent of the area of the Serra da Canastra.

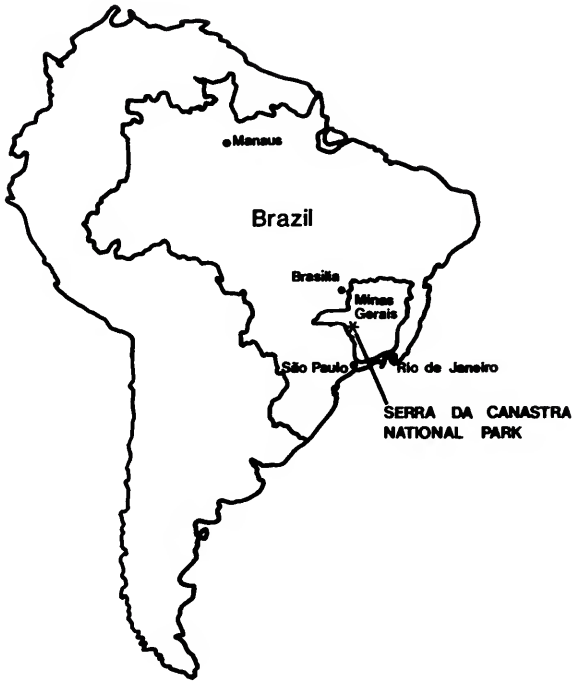


FIGURE 2.—Location of the Serra da Canastra National Park, Minas Gerais State, Brazil, South America.

Approximately 35 percent of the area is composed of cerrado vegetation. This habitat type is defined by well-spaced, thick-barked trees (e.g., *Byrsonima* sp. and *Vellozia* sp.), less than 5 m in height. Trees of the cerrado are typically drought- and fire-resistant with thick tortuous stems, limbs, and branches. Understories are composed of a variety of annual plant species (e.g., Gramineae, Cyperaceae, and Leguminosae) whose presence is often influenced by disturbance factors such as annual burning or clearing of brush to "improve" pasture for cattle grazing.

Many streams and rivers, including the Rio São Francisco, originate in the highlands of the Serra da Canastra. Along these waterways and at their headwaters are found narrow strips of seasonal tropical forest. This riparian habitat type accounts for perhaps 15 percent of the area and is composed of a wide variety of tree species. In this habitat type, understories vary from relatively open ones in drier areas to thick tangles of

vines, herbaceous and shrub species in more mesic areas.

The climate of the region is subtropical with well-defined wet and dry seasons (Figure 3). November through February are typically the wettest months and have a mean temperature of about 22°C. June through August are the driest months and have a mean temperature of approximately 18° C. Frosts occur rarely in the Serra da Canastra. Yearly rainfall varies from about 1300 to 1700 mm. Winds average 18.9 km/hr and are predominantly from the East (Pádua, 1978).

A final characteristic common to all regions of the Serra da Canastra is the ubiquitous presence of humans and their activities. Accessible parts of each range have been annually burned and heavily grazed by cattle during the past several generations. Cowboys tending cattle ride or walk over much of the area on a daily basis. Temporary and permanent human dwellings, as well as dirt roadways, are scattered throughout the area.

Within this hill country (20° South latitude, 46° West longitude) the Serra da Canastra National Park is located. The park was created by Brazilian federal decree in 1972. At the time of my study, however, the land had not yet been purchased by the federal government and was still being used for cattle grazing by local ranchers. Today, the park is 715 $km^2$ in area and is fenced and regularly patrolled by guards in automobiles. A dirt road traverses the park from the city of São Roque de Minas on the east to Sacramento to the west. Upland seasonal grassland is the most common habitat type within the park. The study area for my research consisted of the eastern half of this park and the areas adjacent to it to the east and north. My wife and I lived in the park from July 1978 through May 1980.

## Literature Review

The first detailed description of the maned wolf and its habits was published by the famed naturalist Don Félix D'Azara in 1801. He referred to the maned wolf by its Paraguayan name *Agouara Gouazou* (his spelling) which he translated as "large fox." Simpson (1941) added that this name originated in the language of the Tupi-Guarani Indians and has been shortened to *guará*. Rengger (1830) suggested that the name

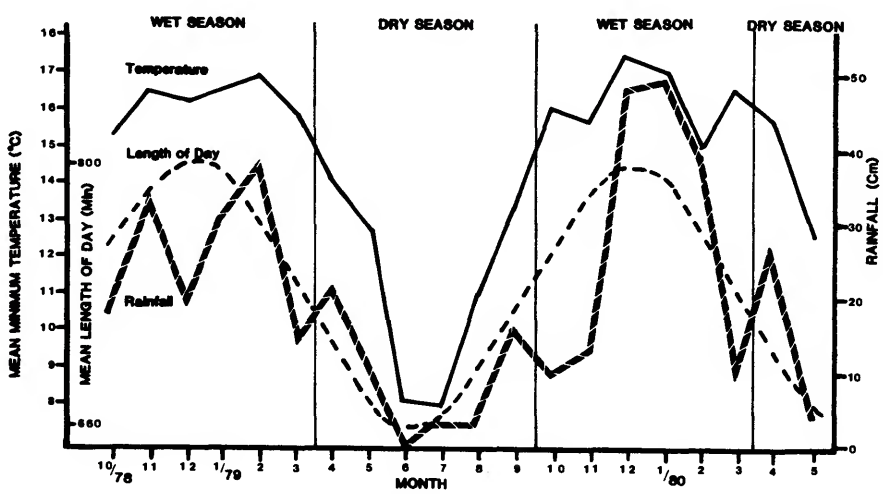


FIGURE 3.—Definition of wet and dry seasons: temperature (= the mean of daily minimum temperatures for each calendar month); length of day (= the mean number of minutes of daylight for the days in each month); rainfall (= total measureable precipitation per month).

*Aguará-guazú* was onomatopoeic for the vocalization of the maned wolf. The animal is now known throughout Brazil as *lobo guará*, in Bolivia as *boroche*, *aguará guazú* in Paraguay and Argentina, and *lobo de crin* in Bolivia and Peru.

The taxonomic relationships within the family Canidae have been relatively unstable since Gray (1825) coined the family name in its present form. Classification of the South American forms at the generic level has been the most unstable (see Cabrera, 1931, and Clutton-Brock et al., 1976, for reviews). The maned wolf has largely escaped these problems of technical nomenclature of the canids and has not been challenged as a distinct genus since clarification of its current scientific name by Osgood in 1919 and 1934. The maned wolf is monotypic, and no geographic races are recognized.

The identification of the canid groups that are the maned wolf's nearest relatives remains an unsolved problem: Clutton-Brock et al. (1976), using morphological character analysis, concluded that the maned wolf is weakly related to the *Dusicyon* group. Chiarelli (1975) writes that the karyotype of *Chrysocyon* is very similar to that of *Canis*. However, the diploid number of the former is 76, while that of the latter is 78 (Newnham and Davidson, 1966). Interbreeding between these two genera is not likely (Bastos, 1978). Gel electrophoresis has been used to differentiate between the serum proteins of various carnivores including the maned wolf and domestic dog (*Canis familiaris*) (Durr and Schmitt, 1970), but a relatively low incidence of polymorphic loci has generally limited the effectiveness of this technique in the Canoidea (Seal, 1975).

Pocock (1927), Langguth (1969), and Studer (1904) have described the external characters and the morphology of the maned wolf and have compared these data with those from other South American canids. Whereas the caeca of most canids are convoluted, the caecum of the maned wolf is short and cylindrical (Flower, 1879), as it is in the bush dog (*Speothos venaticus*), the crab-eating fox (*Cerdocyon thous*), and the short-eared dog (*Atelocynus microtis*) (Langguth, 1969). Sokolowsky (1927), speculating on the adaptive significance of the long legs of maned wolves, surmised that this species is not adapted for swift running, as stated by Stains (1975), but rather for efficient vision and travel in tall vegetation.

Since no fossil remains of the maned wolf have been found outside of the Brazilian Central Highlands, it has been assumed that the maned wolf evolved in that region (Langguth, 1975) either during the beginning of the Pleistocene Epoch (Simpson, 1980) or well before the Pleistocene (Langguth, 1969). The present range of the maned wolf includes the following areas: all geographic regions of Brazil (excluding the Amazon Basin, parts of the arid Northeast, and the Atlantic coast); the provinces of Formosa, Corrientes, and Chaco in Argentina; most of Paraguay; eastern Bolivia; and the Pampas del Heath in Peru (Cabrera, 1958; Cabrera and Yepes, 1960; Paiva, 1973; Schaller, 1975; Hofmann et al., 1975–1976; Schaller and Vasconcelos, 1976; Dietz, in press; Breyer, in prep.).

Acosta (1972) described hand-rearing a litter of maned wolf pups. These data were used by Bekoff and Jamieson (1975) to compare the maned wolf's physical development with that of other canids. The growth parameters for pups were established by Acosta (1972), Encke et al. (1970), and by Seidel (1972). Information on the type of enclosure and diet necessary successfully to maintain maned wolves in captivity has been summarized by Crandall (1964), C. Carvalho (1976), and by Brady and Ditton (1979). The longevity of maned wolves in captivity has been estimated at from 12 to 15 years (Silveira, 1969).

Female maned wolves are monestrous and may copulate several times during an estrus of about five days (Lippert, 1973; Kühme, 1975). Copulatory behavior has been described by Lippert (1973). Copulation by captive maned wolves has been observed during the months of October through February in the Northern Hemisphere (Encke, 1971; D. Altmann, 1972), and from August through October in South America (Acosta, 1972). The birth of from two to five pups, a normal litter size for this species, follows a ges-

tation period of about 65 days (Faust and Scherpner, 1968). A record of seven pups in one litter was recorded in the São Paulo Zoo (C. Carvalho, 1976). Parturition has been described by Hammerling and Lippert (1975), and the studbook record for the species has been published by Roeben (1975) and by Matern (1980).

In addition to mediocre reproductive success, maned wolves suffer from several parasitic and disease problems, including giant kidney worm (*Dioctophyma renale*) (Giovannoni and Molfi, 1960; Lamina and Black, 1966; Matera et al., 1968). This parasite is commonly fatal in captive and probably also in free-living maned wolves. Silveira (1969) suggested that the Solanaceae eaten by maned wolves might have an inhibiting action on this parasite, but the methods used to test this hypothesis were rightly questioned by C. Carvalho (1976). Other endoparasites found in maned wolves are mentioned by Encke et al. (1970), and by C. Carvalho (1976). Bush (1980) reviewed the diseases and medical management of maned wolves in captivity; two recent medical problems include susceptibility to parvovirus (Fletcher et al., 1979) and cystinuria (Bovée et al., 1981).

Maned wolves in captivity lead essentially solitary existences during the reproductive period. Pairs composed of animals of opposite sexes are easier to house in the same enclosure than same-sex animals. Individuals maintain separate preferred resting sites and do not usually rest in close association (Encke, 1971; D. Altmann, 1972; Kühme, 1975). Kleiman (1972) contrasted the solitary behavior of the maned wolf with the highly gregarious nature of the bush dog (*Speothos venaticus*). The vocalizations of maned wolves have been described by Brady (1981), and the behavior of pups by Encke et al. (1970) and Biben (1983).

The wolf feeds mainly on small vertebrates and on fruits (Azara, 1801; Cabrera and Yepes, 1960; C. Carvalho, 1976). F.W. Miller (1930) and Dennler de la Tour (1968) describe the stiff-legged pounce used by maned wolves capturing small prey. Roosevelt (1925) and Krieg (1948) write that the wolf often preys on small domestic stock, but this allegation is refuted by Cabrera and Yepes (1960). Krieg (1928, 1940, 1948) refers to the wolf as the "savanna stroller" and comments on its solitary nature. Dennler de la Tour (1968) also notes that the wolf is usually seen alone and hints that individual territories may be maintained.

The maned wolf is classified by the International Union for the Conservation of Nature and Natural Resources as "vulnerable" (IUCN Red Data Book, 1982), and classified by agencies of the Brazilian government as "endangered" (J. Carvalho, 1968; Coimbra Filho and Magnanini, 1968). Silveira (1968) estimated that only 1500–2200 maned wolves remain in 650,000 $km^2$ in Brazil, and Meritt (1973) details pathways by which wolves captured in Paraguay and northern Argentina were exported out of Paraguay in 1971. However, in spite of what appears to be a rather bleak future for the maned wolf, little research is currently underway on this species, and no objective suggestions have been formulated concerning its conservation.

## The Field Study

### Methods

#### *Capture Procedure*

Political considerations and the likelihood of breaking the long and apparently fragile limb bones of captured maned wolves precluded the use of steel leghold traps for trapping. Interviews with area residents produced several models of live-traps successful in capturing wolves. From these suggestions, I designed and had built seven wooden live-traps (Figure 4). Each weighed about 110 kg and was constructed of durable native hardwoods. Bolts permitted disassembly for transport. The trap design was an open-ended box with a falling door released by a treadle mechanism located at the back of the trap. For bait, a live chicken (supplied with food and water) was supported on a platform above

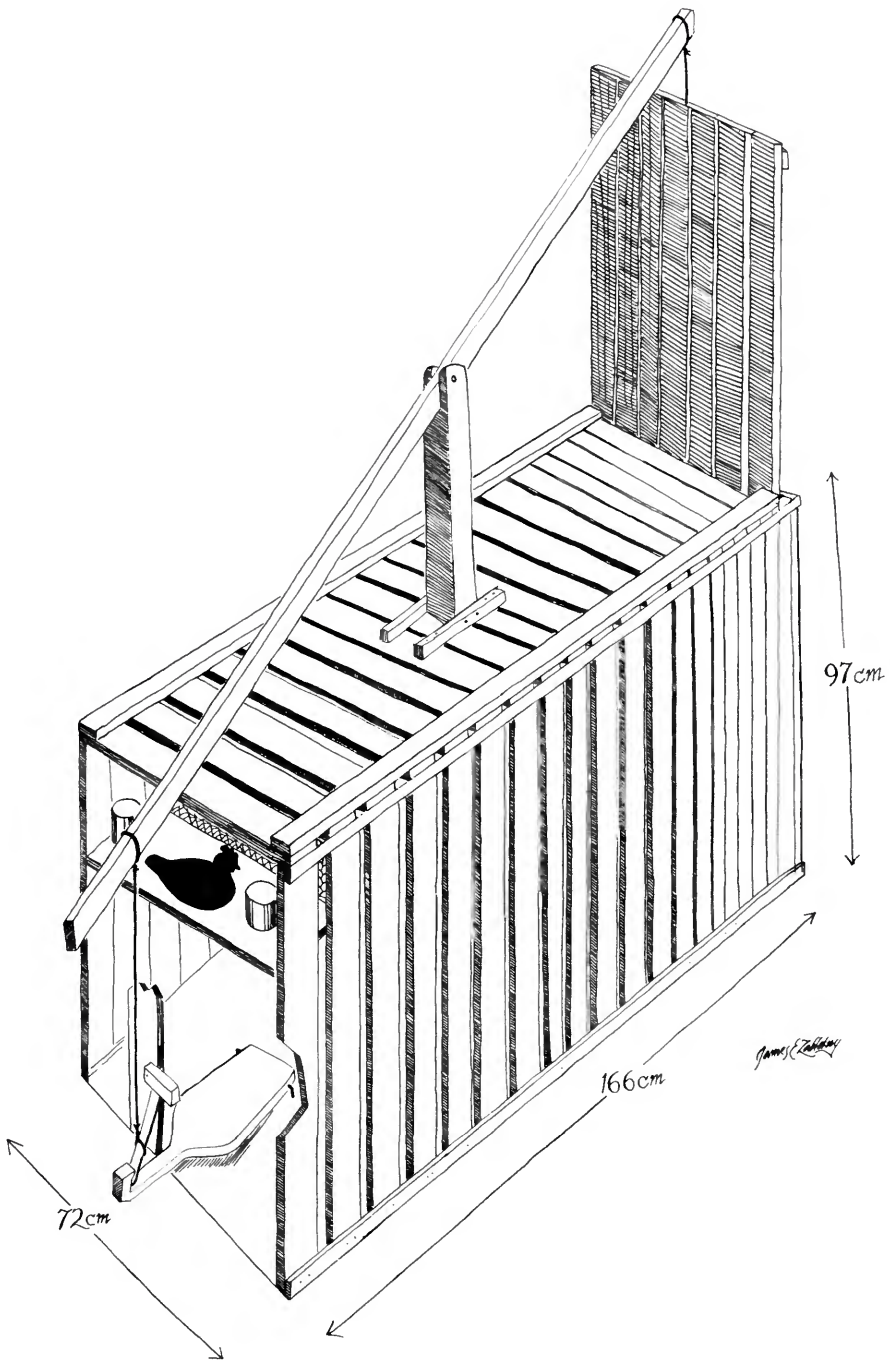


FIGURE 4.—Wooden live-trap used to capture maned wolves. Trap is baited with a live chicken.

the treadle; the chicken was separated from the inside of the trap by a wall of light chicken-wire. All captured wolves perforated the chicken wire and consumed the chicken.

Initial attempts using random distribution of traps were unsuccessful. Through interviews, I established the locations of recent maned wolf activity and set traps within a few meters of major trails. Major trails were determined by the quantities of urine, feces, and tracks found there. All such traps were successful in capturing resident maned wolves. Traps were placed in pasture, tall grass, or scrub brush and were not camouflaged or hidden. When a trap repeatedly captured the same wolves, that trap was temporarily closed or was moved to a new area of wolf activity.

Since the objective of trapping was to place radiotransmitters on all resident maned wolves, trap placement was determined by signs of wolf activity and not by an area grid design selected a priori. The size and topographical irregularity of the area, and the general lack of roads prevented examination of all traps daily. Each trap was assigned to a resident of the study area and was placed so that he could check that trap from a distance. Residents were reimbursed for rapidly reporting a wolf capture.

### *Handling Procedure*

The first capture of a wolf involved the collection of a urine sample for use in testing for cystinuria. Since trapped maned wolves urinated when first approached, I was able to collect urine samples from eight wolves by using one stick to distract the wolf and simultaneously inserting a second stick, with a piece of filter paper attached, between the legs of the wolf to collect the urine as it was voided. The urine absorbed onto the filter paper was analyzed chromatographically by K. Bovée, School of Veterinary Medicine, University of Pennsylvania.

Immobilization involved an intramuscular injection by means of a syringe recessed into a hole in the end of a broomstick, using 20 mg Sernylan (Parke-Davis); 7.5 mg Rompun (Haver-Lockhart); 0.75 mg Acepromazine (Haver-Lockhart). This dose usually rendered the wolf immobile within 10 minutes and allowed about two hours of working time before the animal began to regain consciousness. All immobilized maned wolves recovered physical control quickly and apparently completely.

Whole blood was collected from a superficial vein of a limb and a portion was mixed with anticoagulant (KEDTA) for serological determinations. Feces from the trap and blood samples were immediately sent for analysis to the School of Veterinary Medicine, Federal University of Minas Gerais, Belo Horizonte.

Tooth wear (after Gier, 1957) was used to classify each wolf according to a relative age class: young, middle-aged, or old. All ectoparasites found were counted and collected for future identification. Minor wounds were treated with a topical spray antiseptic (Topazone, Eaton Labs.) and a prophylactic dose of 2 ml Longicil Fortified Antibiotic (Penicillin G; Fort Dodge Products) was applied subcutaneously. Chloromycetin Ophthalmic Ointment (Fort Dodge Products) was used to reduce drying of the eyes during immobilization. A single Rototag (size no. 5; Dalton, England) was affixed to the lateral margin of each pinna. A radiotransmitting collar was fitted around the neck of each wolf. All wolves were weighed (Figure 5) and measured.

Transmitters (Wildlife Materials) weighed about 250 g, were equipped with bimodal activity-monitoring switches, and were fastened to collars of nylon webbing, which were riveted around the neck. The sizes and shapes of collars were based on models of the necks of captive maned wolves from the San Diego Zoo (courtesy of Dr. P.T. Robinson, San Diego Zoo). A collapsible three-element yagi antenna (Wildlife Materials) proved satisfactory under field conditions in the Serra da Canastra. Recapture of a wolf was common and involved only testing the radiotransmitter and photographing the wolf prior to its release.

### *Location by Radiotelemetry*

Radiotelemetry permitted the determination on a year-round basis of home ranges, activity patterns, habitat preference, and social behavior.

FIGURE 5.—Weighing an immobilized maned wolf in the Serra da Canastra.

Wolves were located on a daily schedule based on four 6-hour time blocks: 0601–1200, 1201–1800, 1801–2400, and 0001–0600 hours. Although the accentuated topographic relief in the area restricted my capacity to travel at night and often reduced the radius of transmission of a transmitter to a few hundred meters, an effort was made to locate each wolf at least once every 24-hours. Attempts to radiolocate wolves were dispersed over time so that each time-block was represented in a given month.

I used triangulation based on two or more vectors to determine the location of each wolf (e.g., Craighead and Craighead, 1972; Craighead et al., 1973; Seidensticker et al., 1973). For each location, I recorded the time of day, activity level, and habitat type. After 30 seconds of monitoring I classified a wolf as: inactive (no activity recorded during the interval), intermittently active (activity not continuous during the interval), or constantly active. These activity classes were established by testing radiocollars on domestic dogs.

Radiolocated wolves were visually monitored for individual and social behavior. Observation was attempted periodically when a wolf was known to be active or in a location when and where visual observation was likely to be successful.

If a wolf had not been observed for approximately a month, or if it was inactive and in the same location for several days, radiotelemetry was used to approach the animal to determine its physical condition. The constant movement of cattle and ranch hands throughout my study area often displaced these maned wolves in a similar manner. Wolves fled for short distances, and it is unlikely that my interference had any significant additional effects on their behavior or activity patterns.

### *Determination of Food Habits*

SCAT COLLECTION.—Food habits were determined by the collection and analysis of fecal droppings (scats). Only scats 25 mm or larger in diameter were collected, based on a comparison of known maned wolf scats and those of other canid species in my study area. After several months of field work, additional characteristics of maned wolf scats, including odor, texture, and site, became evident to me.

All maned wolf scats found were collected for analysis, but scheduled collection was limited to the three home ranges of the maned wolves that I intensively studied. A goal for collection of at least 50 scats per home range per month was arbitrarily set and usually achieved. Scats collected from the interface between two maned wolf ranges were omitted from analysis relating to home ranges but were included in other analyses. All feces found in a single location (~0.5 m in diameter) were classified as a single scat except when obvious differences in dates of deposition were evident.

SCAT ANALYSIS.—Scats were air-dried and stored until analysis. All components of each scat were identified and grouped into major food types. A reference collection of fruits and animals collected in the study area was used to identify

scat components. I measured the volume of the major scat components by compacting the material in a graduated cylinder using a close-fitting dowel.

The relative importance of food items in collected scats was calculated using relative volume (total volume of that component as a function of total volume of all components) and frequency of occurrence (number of scats containing that component as a function of the number of occurrences of all components). Data analyses were performed using a series of SPSS programs (Statistical Package for the Social Sciences, Version 8, Vogelback Computing Center, Northwestern University). The quantitative problems relating to the use of scat analysis in determining food habits have been documented (e.g., Floyd et al., 1978; Meriwether and Johnson, 1980; O.J. Murie, 1946).

CENSUS OF AVAILABLE FOOD ITEMS.—Published accounts of the food habits of maned wolves indicated that small mammals and native fruits were perhaps the items most commonly exploited by this species (e.g., Cabrera and Yepes, 1960; C. Carvalho, 1976). To determine how maned wolves use available trophic resources, the relative abundance of small mammals (Dietz, 1983) and of fruits was estimated on a monthly basis in each of the three major habitats in the park.

The trap lines for small mammals were also used as transect lines for the estimation of relative diversity and abundance of fruits available to maned wolves. The 5 hectare area sampled in each habitat was arbitrarily defined by a strip 10 m wide running the length of the trap line. Any fruits larger than 1 cm in diameter and less than 1 m above the ground level were defined as available to maned wolves. Relative abundance of a fruit species was estimated by the number of individual plants in fruit in the sampled area.

Interviews with area residents were used to determine which fruit species might be eaten by maned wolves. The months when these 43 species were in fruit were noted and examples incorporated into the reference collection.

## RESULTS

### *Physical Characteristics of Captured Maned Wolves*

My observations are in general agreement with previously cited descriptions of maned wolf physical attributes and, therefore, are not stressed. However, as published data on the hematology and blood chemistry of this species are unavailable for free-living individuals, I have included information on these aspects in Tables 1 and 2.

PELAGE, WEIGHTS, AND MEASUREMENTS.—Photographs of the nine adult maned wolves captured in the Serra da Canastra revealed almost no observable individual variation in pelage coloration. One male, Lambda, was slightly darker on the cheeks and muzzle, but at distances greater than about 50 m I found it impossible to identify individuals without the aid of radiotelemetry.

The guard hair on the bodies of captured wolves was about 8 cm in length, straight, and golden-red in color. No underfur was present on these adult wolves. The distal portion of the muzzle was black, as was the antebrachium distal from the elbow and the hindlimb distal from the tarsus. Of the dorsal erectile mane, approximately the cranial half was black. Black from the mane also radiated laterally over the scapulae. The inner aspects of the pinnae were white as were the intermandibular and throat regions. The distal half of the tail was also white. The length of white on the tail and of black on the forelimb, hindlimb, and on the mane were measured on five of the captured wolves (Table 3).

Weights and selected measurements of nine captured adult wolves are also presented in Table 3. All comparisons of these values among age classes, and all but one comparison between sexes were not significantly different (Student's t-test for unpaired observations; Steel and Torrie, 1960; $p > 0.05$). However, sampled male wolves had significantly longer pinnae than sampled females ($p < 0.05$).

HEMATOLOGY AND BLOOD CHEMISTRY.—I collected whole blood for hematologic and serum

analysis from eight adult maned wolves in the Serra da Canastra. In addition, the veterinarian at the Belo Horizonte Zoological Garden contributed blood samples from two captive maned wolves (Zoo 1 and Zoo 2) recently acquired by that institution. One of the latter two wolves was a female; the sex of the other was not recorded. These data (Tables 1 and 2) may be compared with values from other maned wolves, but small sample sizes, difficulties during collection and transportation of blood samples, and the lack of information concerning environmental or physiological conditions suggest that a degree of caution should be used.

### *Description of Home Ranges in the Study Area*

During the two years of this study, I captured eight maned wolves in the Serra da Canastra and three wolves elsewhere. Radiotelemetric and visual observations of the eight wolves residing in the study area allowed the definition of three mutually exclusive home ranges (Figure 6). I named these ranges the West Range, the East Range, and the Taperão Range. Portions of each range were located within the boundaries of the Serra da Canastra National Park. Each range was occupied by a single male-female bonded pair of maned wolves.

WEST RANGE.—Connecting peripheral points on a map of plotted radiotelemetric locations yields a polygon with an area of 21.7 km$^2$. However, because one series of ridges and valleys, measuring about 4 km$^2$, was difficult to reach from my field headquarters, this estimate is probably smaller than the area actually used by the resident pair of wolves.

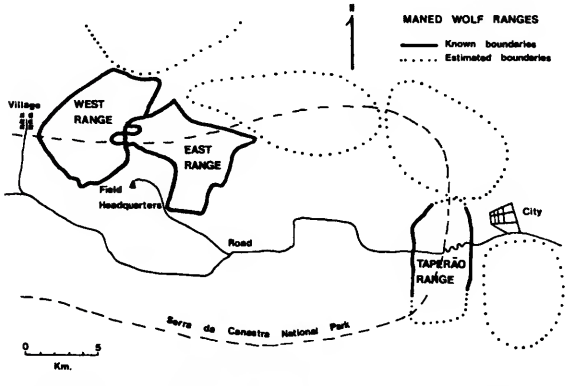


FIGURE 6.—Locations of home ranges of maned wolves in the study area.

EAST RANGE.—Directly northeast of my field headquarters and adjacent to the West Range was the East Range (Figures 6, 7). The pairs of wolves that successfully used this range were more easily located than the wolves of the other two ranges. Therefore, my estimate of the area of this range, 30.0 km$^2$, is probably the most accurate of the three.

TAPERÃO RANGE.—The Taperão Range (Figure 6) was located about 2 km southwest of the city of São Roque de Minas, and about 28 km east of my field headquarters. Ranchers and farmers declared that the movements of the resident wolves had remained unchanged for many years. With the help of these farmers, I first trapped a male maned wolf, Beta, on 10 September 1978.

The Taperão Range was characterized by extremes of topographic relief. Only one road was usually passable by automobile. Any of a number of large ridges effectively blocked the transmitter signal. Therefore, the area of this home range, 12 km$^2$ as calculated from radiotelemetric data, is an underestimation. A more accurate estimate, based on single radiotelemetric vectors and visual sightings, is about 24 km$^2$. With the exception of scat collection, data were collected only opportunistically in the Taperão Range.

OTHER RANGES.—In addition to the three described home ranges, there were several other ranges in the region (Figure 6). One such range abutted the West Range to the north, and a second range was adjacent to, and east of, the East Range. Between this second range and the city of São Roque de Minas was a third range, while a fourth existed to the south of São Roque and east of the Taperão Range. Access to these additional ranges was difficult and I made no attempts to capture their resident maned wolves. Pairs of wolves were sighted in three of the four

FIGURE 7.—Part of the East Range, Serra da Canastra National Park.

ranges, and reproduction took place in all four ranges. Reports by area residents of the numbers of wolves vocalizing in these areas and my own subjective estimates of the amounts of wolf-sign present suggest that two wolves occupied each of these additional ranges.

Radiolocations indicated that maned wolves spent approximately 34 percent of their time in grassland, 43 percent in cerrado, and 24 percent in forest (Table 4). After transformation to reflect equal sample sizes for both sexes, a chi-square test of goodness of fit (Steel and Torrie, 1960), suggested that males used grassland habitat significantly more than did females ($p < 0.05$), and that females used cerrado habitat significantly more than did males ($p < 0.025$). No significant difference between sexes was found in the use of forest habitat.

G-tests of independence (Sokal and Rohlf, 1969) indicated a significant relationship among male-female pairs with respect to their use of cerrado ($p < 0.005$) and of forest habitat ($p < 0.005$) (Table 5).

Seasonal differences in habitat use were determined by dividing the radiolocations into those occurring during the wet and dry seasons (Table 6). Results of chi-square tests within seasons indicate that grasslands were used more often than expected during the wet season ($p < 0.025$), and forest habitat was used more often than expected during the dry season ($p < 0.025$). A possible biological significance of these results is that the grassland affords less cover and supports a lower relative abundance of small vertebrates during the dry season when pastures are burned by local ranchers.

The preceding analyses are biased in two ways: first, the majority of the radiolocations were during the day. Thus, because these wolves were largely nocturnal, habitat types associated with daytime rest sites would be overrepresented. Second, although the three defined habitat types did not differ among home ranges with respect to relative availability, those three habitat types were not equally abundant in the study area. Therefore, the contribution of smaller habitat

types would be overemphasized in the above analysis. To correct for these biases, I divided radiolocations into day (1601–1800 hours), and night (1801–0600) observations. A correction factor was applied to adjust for differences in relative abundance of the three habitat types. I placed a confidence interval using the Bonferroni z-statistic (after Neu et al., 1974) on the observed proportion of occurrence of wolves in each habitat (Table 7); results indicate that maned wolves of the Serra da Canastra were less likely to be found in grassland habitat than in other types of habitat at any time. During the day, wolves were most often found in cerrado; at night, they were most commonly located in forest habitat.

### *Activity Patterns*

DAILY AND SEASONAL VARIATION.—Results include 763 radiolocations of eight wolves over 20 months (Figure 8). A maximum of two locations per wolf per time block are included in the analysis. Radiotelemetric data collected during daylight hours (0601–1800) indicate that wolves were active during 34.7 percent of the time, or, 35.0 percent of the six hours prior to noon and 33.8 percent of the six hours following noon. The majority (53.8 percent) of these active observations were classified as intermittently active, and the remainder (46.2 percent) as constantly active; that is, wolves spent approximately 115 minutes travelling from place to place during daylight hours.

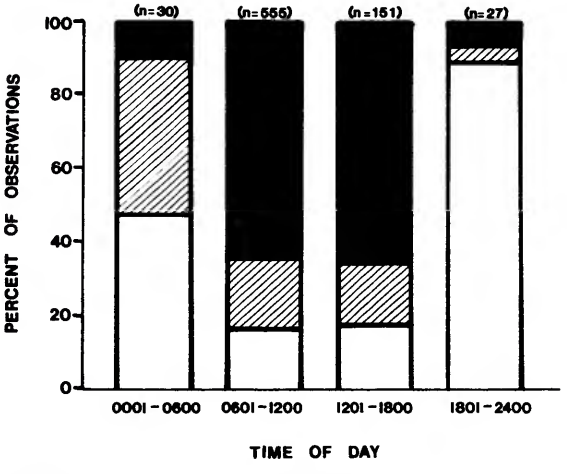


FIGURE 8.—Activity of maned wolves during six-hour time blocks. Total number of radiolocations for each time block (n) are classified according to level of activity (shading = inactive; hatching = intermittently active; white = constantly active).

The maned wolves were more active at night than during the day. Ninety-one percent of the radiotelemetric observations between 1801 and 0600 hours were of constantly or intermittently active wolves. Between 1801 hours and midnight, 96 percent of the radiolocations of active wolves were classified as constantly active. During the six hours following midnight, 48 percent of the radiolocations were of intermittently active wolves and 52 percent were of constantly active wolves. Thus, wolves spent about eight hours (five hours before midnight and three hours after midnight) moving from place to place at night.

Although a chi-square test of independence did not indicate a dependent relationship between level of activity and four male-female pairs ($p = 0.33$; Table 8), the same test did indicate a relation between activity and sex ($p = 0.012$; Table 9). Further, when numbers of intermittently active and of constantly active observations were pooled to form a single class for each sex, results indicated that males were more active than females (G-test; $p < 0.01$). Again, using combined numbers of observations of constantly active and intermittently active wolves, females were active 34.4 percent of the time and males were active 44.0 percent of the time.

OBSERVATIONS ON INDIVIDUAL ACTIVITY.—Data collected during 16 monitoring sessions of from two to six hours in length added descriptive detail to the picture of temporal relationships among maned wolves.

During daylight hours, the wolves rested in thick cover—often in riparian forest or in the grass and shrubs at the headwaters of small streams. Individuals usually remained in the same patch of cover or moved only a few meters during the day. At intervals of about 45 minutes, however, each wolf could be expected to move

for a few seconds before again settling down. The transmitted radio signals suggested postural changes or perhaps standing up and turning around before again lying down. Shortly after sunset (between the hours of 1750 and 1845), the wolves left the areas where they had been resting during the day and began to hunt and travel throughout their ranges. These movements continued for much of the night with occasional pauses of up to about 20 minutes. Occasionally wolves travelled across a home range with only brief stops. At other times, an entire night might be spent hunting in a small area. Usually by 0700 hours, but occasionally as late as 0840 hours, the wolves again retired to thick cover for the day. Wolves appeared to remain active longer during rainy or foggy days than during days of bright morning sunshine.

*Social Organization and Communication*

RELATIONSHIPS OF INDIVIDUALS WITHIN PAIRS.—Results based on 1537 trap-nights (Table 10), 828 precise radiotelemetric locations, nearly as many single directional vectors, and approximately 50 visual sightings of eight maned wolves indicate that the maned wolves of the Serra da Canastra displayed facultative monogamy (see Kleiman, 1977) characterized by a long-term pair bond between male and female. Although the male and female, as a pair, had completely overlapping ranges, very little time was spent in close association. According to local observers, family groups were rarely seen.

*Beta:* This wolf, a middle-aged male, was captured in the Taperão Range on 10 September 1978 (Figure 9). He was observed on numerous

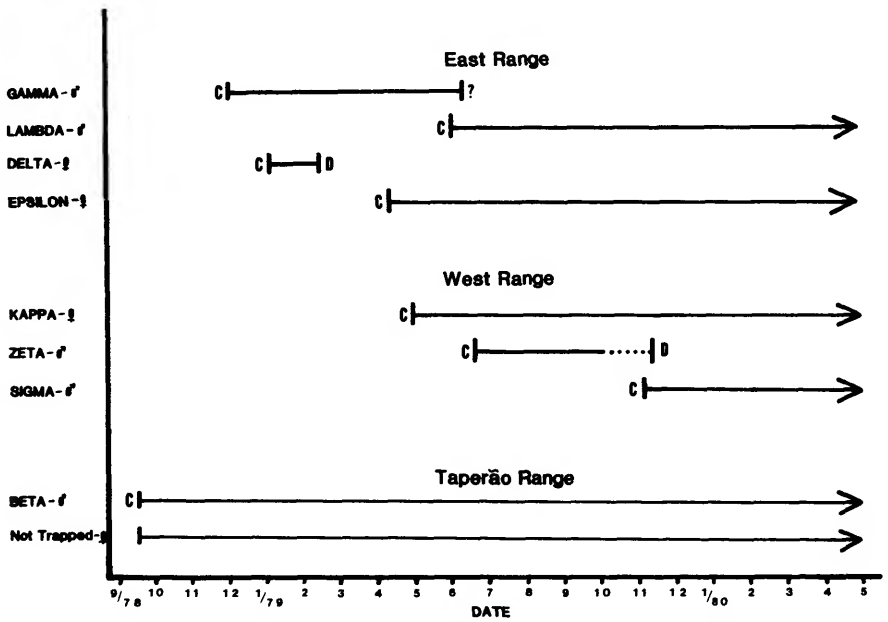


FIGURE 9.—A chronological representation of the relationship among wolves inhabiting the East, West, and Taperão ranges. (C = date of initial capture of a maned wolf; D = date by which a maned wolf was known to have died; maned wolf Zeta died some time during the period indicated by the dotted line.)

occasions in the company of a small female wolf that apparently shared that range. These wolves shared part, if not all, of the same home range estimated to be 24 $km^2$. During the 20 months that Beta carried a transmitter, he was observed either alone or with the same female wolf.

In May 1979, the signal of his transmitter ceased. I thought that perhaps Beta had been replaced by another wolf and set traps accordingly. On 18 June 1979, Beta was retrapped and fitted with a new transmitter. The external antenna of his transmitter had been bitten off at its base. The transmitter was also deeply gouged by the teeth of a large carnivore, and one of the rivets attaching the transmitter to its collar had been pulled loose. This damage was probably done during a social interaction with another wolf.

*Gamma and Delta:* Gamma, a middle-aged male wolf, was first captured on 15 December 1978 in the East Range (Figure 9). Although severe seasonal rains initially complicated radio telemetry, I learned the general outline of the East Range, that the perimeter was well defined, and that it was stable (Figure 10).

An old female wolf, Delta, was taken in the same trap as was Gamma, but about one month later, 18 January 1979. At the time of her capture, she appeared weak and disoriented, often shaking her head from side to side. Closer examination revealed that the left pinna and inner ear of this wolf was severely infested with screw-worm larvae (*Cochliomyia hominovorax*). A single application of a lindane-based product (Myzin Smear, Fort Dodge Products) was successful in curing this infestation by the time of her second capture on 4 February. On 5 February this wolf suffered a compound fracture of the right radius and ulna. She never recovered from this injury and died of apparent starvation about 25 February. Necrospy revealed that the screw-worm infestation had caused erosion of the left tympanic bulla and surrounding temporal bone.

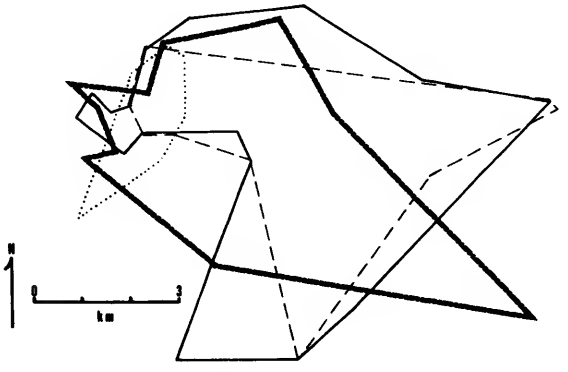


FIGURE 10.—East range occupied sequentially by maned wolves Delta (dotted line; n = 18 radiolocations; female) and Gamma (striped line; n = 20 radiolocations; male); Epsilon (dashed line; n = 220 radiolocations; female); and Lambda (solid line; 225 radiolocations; male). Polygons represent the connected peripheral locations for each wolf.

The number of radiolocations for Delta were few (n = 18). In addition, during three of the six weeks that this wolf carried a radio collar, her locomotion was severely hampered by her broken leg. Nevertheless, the portion of her range that I was able to identify almost completely overlapped that of Gamma (Figure 10), and the area she used corresponded to that most intensively used by later occupants of this range. These facts indicate that Delta was the mate of Gamma and that both were residents of the East Range.

*Epsilon and Lambda:* In late April, a young adult female wolf, Epsilon, was captured in the East Range in one of the traps in which Gamma had been recaptured. Visual sightings of wolves and the amount of sign present in the East Range indicated that Epsilon was probably trapped shortly after her arrival in this area. She carried a radiotransmitter in this range for the duration of my study.

About one month after the capture of Epsilon, it became increasingly difficult to locate Gamma. While Epsilon used the western half of the East Range, Gamma travelled widely in the eastern half of the range. During the month of June, Gamma was often outside the range of my radiotelemetric equipment. On 25 June 1979, he was located for the last time. I believe that either he was killed by ranchers or he permanently left the

study area and crossed a series of ridges to the east of the East Range.

Ten days before the last location of Gamma in the East Range, a young male wolf, Lambda, was taken in the same trap that had captured both Gamma and Epsilon (Table 10). Lambda was captured an additional 21 times and radiolocated 225 times in the East Range (Figure 10). After the captures of Epsilon and Lambda, no additional maned wolves were observed or trapped in this range.

In summary, the East Range was occupied by maned wolves Gamma (male) and Delta (female) for an unknown period of time prior to their respective captures in December 1978 and January 1979. About two months after her death, Delta was replaced by Epsilon, a young female new to the East Range. Gamma did not closely associate with Epsilon. About 10 days before Gamma's departure, a young male, Lambda, was captured in the East Range and rapidly took over most of the area formerly used by Gamma. Based on this circumstantial evidence, Lambda may have been responsible for the eviction of Gamma from the East Range. The areas used by Lambda and Epsilon, a total of 30 $km^2$, overlapped almost completely and differed little from that of former inhabitants Gamma and Delta.

*Kappa, Zeta, and Sigma:* Reported wolf activity to the west of the East Range prompted me to extend trapping efforts to that area. On 15 May 1979, Kappa, a young adult female wolf, was taken in what I named the West Range. She carried a radiotransmitter in this range for the remaining 12 months of this study. Seven weeks after the capture of Kappa, a middle-aged male wolf, Zeta, was taken in the same trap. The home ranges of these two wolves overlapped extensively (Figure 11) for about 14 weeks. On 17 October 1979, Zeta was located for the last time. Nearly six weeks later I followed the signal of his transmitter to the bank of a swollen stream. The nylon collar had been cut with a sharp instrument. Zeta had probably been killed by an area farmer and the removed transmiter thrown into a deep pond. A flash flood washed the transmitter up onto the shore on the day that I received the final radiosignal.

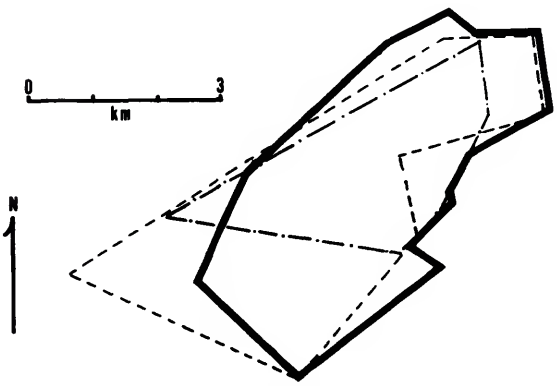


FIGURE 11.—West Range occupied by maned wolves Kappa (solid line; n = 106 total radiolocations; female), Zeta (dashed and dotted line; n = 25 radiolocations; male), and Sigma (dashed line; n = 46 radiolocations; male). Sigma replaced Zeta in this range after Zeta's death. Polygons represent the connected peripheral locations for each wolf.

On 18 November, a middle-aged male wolf, Sigma, was trapped in the West Range. Sigma took over the range formerly occupied by the missing Zeta (Figure 11), and on several occasions was observed in close association with Kappa.

The maned wolves of the Serra da Canastra led predominantly solitary existences. Wolves were never observed resting together, and they rarely travelled or hunted together. On only 25 occasions during this study were two adult wolves observed in close association. Groups of more than two adults were never seen. Lambda and Epsilon were seen in close association on 17 occasions in the East Range (Figure 12). Other data, such as the distribution of wolf feces and tracks, indicate that social activities involving both individuals were most common in September 1979 and were least common during March through May of the following year.

During periods when the members of a dyad were not often in close association, the location of one maned wolf was not independent of that of its mate. Both individuals used the same trails and resting places, but not simultaneously. In all

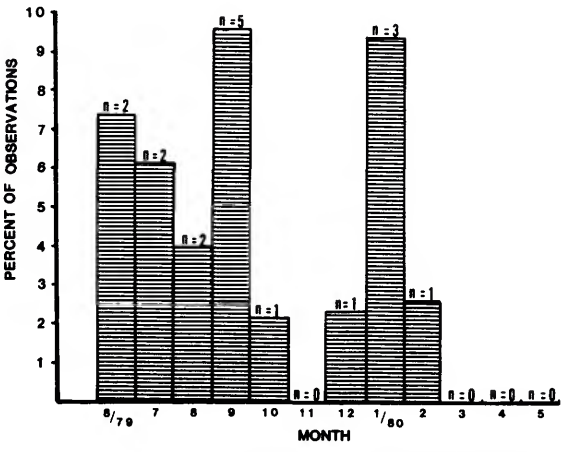


FIGURE 12.—Percent of radiotelemetric locations per month in which Lambda and Epsilon were found in close association (n = number of such observations).

but the Taperão Range, both members of a pair were taken in the same trap. Capturing one wolf often facilitated the prompt capture of its mate in the same trap. However, precedence in the use of traps and favorite resting places was not sex-specific.

VOCALIZATIONS.—High-amplitude vocalizations produced by maned wolves bear little resemblance to the variable and oscillating howls of the gray wolf (*Canis lupus*) or of the coyote (*C. latrans*). The vocalizations of maned wolves more resemble an extended variation of the bark of a large domestic dog. Each bark lasted approximately 0.7 second, was repeated at regular intervals of from 2 to 4 seconds, and sounded something like "oo-wáhh." Wolves repeated this call from 2 to 23 times in succession with an average of about 9 repetitions. Both sexes bark, but recognition by the author of an individual by its call was not possible. Occasionally as many as three wolves were heard barking simultaneously, and in at least two instances, wolves of two adjacent home ranges were heard exchanging vocalizations.

Wolves were heard barking on 46 occasions (Figure 13) of which 29 occurred in the East Range. These data indicate that maned wolves vocalized at all times of the year, and that a peak in frequency occurred during the months of June through August 1979. This higher incidence of vocalization might have been related to the replacement of Gamma by Lambda in June 1979 and to the subsequent reproductive behavior of Lambda and Epsilon.

The only additional vocalization that I heard was a low-volume growl produced when a trapped wolf was first approached by a human. When approached more closely, the trapped wolf invariably began a series of extended barks. Artificial predator calls and my own attempts to imitate the extended barks of maned wolves produced no discernible response in wolves in the Serra da Canastra.

DEPOSITION OF FECES AND URINE.—Feces were most commonly encountered in the vicinity of favorite resting sites, at den sites, and on or near prominent points such as rock outcrops, fence lines, trail intersections, or termite mounds. Scat grouping, elevation above surrounding ground level, and substrate often differed between these location types.

I examined three den sites recently used by maned wolves (see "Reproduction"); one had scats deposited by one or more adults and by two pups. Scats of 1 cm or less in diameter were found within a few meters of the den, while slightly larger scats were found farther from the den. Apparently, as pups grew they wandered and defecated farther from the den. All scats deposited by adults were located within a radius of 50 m from the mouth of the den, and all were deposited at ground elevation. Outside of this perimeter, I found no scats in the region of the den. I often found one, and occasionally two or three, concentrations of scats near vicinities of frequently used resting places. In three cases, these "latrines" were about 20 m from a favorite resting place of a pair of maned wolves, consisted of a low, flat rock, and contained between 10 and 20 scats. Several scats were also found on trails and rocks near these concentrations. These latrines were probably used by both wolves residing in a home range.

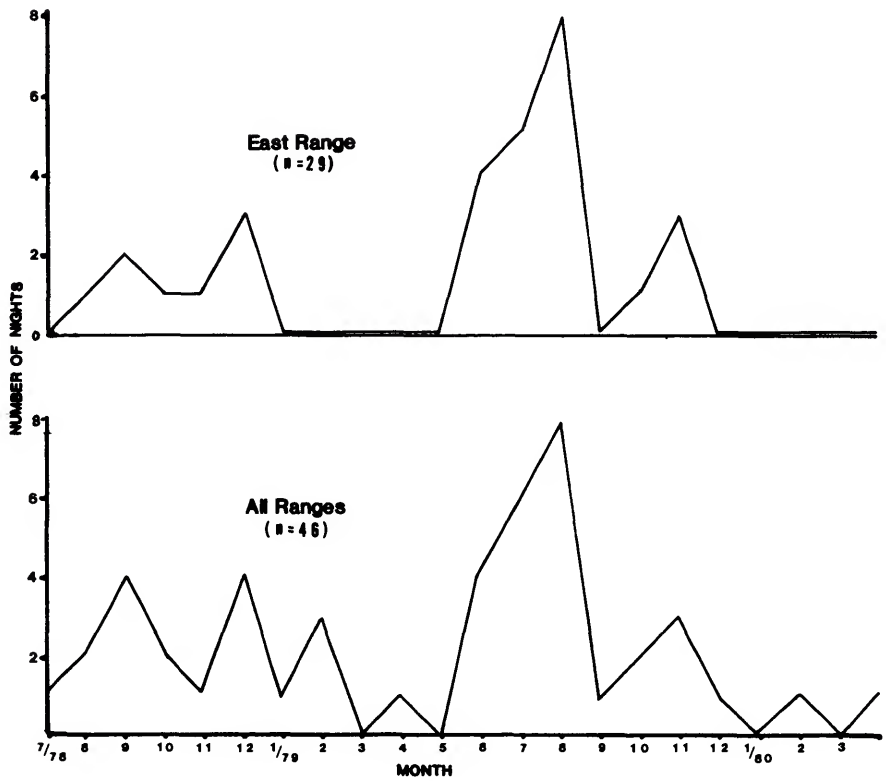


FIGURE 13.—Number of nights per month during which maned wolves were heard vocalizing in the East Range and in all ranges in the study area (n = the total number of observations).

Scats on trails were not distributed in a random fashion throughout a home range. When travelling from place to place, a maned wolf not actively hunting usually followed the path of least environmental resistance. Often-used trails were customarily located along open ridge tops, and scats along these important routes were deposited individually at intervals along trails. When I collected scats that had remained undisturbed along a trail for several weeks, maned wolves often replaced them with fresh scats within a few days.

Sixty-five percent of the 740 collected scats were found on rocks, dirt piles, or termite mounds elevated above the surrounding ground level (Table 11). The mean elevation from surrounding ground for all collected scats was 39.4 cm, and scats were collected from atop termite mounds up to 170 cm in height.

A few additional observations imply that defecation serves a defensive or alarm function. When startled or confronted at close quarters, those animals (a male and a female) sprang onto rocks about 60 cm high and defecated before fleeing. Finally, one night I observed the meeting of two wolves coming from opposite directions along the same trail. One of the two defecated on the trail and one barked repeatedly.

Little information was collected concerning urine-marking by maned wolves. The odor of the urine of maned wolves was prevalent along frequently used trails, indicating that urine-marking may have been employed in the same context as the elevated deposition of feces. No scratch marks were observed at the urination sites or with feces. In addition to urination by all wolves within traps, two individuals urinated im-

mediately after being released from traps—again suggesting a parallel between the alarm or defensive function of feces deposition and urination. All trapped wolves and a free female wolf were observed to use a squatting posture during urination. A free male was observed on two occasions to cock a hind leg when urinating.

In summary, maned wolves deposited feces and perhaps urine selectively with respect to location. Feces near a den site were deposited at ground level and were restricted to the area immediately surrounding the mouth of the den. Latrines in the vicinity of resting locations were used by both occupants of the home range and contained large concentrations of scats. Finally, scats found throughout the remainder of a home range were physically elevated, individually located, spaced at intervals and replaced after removal. I presume that these elevated and spaced feces served to advertise the presence of a maned wolf and may have aided indirectly in the defense of territories. Reduced dispersal of scats in the area of the den site and resting sites perhaps served to emphasize the ownership of those areas to unfriendly conspecifics or other predators.

RELATIONSHIPS BETWEEN ADJACENT PAIRS OF WOLVES.—The maned wolves studied maintained strict territoriality, i.e., boundaries of the ranges of each bonded pair were fixed and were almost never transgressed by wolves of an adjacent range. In most cases, the limits of these ranges were composed of physically identifiable landmarks, such as roads, ridges, or streams. Where they could be identified, the interfaces between adjacent territories were only a few meters wide. For example, a north-south road divided the West Range and the East Range. The wolves of each range used the areas on their respective sides of the road but neither pair used the road *per se* or crossed to the opposite side. Scats were liberally deposited along trails on either side of the road, and wolves were occasionally heard vocalizing back and forth across the boundary.

Home range boundaries appeared to remain constant over time. The two exceptions concerned those of wolves that had died or left the area. These two observations give some insight into the type of territoriality maintained by these maned wolves.

When Delta (female) died and Gamma (male) died or abandoned the west portion of the East Range, the interface between the West Range and the East range was the Gameleira Road (Figure 14). Within several weeks, these wolves were replaced by Epsilon (female) and Lambda (male). However, just prior to, or perhaps shortly after, the arrival of the latter pair, one or both wolves of the West Range extended their territory into the region referred to as Antônio's Area in the East Range. Within six weeks, all four resident wolves were observed at least once in this area of about 0.8 km$^2$. From early July until October, only Zeta (male) was found using Antônio's Area, indicating that a portion of the East Range had been annexed to the West Range. When Zeta was killed in late October or early November, Antônio's Area remained vacant for about four weeks before being repossessed by Lambda, the male of the East Range. He was the only wolf known to use this area for the remaining five months of the study.

A second region of contention along the border of the West and East ranges was a 0.75 km$^2$

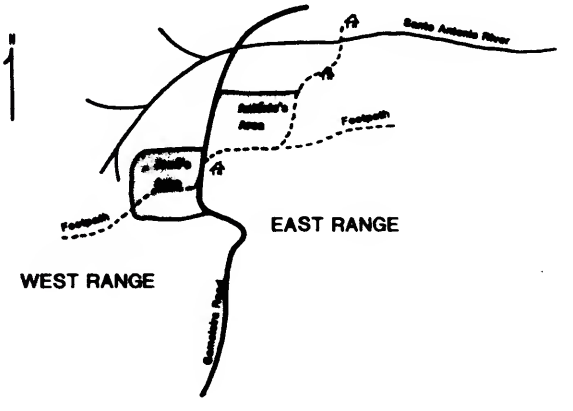


FIGURE 14.—Areas of dispute between maned wolves residing in the West Range and in the East Range. Antônio's Area was successively occupied by maned wolves of the East Range, West Range and East Range. José's Area was taken over by Lambda (East Range) after the death of Zeta (West Range). The Gameleira Road divides the two ranges.

pasture referred to as José's Area. This region was used occasionally by both wolves of the West Range until November 1979. After the death of Zeta, resident male of the West Range, José's Area was taken over for the duration of the study by Lambda, resident male of the East Range. Subsequent to this appropriation, the only wolf observed in this area was Lambda. José's Area had apparently also been added to the East Range.

The territoriality maintained between adjacent pairs of maned wolves was dynamic and expansive in nature. An area left vacant in one range by the death or departure of its owner resulted in appropriation by a wolf of the adjacent range. All successful appropriations were accomplished by male wolves; female wolves were not subsequently observed in these areas, suggesting a system in which males competed to secure territory rather than mates. These new additions to the territories of males may later be acquired by their mates during periods of decreased social distance associated with the breeding season.

LONERS OR NOMADIC MANED WOLVES.—On three occasions, maned wolves other than radiocollared individuals were observed in the vicinity of the West and East ranges. One sighting took place on the boundary between the West and East ranges, and the other two sightings were made along the southern boundary of the East Range. A skilled dog trailed one of these wolves north along the eastern periphery of the East Range for several kilometers before losing the scent at a river. Finally, on one occasion, a set of wolf tracks not attributable to a radiocollared wolf was followed from the northern extreme to the southern extreme of the interface between the West and East ranges. These observations suggest that maned wolves without fixed ranges travelled the peripheries of occupied ranges and presumably filled vacancies created by death or abandonment. Maned wolves Lambda, Epsilon, and Sigma replaced previous resident wolves and could have been loners prior to inheriting their respective ranges. No general statement can be made about the gender and age class of these wolves (a young male, a young female, and a middle-age male) as a group.

### *Feeding Ecology*

SEASONAL AVAILABILITY OF TROPHIC RESOURCES.—The numbers of available fruit species determined by questionnaires (Figure 15, Curve A), and monthly transect-lines (Figure 15, Curve C) were greater during the wet season than the dry season. The seasonality of 14 species of fruits identified in maned wolf scats (Curve B in Figure 15) suggests a similar seasonal fruiting pattern between the fruits available to and consumed by maned wolves.

The fruit lobeira (Figure 16) was considered apart from other fruits. This species is common in the Serra da Canastra but is not ubiquitous. Since this species prefers more organic soils than were prevalent in the national park, lobeira in this region was commonly located in richer soils and along horse-trails and near corrals. The species is everbearing, and I noted no quantitative differences in fruit production between seasons.

The results from the small-mammal trapping study (Figure 17; Dietz, 1983) suggest that small

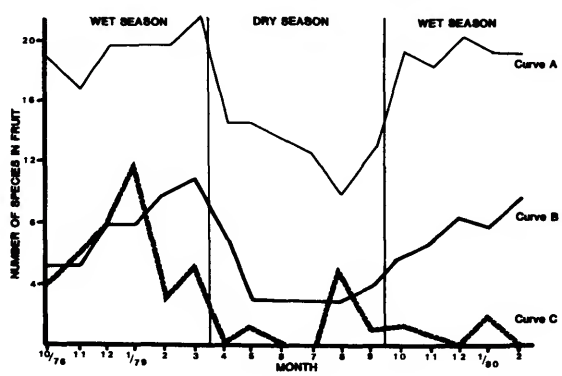


FIGURE 15.—Seasonal availability of fruit species in the study area. (Curves: A = the months during which 43 plant species reported consumed by maned wolves were in fruit; B = the months of fruiting of 14 species known to be consumed by maned wolves; C = the estimated total number of species fruiting per month as determined by transect-lines.)

FIGURE 16.—Lobeira (*Solanum lycocarpum*), "fruit of the maned wolf."

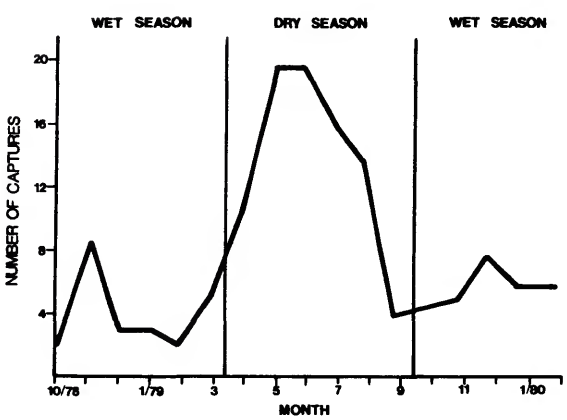


FIGURE 17.—Numbers of small mammals captured by author.

mammals were more abundant, or at least were more readily caught, during the dry season than during the wet season ($\chi^2 = 46.5$, 2 d.f., $p < 0.005$). Coleopteran beetles were extremely common during the months of October and November. Large volant ants swarmed during the month of November.

FOOD HABITS OF MANED WOLVES IN THE STUDY AREA.—The diet of maned wolves of the Serra da Canastra, based on a complete list of food items identified in scats (Tables 12, 13), is typical for a generalist omnivore; of 41 identifiable items, 20 were animal in origin, 20 were of plant materials and one was inorganic. Approximately 49 percent of the 2056 occurrences of food items in the analyzed scats were animal

material and 51 percent were plant material.

The components of the list of food items were divided into categories based on taxonomic relationships and on questions of interest. For example, the endangered status of the giant anteater (*Myrmecophaga tridactyla*) suggested that this species be included as a separate category (Table 14).

In terms of volume and occurrence in scats, the fruit *Solanum lycocarpum* was the single most important food item in the diet of the maned wolves of the Serra da Canastra. The regional common name for this fruit, "lobeira," freely translated means "fruit of the maned wolf." Larger examples of this fruit weighed about 450 g and resembled large tomatoes: green before, and yellow upon, ripening. Although plants of this species produced ripe fruit in our corral, I never observed ripe fruit in any other region. This, I assume, was due to domestic and wild fauna feeding on the fruits before or as soon as ripening took place. Maned wolves apparently did not await ripening before consuming it, as evidenced by large pieces of the green fruit in fresh feces.

Small mammals and birds occurred in 69 and 33 percent, respectively, of examined scats. The majority of small mammals consumed were probably cricetid rodents; however, specific identification was not attempted. The relatively high incidence of grass in the examined scats cannot be explained on nutritional grounds. Ingestion of grass has been observed in captive maned wolves (Kühme, 1975; Brady and Ditton, 1979), and D. Altmann (1972) reports that consumed grass is defecated within seven minutes of ingestion. Lloyd (1980) suggested that grass is often eaten accidentally by foxes catching small prey. A. Murie (1944) noted roundworms in wolf (*C. lupus*) scats composed largely of grass and speculated on the beneficial scouring action of grass. Lever (1959) mentioned the diuretic and emetic actions of some grasses on red foxes. On one occasion, I observed a maned wolf investigate and consume a clump of grass that had previously been urinated upon by another wolf.

At least six species of armadillo were common in the study area, and four were identified by their dermal scutes in 8.6 percent of examined wolf scats: *Dasypus novemcinctus* (in 31 scats), *Dasypus septemcinctus* (2), *Dasypus* sp. (2), and *Euphractus sexcinctus* (5). In most cases, ants and soil were also found in scats containing armadillo scutes, indicating that the former two items were perhaps ingested incidentally. Carcasses of armadillo preyed upon by maned wolves usually consisted of an intact but deeply scratched carapace and head. The ventral musculature and viscera, except the descending colon, were removed by the wolf. Maned wolves apparently surprise armadillos above ground and then use teeth and claws to turn the prey onto its dorsum, thereby exposing the more vulnerable venter.

Insect material was found in 14 percent of examined scats but comprised only 0.3 percent of total scat volume. This is in marked contrast with scats of sympatric foxes *Dusicyon* and *Cerdocyon*, which contained high percentages and volumes of insect remains. Maned wolves apparently do not forage as intensively for insects as do these smaller canids.

Small amounts of the hair of giant anteaters were found in 0.7 percent of wolf scats. These long, flat hairs were typical of the tail and dorsal mane of the giant anteater and were never found in sufficient quantity to suggest that a maned wolf fed on an anteater. Maned wolves may have removed a few hairs from the carcasses of dead anteaters, or may have occasionally attacked live anteaters. However, my observations indicate that during apparently chance encounters between maned wolves and giant anteaters, neither animal paid any noticeable attention to the other.

Seasonal changes in the food habits of the maned wolves of the Serra da Canastra were determined empirically by categorizing scats by collection date: dry season or wet season. Weathering and insects destroyed scats rapidly; therefore the differential survivorship of scats from one season to the next was ignored for the purposes of this analysis.

Lobeira, the main staple in the diet of these

maned wolves, was consumed consistently across seasons (chi-square, $p > 0.90$), whereas small mammal remains and foliage were encountered more often in dry-season scats (Table 15). Conversely, fruits (except lobeira) and insect remains were more prevalent in scats collected in the wet season.

The seven food items most important in terms of volume and of occurrence in scats were divided according to home range to test if use of trophic resources varied between wolf pairs. There were no differences in the percent of occurrences of these items between home ranges (chi-square, $p > 0.05$).

In summary, the numerically most important dietary components of the maned wolves of the Serra da Canastra were lobeira, small mammals and miscellaneous fruits. Consumption was apparently consistent with relative availability for all three of these classes of food items: lobeira was available and consistently consumed during both the wet and dry seasons; small mammals were most numerous and were consumed in greatest numbers during the dry season; fruits other than lobeira were most abundant and most often consumed during the wet season. Insects appeared to be most available and consumed most often during the wet season.

Maned wolves at the Serra da Canastra are, therefore, opportunistic generalists in their foraging habits. They feed on those food types that are most abundant, shifting to alternative resources when they become abundant. Trophic resource use did not differ between mutually exclusive home ranges.

EXPLOITATION OF DOMESTIC STOCK BY MANED WOLVES.—Beef carrion was usually available throughout the study area in the form of cattle dead from disease or injury. These carcasses were not exploited by area ranchers and would seemingly represent a large store of available protein for resident maned wolves. However, I neither located a radiocollared wolf, nor found a track or scent post, in the vicinity of cattle carcasses. Only one rancher reported having seen a maned wolf feeding on carrion: the wolf was seen with its head inside the abdominal cavity of a recently dead steer and was tugging at the viscera.

Interviews with area residents suggest that maned wolves never preyed upon calves or the adults of cattle, sheep, or pigs. Maned wolves may very rarely take newborn lambs in this region. Wolves occasionally prey on young pigs and frequently take domestic chickens.

The maned wolf's preference for chickens results in more human-related wolf mortality than any other interaction. Most Brazilians in the Serra da Canastra maintain flocks of chickens for eggs and meat, but the flocks are not shut in at night. A marauding wolf may kill one or many chickens in a single or multiple visits. The wary wolf becomes quite the opposite when approaching a flock of chickens. Wolves attacking my chickens advanced with bodies close to the ground and their gaze fixed on the prey.

Farmers can effectively defend barnyard fowl from predation by maned wolves by enclosing the roosting birds at night and by the acquistion of reliable watch dogs.

Radiotelemetric data suggest that some maned wolves attacked chickens with greater frequency than others. Of 23 reported incidents of predation on domestic stock, 14 (61 percent) took place from September through November, the time when maned wolf pups are most likely to be at den sites. Increased energy requirements imposed by nourishing the young may force the adult female and perhaps the male to exploit domestic stock to a greater degree at this time of year.

### *Reproduction*

DENNING.—I examined three den sites, and was informed of another, in which maned wolf pups had recently been raised. These dens were above ground, took advantage of natural features, and were located in open grass pasture. All were within a few hundred meters of roads frequently used by ranchers in cars or on horses. One den was situated in a clump of grass at the

base of a hillside; a second den was found in a shallow crevice formed by several large rocks. The third den, from which two pups were captured, was located in a grass-covered gully formed by previous water erosion. The cavity of this den was 30 to 100 cm deep and about 60 cm wide. Near the opening of the den, grass had been trampled and flattened. Wolf scats and chicken feathers were strewn within a radius of approximately 50 m. The fourth den was within the hollow of a termite mound excavated perhaps by a giant anteater. I obtained no evidence to indicate that maned wolves either excavated or enlarged abandoned underground dens.

PARTURITION AND LITTER SIZE.—None of the radiocollared wolves succeeded in raising a litter during my study. However, observations of Epsilon and Lambda during the last two weeks of August 1979, suggest that Epsilon may have whelped at that time. Radiotelemetry at this time indicated that Epsilon rarely moved from a dry creek bed near the west border of the East Range. Lambda was usually within a few hundred meters of her location and was never found farther than 2 km from the creek bed. Wolves were heard barking in this area on five nights during this period. The area immediately surrounding the possible den site was littered with scats. I did not examine the den site at close quarters until after the animals had abandoned the site and, therefore, have no direct evidence that whelping took place.

Interviews with area residents produced some data on 27 litters, as well as on one pregnant female near term and on one lactating female. To estimate dates of birth, information concerning the sizes of pups from 21 litters was compared with a theoretical growth curve based on interviews, my own observations, and published information (Acosta, 1972). Results (Figure 18) indicate that whelping may begin as early as February and reach a peak between June and September. Seventy-one percent (n = 15) of observed litters were estimated to have been born during these latter four months. The mean number of pups observed in 17 litters was 2.47, and the range was one to five pups (Figure 19). Weights and measurements of a litter of two female pups, estimated to have been born during the last two weeks of June 1978, are presented in Table 16.

PARENTAL CARE OF PUPS.—If Epsilon did produce a litter during the last two weeks of August 1979, inferences about the behavior of Lambda, her mate, are perhaps warranted. Although he was not located in the vicinity of the den site with the same regularity as Epsilon, his persistence in that area suggests that he may have played some role in the early care of the pups. On the morning of 25 August, my field assistant watched Lambda hunting in an area about 500 m from the den site and saw the wolf pounce on and seize a small animal in its jaws. Lambda carried his prey directly to the den site where Epsilon was located. Since Epsilon's pups would not yet have been old enough to ingest solid food, Lambda probably carried this food item to his mate. Beginning on

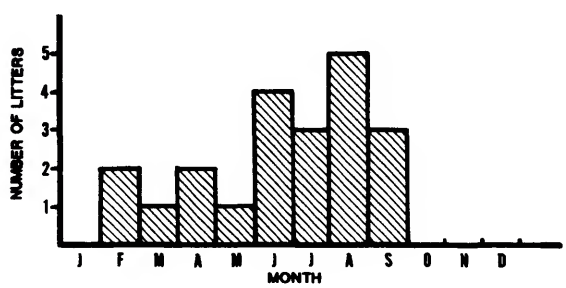


FIGURE 18.—Estimated months of birth of 21 litters of maned wolves seen by residents of the Serra da Canastra. Stature of pups was used to estimate months of birth.

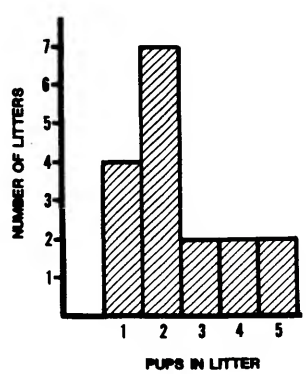


FIGURE 19.—Numbers of pups in 17 maned wolf litters observed by residents of the Serra da Canastra.

about 26 August, this pair of wolves again began to travel widely about their range and no longer spent a disproportionate amount of time at the den site. Although these wolves were observed together several times during the month of September, thorough searches revealed no evidence of pups at the den site.

Some inferences concerning parental care of pups at the den can also be drawn from information collected during interviews of area residents: of 24 litters of maned wolf pups observed by area residents, 16 were unaccompanied by adult wolves, 6 each had one adult wolf present, and 2 litters had 2 adult wolves present. If the only adult wolves participating in raising a litter are the parents of that litter, then at least some males associate with the female and her pups before the pups disperse.

I recorded six reliable reports by area residents who experienced aggressive attacks by single adult maned wolves as a result of human interference with litters of pups. In four cases, the advances were accompanied by threats and attempts to bite the offending humans. Three of the six attacks took place while cowboys were burning pasture, which flushed the wolves. Subsequently, the maned wolf pups were captured. In one case a wolf (identified as a female) advanced to within 4 meters of a cowboy who then released two pups. The adult wolf picked up both pups simultaneously in its mouth and carried them over a nearby hilltop. In another case, a cowboy captured a wolf pup and carried it 6 km to his ranch. An adult wolf followed him to the ranch and barked in the vicinity until the pup escaped.

A final observation concerns the probable relocation of a litter of pups by an adult female maned wolf. On 26 June 1977, an area resident saw an adult female wolf and two pups at a den site in the East Range about 500 m east of the den site selected by Epsilon. The pups, which did not yet have their eyes open, were located under a bent-over thatch of grass. The following day, the cowboy returned to the site and found neither the adult wolf nor the pups.

### *Parasites, Diseases, and Mortality*

ECTOPARASITES.—On 11 occasions (involving 8 wolves), total ectoparasite loads were estimated and representative parasites were collected for identification. The most commonly observed ectoparasites were ixodid ticks of the genus *Amblyomma*. The majority were *A. cajennense*, but a few *A. tigrinum* were also found (J. Whitaker per N. Wilson, in litt.). From 10 to 50 ticks were counted on each wolf ($\bar{x}$ = 24; SD = 12.1). Most were located in and around the ears.

One individual flea was found during each of 3 of the 11 examinations. The scarcity of this parasite may be related to the lack of underfur in this host. The only other ectoparasites noted were screw-worm larvae (*Cochliomyia hominivorax*) infesting the pinna and inner ear of maned wolf Delta. Chandler and Read (1961) mention that these insects often infest wounds resulting from tick bites; Delta had many ticks in the ears.

One ectoparasite conspicuous by its absence on examined wolves was the cuterebrid skin bot fly (*Dermatobia hominis*). Although the subcutaneous larvae of this parasite were extremely common in cattle and dogs in the study area, none were observed infesting maned wolves.

ENDOPARASITES.—Fresh feces collected from traps, after the release of six captured maned wolves in the Serra da Canastra, and from the cages of two recently captured wolves in the Belo Horizonte Zoological Garden were sent to the School of Veterinary Medicine, Federal University of Minas Gerais, for examination for endoparasitic eggs or larvae. Each examined wolf carried from two to four genera of endoparasites ($\bar{x}$ = 3, SD = 1; Table 18). Six genera of endoparasites were identified: four nematodes, one cestode, and one coccidian protozoan. Three nematodes, *Trichuris* sp., *Ancylostoma* sp., and *Toxocara* sp. were most frequently found, and were detected, respectively, in eight, seven, and four of the eight examined wolves.

Certain parasitic infestations, for example, dioctophymiasis (Mace and Anderson, 1975) probably would not be diagnosed by the sedi-

mentation method used in the above analyses. In addition, because only one fecal sample was examined from most wolves, the results probably underestimated the presence of parasites whose eggs or larvae are found only intermittently. Two additional genera of parasites were found in the second sample of feces than in the first sample from maned wolf Beta.

DISEASES.—The urine of six of eight wolves tested positive for cystinuria (Table 17). Cystinuria is an inherited metabolic disease described for some breeds of dogs and in humans. The significance of the unexpectedly high incidence of this disease in maned wolves is discussed by Bovée et al. (1981). The relationship between the high incidence of cystinuria and dibasic amino-aciduria is not clearly understood. One female wolf, Kappa, also showed abnormal amounts of glucose in the examined urine sample.

MORTALITY IN THE SERRA DA CANASTRA.—I saw the remains of only two wolves that had died of apparently natural causes: a few bone fragments from one subadult, and the nearly complete skeleton of Delta.

I was informed of 19 adult wolves and of 4 subadults that were killed by residents of the Serra da Canastra since approximately 1970. These wolves were killed in the following manners: seven were shot, five were run down and killed by dogs, four were trapped, two pups were taken from a den and subsequently died of disease in captivity, one pup was poisoned in captivity, one adult was killed by a thrown rock, one was clubbed to death, and two died of unknown causes. Sixteen of these 21 deaths took place while wolves were attempting to steal chickens from barnyards; no mortalities were attributed to hunting for sport.

### *Relations of Maned Wolves with Humans*

EFFECTS OF HUMAN DISTURBANCE ON MANED WOLVES.—Published accounts (e.g., Walker, 1975) state that populations of maned wolves tend to retreat before the advancement of human colonization. My observations do not support this assertion, because the home ranges occupied by maned wolves have also been occupied by farmers and ranchers for generations. Disturbance factors, such as annual burning, clearing of brush, and overgrazing throughout the entire area had no observable immediate effects on the movements and activity patterns of adult maned wolves. However, I noted three reports of maned wolf pups captured after being driven from dens by range fires. I observed no direct effects of subsistence-level agricultural practices on maned wolves in this area. Wolves made no apparent attempt to avoid fences, planted fields, roads, or the vicinities of uninhabited houses.

Hofmann et al. (1975–1976) stated that maned wolves in the Peruvian Pampas del Heath were diurnal in an area annually burned but uninhabited by man. My observations indicated that wolves were acutely sensitive to the physical presence of a human on horseback or on foot. Upon detecting a human in its vicinity, a wolf would seek cover in nearby brush or when in grassland would lie curled on the ground with only its ears occasionally moving. When a person approached to within about 2 to 3 m the wolves flushed, would piloerect and often vocalize, and bounded toward the nearest cover. In most instances, retreating wolves stopped at least once, turned broadside to the human, back arched and piloerect, and displayed one or more of the following behaviors: defecation, urination, vocalization, feigned hunting behavior, or olfactory investigation of a nearby rock or clump of grass.

A close encounter with a maned wolf is an extremely rare event in the Serra da Canastra. In two years of field work, I saw only five wolves without the aid of radiotelemetry. Three of these encounters were with wolves stealing chickens from my barnyard. Cowboys and farmers who lived and worked within my study area saw wolves only about once a year.

ATTITUDES OF AREA RESIDENTS TOWARD MANED WOLVES.—The attitudes of the rural residents of the Serra da Canastra toward maned wolves were not confounded by emotional or political conflicts and were based on a relatively accurate evaluation of the ecological role of the

wolves in that area. Maned wolves were not actively hunted for sport or for food but were occasionally killed in retribution for damage done to domestic stock. In these cases, individual offending wolves were selectively eliminated by the farmer or rancher suffering the loss. Excepting females defending pups, maned wolves are generally thought of as timid and fearful of man, and successfully coexist with him in the Serra da Canastra.

FOLKLORE.—The maned wolf has become an important part of Brazilian folk culture and is considered to have more supernatural identification with man than any other species of fauna. Maned wolves are thought to possess inexplicable powers, and a variety of parts of their anatomy serve as ingredients in folk medicines. For example, the right eye removed from a live maned wolf is said to increase the sexual prowess of the bearer after the wolf is released.

Another legend predicts that a large snake can be found in the kidney of a freshly killed maned wolf. The snake in this legend is likely to be the giant kidney worm common in maned wolves. Azara (1801) also mentions this legend for wolves in Paraguay.

During two visits to a locally renowned spiritualist healer (*curador*), I was informed of the recipes for many medicinal preparations based on maned wolf ingredients: A canine tooth from a maned wolf is tied around the neck of a child to cure or protect against dental problems. A piece of hide from a wolf is attached to a saddle or belt to cure the user of kidney or back-related problems. Ingestion of two small pieces of the heart of a freshly killed wolf will protect a snakebite victim from death. Finally, a chronic cough is best cured by drinking hot tea made from the dried feces of a maned wolf.

## Study of Captive Maned Wolves

### METHODS

#### *Facilities and Observation Schedule*

Behavioral observations were conducted on 15 maned wolves captive at the Conservation and Research Center (CRC), National Zoological Park, in Front Royal, Virginia. Wolves were housed in male-female pairs in fenced outdoor enclosures averaging approximately 725 $m^2$ in area (Figure 20). Each pair had access to one heated den and in some cases to an additional unheated den. Adjacent pairs were separated by cinder-block walls. With the exception of daily feeding and cleaning routines, wolves were not often disturbed by humans. Management of maned wolves at this facility was as described by Brady and Ditton (1979).

Preliminary observations indicated crepuscular activity peaks in maned wolf activity. Therefore, behavioral observations were conducted during the period from one hour before sunset to three hours after sunset, and during the period from three hours before sunrise to one hour after sunrise. Prior to each observation session I switched on three to five red floodlights in the enclosures where observations were to take place. Observations were conducted using infrared binoculars from blinds mounted 3 m from ground level adjacent to enclosures.

Scheduled observations were conducted (1) throughout the breeding season of 1981–1982 (12 October 1981 to 23 December 1981) until individuals of male-female pairs were separated prior to whelping; (2) subsequent to the rejoining of pair members following weaning of pups (8 February 1982 to 8 April 1982); and (3) throughout the breeding season of 1982–1983 (13 September 1982 to 20 December 1982). The three breeding pairs observed during these time periods produced five litters. One female apparently aborted late in gestation of the 1981–1982 breeding season. In addition to information concerning these breeding pairs, I recorded data concerning one nonbreeding pair each year. However, the same male was used in both nonbreeding pairs. Although these five pairs formed the nucleus for my behavioral studies, I was able to collect limited amounts of information on three additional nonbreeding pairs also captive at CRC.

I observed maned wolves from 1 to 4 hours per day on an average of five days per week (total

FIGURE 20.—Maned wolves in an outdoor enclosure at the Conservation and Research Center (photo taken from observation tower).

474 hours). Observation sessions with each pair lasted 1 hour and were systematically scheduled to represent all pairs equally. Sampling procedures included recording all occurrences of certain behaviors and of scan sampling at 2-minute intervals for other behaviors (J. Altmann, 1974). Additional information on sampling procedures is presented in the following sections.

Statistical analysis of the following behavioral data generally concerns (1) comparison between sexes of frequencies of behaviors and (2) comparisons between reproductive stages. In the former case I used the test for difference between proportions (Bruning and Kintz, 1977:222). In the latter case I applied a chi-square test for interaction (Steel and Torrie, 1960:366) in which expected values were calculated using means weighted by the appropriate number of hours of observation for compared stages. In both cases, data from breeding pairs were analyzed independently from those of nonbreeding pairs. Data from all breeding pairs were summed for each sex and for each reproductive stage, thus obscuring individual variation.

### *Operational Definitions of Reproductive Seasons*

In view of the lack of histological and physiological information concerning the estrous cycle in the maned wolf, behavioral information was used to define four reproductive stages for breeding pairs. Brady and Ditton (1979) state that 30 days prior to copulation, adult maned wolves show an increase in friendly interactions and in urine marking. I have termed this period of courtship as "proestrus." It as not possible to

record all incidences of copulation by breeding pairs. Therefore, I defined the period ($\bar{x}$ = 7.8 days) during which a female accepted mounting by her mate as "sexual receptivity." I refer to the approximately 55 days following sexual receptivity and prior to separation of pair-members as "gestation." Observations were not conducted during the remaining days prior to birth when male and female were housed separately. Finally, the period subsequent to rejoining of male and female, after weaning and removal of the pups from the mother, is referred to as "anestrus." Data concerning nonbreeding pairs were not divided into reproductive stages.

### *Behavioral Observations*

To test the hypothesis that synchrony of activity does not vary with the reproductive stage I recorded at 2-minute intervals the activity states of both wolves. Individuals on their feet were classified as active; those lying prone were categorized as inactive. A wolf remaining in a den for longer than 2 minutes was presumed to be inactive. Synchrony of activity occurred when pair-members were either both active or both inactive.

Information from the field study indicates that the individual distance maintained between pair-members changes as a function of reproductive stage. To establish the timing of these changes I recorded at 2-minute intervals the distance (in body-lengths) between wolves that were within five body-lengths of one another. I reduced the confounding effects of having only one den available to some pairs by deleting from the analysis those observations in which both wolves were inactive.

Throughout my observations I monitored all occurrences of 30 specific behaviors used in the regulation of individual distance. From these I selected six behaviors that are distance-decreasing and five behaviors that are distance-increasing in function (pp. 30–32). I used the available literature, interviews with personnel involved with care and management of maned wolves, and my own experience to select those behaviors least ambivalent in function. The summed frequencies of distance-increasing behaviors and of distance-decreasing behaviors were compared between sexes and among breeding stages.

To further understand the relationships between sexes and how these relationships change with reproductive stages, I defined and sampled on an all-occasion basis three types of initiative behavior: "Initiation of approach" was defined by one wolf approaching to within one body-length of its mate. Cases in which one wolf did not clearly initiate the approach were not scored. "Initiation of activity" was defined by one of two inactive wolves rising to a standing position. Conversely, "initiation of rest" occurred when one of two active wolves lay down or remained in a den for longer than 2 minutes.

Defecation, urination, and rubbing by maned wolves observed in this study were similar to descriptions of these activities by Kleiman (1967, 1972) and by Kühme (1975). I recorded all occurrences of these behaviors and of straddling (Brady, 1982). Frequencies of these scent-marking behaviors were compared between sexes and among reproductive stages.

Information on free-living maned wolves suggests that individuals of mated pairs are found in close association only during the breeding season. However, because females radiocollared in the Serra da Canastra did not produce viable litters, it was not possible to determine the timing of these changes with respect to reproductive stages. Neither was it possible to identify differences between sexes in bringing about these spatial changes. To address these questions each enclosure was divided into from 76 to 102 quadrats measuring approximately 2.6 m by 3.3 m in area. I assigned latitudinal and longitudinal coordinates to each quadrat and recorded at 2-minute intervals the locations of both animals in the focal pair. These data were computerized and the number of locations in each quadrat determined for each wolf during each reproductive stage. To reduce the cumulative effects of errors in location, and to correct for the differ-

ences in numbers of quadrats per enclosure, I used the following formula to estimate the percent of an enclosure frequently used by a wolf and also shared with its mate:

$$M = \frac{SFQ}{FQ} \times 100.$$

*FQ*, or the number of frequently used quadrats, is defined as those quadrats in which a wolf of specified sex was located during at least 1 percent of the total number of locations for that wolf. *SFQ*, or the number of shared frequently used quadrats, is defined as those frequently used quadrats with locations scored for both members of a pair. Thus *M* is a sex-specific coefficient of mutual use of space in the enclosure. An analagous parameter in free-living maned wolves would be range overlap.

Priority in feeding was recorded during the period October 1981 through December 1982. The staff caring for maned wolves noted whether the male, female, or both wolves initiated feeding when the afternoon ration was presented. No score was recorded when feeding was not initiated within 5 minutes after delivering the food.

## Results

### *Synchrony of Activity*

Results (Table 19) were analyzed for differences between reproductive stages. Excepting sexual receptivity x anestrus, all pairwise comparisons were significant ($p < 0.01$). The percent synchrony among nonbreeding wolves was less ($p < 0.001$) than that for proestrus, the reproductive stage with least synchrony in breeding pairs ($p < 0.001$).

### *Individual Distance*

The number of instances in which individuals of breeding pairs were located within five body-lengths (Table 20) was compared pairwise for the four reproductive stages. Values for each stage were significantly different from those of all other stages ($p < 0.001$). In addition, the value for nonbreeding wolves was significantly less ($p < 0.001$) than that for gestation, the reproductive stage with the lowest relative number of locations within five body-lengths.

In summary, individual distance as estimated by the inverse of the frequency of approaches to within five body-lengths, was at a minimum during the period of sexual receptivity and at a maximum during gestation in breeding pairs. Individual distance was significantly greater for nonbreeding pairs than for breeding pairs during any reproductive stage.

Evaluation of the mean distance between wolves (≤ five body-lengths apart) generally supports the above conclusions. Individuals of breeding pairs were found closest together during sexual receptivity and farthest apart during gestation. However, the mean distance between individuals of nonbreeding pairs was approximately equal to that for breeding pairs during sexual receptivity. Thus it appears that although members of nonbreeding pairs were rarely in close proximity, the distance between them on these occasions was small in comparison with that for breeding pairs.

### *Distance-increasing and Distance-decreasing Behavior*

Occurrences of the following behaviors were monitored throughout the study.

MOUNT.—Distance-decreasing. A wolf, usually the male, places one or both forepaws over the back or hips of its mate. Observed most often in a sexual context but occasionally during play.

PRESENT.—Distance-decreasing. The female averts the base of the tail exposing the anogenital region. During estrus this behavior may be accompanied by lordosis and/or by "trapping" of the male. In the latter case the female positions herself so that the male is forced to pass near her, e.g., in an open gate. She then turns away from him and presents. Presenting is rarely seen outside proestrus and sexual receptivity.

INVESTIGATION OF ANOGENITAL REGION.—Distance-decreasing. A pair-member sniffs and/or licks the anogenital region of its mate. This

behavior was most common during proestrus and sexual receptivity but was frequently seen at the onset of activity bouts during all reproductive stages. Males were observed performing this behavior significantly more often than were females ($n = 190$; $p < 0.001$).

INVESTIGATION OF MUZZLE.—Distance-decreasing. A maned wolf sniffs and/or licks the muzzle of its mate. This behavior was often used in greetings and preceded investigation of the anogenital region. I occasionally observed muzzle investigation following feeding and surmise that this behavior may transmit information about the recent feeding history of the recipient. There was no significant difference between sexes in the number of observed occurrences of this behavior ($n = 117$; $p > 0.05$).

TAIL-UP, TAIL-OUT.—Distance-decreasing. These actions form part of a behavioral continuum in which the sender elevates its extended tail a minimum of about 30° to a maximum of about 180° from the pendent position (see Kleiman, 1972:798) for a duration of from one to several seconds. These tail postures range in function from low-level appeasement to a compelling invitation for social contact. For example, a maned wolf passing unusually close to its resting mate might send a tail-out of 1-second duration. The tail-up display by maned wolves does not appear to be related to expression of dominance as in *Canis lupus* (e.g., Zimen, 1975) and *Canis familiaris* (e.g., Fox, 1978), but rather to the regulation of individual distance. Tail-up and tail-out were both performed significantly more often by males than by females (tail-up: $n = 229$, $p < 0.01$; tail-out: $n = 376$, $p < 0.001$).

YAWN.—Distance-increasing. The yawn was one of the behaviors most frequently observed in these maned wolves ($n = 811$). Yawning was most often performed by males and was never observed occurring synchronously or in sequence by pairs. Thus, Ewer's (1968) hypothesis that yawning in the Canidae is a social ceremony serving to rouse and synchronize the moods of group members is not substantiated by this study. Yawning apparently functions as a low-level aggressive display and was often illicited when a pair-member approached unusually close to its mate. In most cases the wolf receiving the yawn altered its course to increase distance between individuals.

AVOIDANCE.—Distance-increasing. I defined avoidance as one wolf moving out of the way or clearly altering its course to make way for its mate. Males avoided females significantly more often than females avoided males ($p < 0.001$). However, these data are not homogeneous across pairs. In the five observed pairs the percentages of total occurrences of avoidance behavior contributed by males were 95, 94, 61, 42, and 34. Thus, in two pairs the majority of avoidance behavior was exhibited by males, in two pairs each sex behaved in roughly equal percentages, and in one pair the female avoided the male more often than conversely.

Avoidance behavior was at a maximum during anestrus and at a minimum during sexual receptivity (proestrus = 1.15 occurrences/hour of observation; sexual receptivity = 0.32; gestation = 1.14; anestrus = 1.36).

GAPE.—Distance-increasing. This agonistic display consisting of opening the jaws, was usually accompanied by lowering the head, flattening the ears laterally, and occasionally by growling. The gape was often used in defense of food or a favored resting place, or in retribution for an invasion of individual space. I found no significant difference between sexes in the frequency of occurrence of gapes. Occasionally a wolf began to gape at its mate and then terminated the display in a yawn, usually when the stimulus apparently inducing the gape was suddenly removed, e.g., the approaching mate reversed its direction. This grading of a gape into a yawn suggests a motivational relationship between these two behaviors.

FULL PILOERECTION.—Distance-increasing. A maned wolf in full agonistic display can erect its white throat-patch and its dorsal mane from between its ears to the tip of its tail. This impressive piloerection may be accompanied by broadside positioning and by cat-like arching of the back—both presumably to maximize visual impact. Full piloerection was defined as the raising of the

dorsal mane from the ears to at least the rump and was observed on 68 occasions with no significant difference in frequency detected between sexes.

BITE.—Distance-increasing. Biting occurred in three contexts: copulation (never observed during scheduled observations), intense play, and intense agonistic encounters. Bites during play were inhibited and were uncommon. Intense aggressive interactions were usually ritualized and involved the distance-increasing behaviors described above. Uninhibited aggressive bites were very rare and were usually directed to the recipient's shoulder or flank. No bite wounds were noted during the 1981–1982 breeding season, but five were recorded during the following year: a female with a wound at the base of the tail during late anestrus; a female with a wound on the left shoulder during proestrus, and another on the left flank during early anestrus; a nonbreeding male with two wounds to the left shoulder. The increase in the number of adult maned wolves housed at these facilities during the 1982–1983 breeding season may have precipitated aggressive interactions.

Total frequencies of distance-increasing and distance-decreasing behavior for each sex (Figure 21) were not independent of reproductive stage ($p < 0.005$). In addition, the frequency of distance-increasing behavior by males was significantly greater than that for females during all reproductive stages ($p < 0.05$). The frequency of distance-decreasing behavior for males was also greater during proestrus ($p < 0.05$) and anestrus ($p < 0.001$).

Examining Figure 21 it becomes apparent that the rates of distance-increasing behavior remained relatively more stable across reproductive stages than did those of distance-decreasing behavior. The major variation from the mean (for all reproductive stages) for distance-increasing behavior was a 43 percent decrease by females and a 46 percent decrease by males during sexual receptivity. However, distance-decreasing behavior during gestation declined from 124 percent above the all-stages mean to 66 percent below the mean for males, and from 62 percent above the mean to 62 percent below the mean for females.

Males of nonbreeding pairs performed proportionally more distance-increasing and distance-decreasing behavior than did females ($p < 0.001$). In addition, neither the percentages of distance-increasing nor distance-decreasing behavior exhibited by each sex in nonbreeding wolves differed significantly ($p < 0.01$ from those in breeding pairs (all-stages means). However, the frequencies of distance-increasing and distance-decreasing behaviors in nonbreeding wolves approximated those for the reproductive

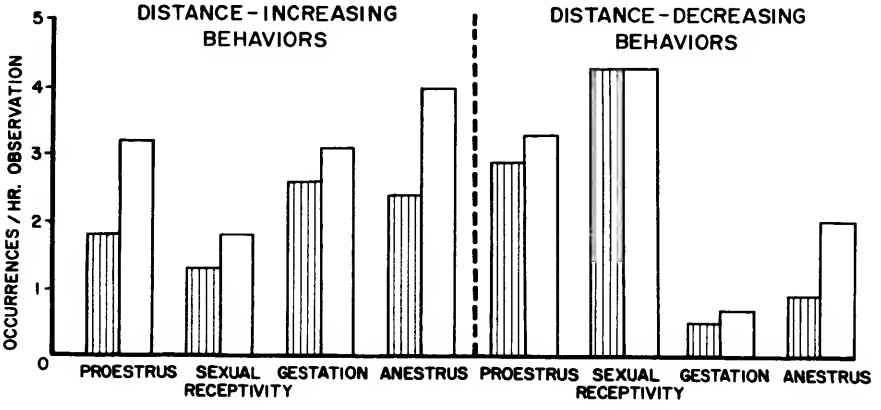


FIGURE 21.—Total frequencies of selected distance-increasing and distance-decreasing behavior for three pairs of maned wolves (striped bars = females; solid bars = males).

stage with the lowest frequencies in breeding pairs (distance-increasing: nonbreeding male = 0.67 occurrences/hr observation, female = 0.37; distance-decreasing: male = 0.91, female = 0.43). In summary, although nonbreeding pairs did not differ from breeding pairs with respect to relative rates of behavior performed by each sex, in absolute terms the rates for nonbreeding pairs were lower than those of breeding pairs.

### *Initiative Behavior*

There was no significant difference between sexes with respect to the all-stages frequencies for *initiation of approach* ($p > 0.01$; Figure 22). However, approaches during gestation were initiated significantly less often by females than by males ($p < 0.001$). Frequencies of approach initiation were highest during sexual receptivity

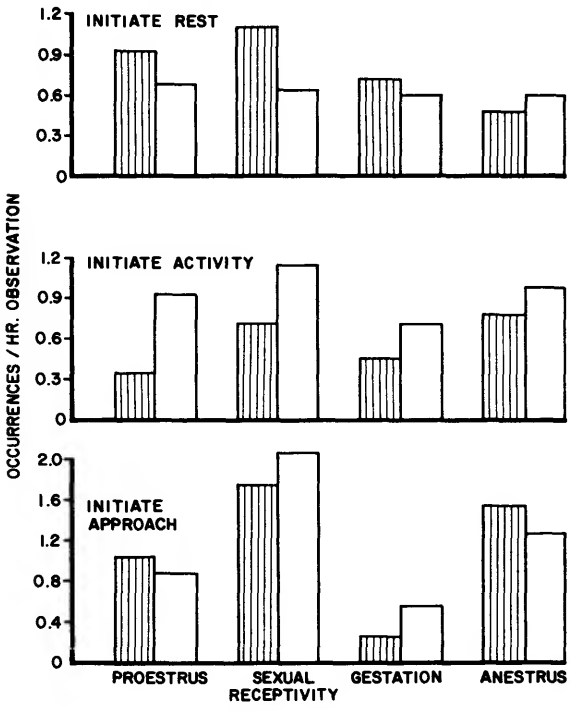


FIGURE 22.—Frequencies of initiative behaviors for three breeding pairs of maned wolves (striped bars = females; solid bars = males).

(male = 128 percent above the all-stages mean; female = 86 percent above the mean) and lowest during gestation (male = 38 percent below the mean; female = 76 percent below the mean). The frequencies of approach initiation for nonbreeding pairs were significantly greater by males ($p < 0.05$) and were approximately equal to those for breeding pairs during gestation (male = 0.33 occurrences/hr observation; female = 0.23).

*Initiation of activity* was performed significantly more often by males than by females ($p < 0.001$) irrespective of reproductive stage in breeding and in nonbreeding pairs, and also for each stage considered individually in breeding pairs ($p < 0.05$). Frequencies for nonbreeding pairs were small in comparison with those for breeding pairs (male = 0.35 occurrences/hr observation; female = 0.12).

In contrast, *initiation of resting* was performed significantly more often by females than by males in breeding pairs ($p < 0.05$) and in nonbreeding pairs ($p < 0.001$). The only exception to the above was during anestrus, when males initiated rest more often than did females ($p < 0.05$). Frequencies for initiation of rest by nonbreeding pairs were lower than those for breeding pairs (male = 0.04 occurrences/hr observation; female = 0.45).

### *Scent Marking*

Straddling consists of the wolf swinging a hind leg over a bush or tuft of grass taller than its back. The wolf then advances until the bush bends beneath its tail and anogenital region. This behavior was often accompanied by alternately elevating the hind limbs, by yawning, and by shaking the mane. Straddling was usually maintained for several seconds and until the straddling wolf was in the visual field of its mate. In four instances I failed to find urine on or beneath straddled vegetation. However, on various occasions I observed wolves sniffing and/or rubbing on shrubs recently straddled by their mates. Thus, it is likely that some olfactory information,

perhaps from the anal glands or genitalia, is deposited on straddled items. I found no significant difference in frequency of straddling between sexes in breeding or nonbreeding pairs ($p > 0.1$; Figure 23). There were, however, differences in frequencies of straddling among reproductive stages for both males and females ($p < 0.005$). Straddling was most common during proestrus and least common during anestrus in breeding pairs. Straddling was very rare in nonbreeding pairs (male = 0.01 occurrences/hr observation; female = 0.01).

Rubbing by these maned wolves was always accomplished from a standing position and usually included sliding the head and neck along an elevated object or on the ground. I never observed a maned wolf rubbing on feces, but rubbing on recently deposited urine, either its own or that of its mate, was very common. The frequency of rubbing behavior (Figure 23) did not differ between sexes ($p > 0.1$), with all breeding stages combined. However, during proestrus and gestation females rubbed more than did males ($p < 0.005$), and during anestrus males rubbed more often than did females ($p < 0.001$). Frequencies of rubbing were not independent of reproductive stage for males or females of breeding pairs ($p < 0.005$). Males rubbed most during anestrus and least during proestrus; females rubbed most during gestation and least during anestrus. Rubbing by nonbreeding wolves did not differ between sexes ($p > 0.01$) and was infrequent in comparison with rates for breeding wolves (frequency for females = 0.11 occurrences/hr observation; male = 0.13).

Each wolf had two or three sites where it deposited virtually all of its feces. These sites were usually but not always shared by both pairmembers, and were sometimes used in excess of two years. With two exceptions (on a table and on a den roof), middens were located at ground level. Placing five cross-sections of logs ranging in height from 10 to 40 cm into enclosures produced no observable changes in defecation patterns. Defecation, often accompanied by an extended-bark vocalization, was a common response to the presence of an unfamiliar person in an enclosure and suggests that defecation has an aggressive or alarm function in maned wolves. Also of interest is the observation that maned

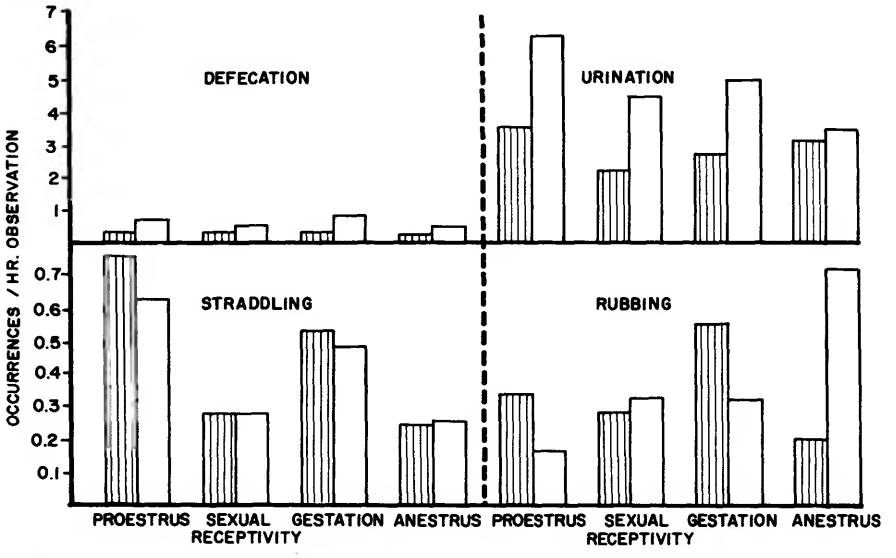


FIGURE 23.—Frequency of scent marking by defecation, urination, straddling and rubbing by breeding pairs of maned wolves (striped bars = females; solid bars = males).

wolf pups practiced locus-specific defecation as soon as they became mobile, but maintained the midden separate from that of their female parent.

Defecation by males was more common than by females for nonbreeding pairs. Males of breeding pairs defecated more than females during all reproductive stages except sexual receptivity ($p < 0.001$). The lack of significance during sexual receptivity ($0.05 < p < 0.1$) may be due to small sample sizes (12 occurrences for males; 6 for females). Although defecation rates by females were independent of reproductive stage ($p > 0.1$), those for males were not independent of reproductive stage ($p < 0.005$). Defecation rates for both sexes were slightly higher during gestation and lowest during anestrus in breeding pairs. Rates for nonbreeding pairs were 0.11 occurrences per hour of observation for females, and 0.47 for males.

Urine was most often deposited on elevated objects throughout the enclosure, but also on level ground and on walls. Although some objects were marked more often than others, I only noted locus-specific urination practiced by females during gestation, and then usually along the fences nearest other maned wolves. Sequences in which the urine mark of one wolf was marked, or rubbed and then marked by the mate, were common throughout the study and were practiced with approximately equal frequency by both sexes. With the exception of anestrus for breeding pairs ($p > 0.1$), rates of urine marking were greater for males than for females in nonbreeding and in breeding pairs, when reproductive stages were combined or when considering each stage individually ($p < 0.001$). Rates of urine marking for males and for females were found not to be independent of reproductive stage in breeding pairs ($p < 0.005$). Rates were greatest during proestrus for both sexes, least for females during sexual receptivity, and least for males during anestrus. Rates of urine marking by nonbreeding wolves (female = 0.39 occurrences/hr observation; male = 1.5) were less than those for breeding pairs.

*Vocalization*

Kleiman (1972) and Brady (1981) have described the high-amplitude roar-bark or extended-bark of the maned wolf. The latter author postulated that this call functions primarily as a spacing mechanism within sexes. During the field study, I noted several exchanges of vocalizations between pairs and between pair-members, indicating that the function of this call might also be related to localization between and within pairs.

I intended to determine at CRC the frequency and duration of vocalization bouts and to identify participants during each reproductive stage. However, because my observations were mainly at night, and I could not identify individual wolves by their calls, it was often impossible to identify individual vocalizing wolves. The smallest identifiable unit was often of the focal pair. Also, since the reproductive stages of breeding females were not entirely synchronous, it was necessary to combine data from the proestrous, sexual receptivity, and gestation stages into a single breeding season.

Results (Table 21) show that these wolves vocalized more often, engaged in more bouts involving more than one wolf, and used more barks per occurrence during the combined breeding stage than during the single anestrus stage ($p < 0.005$). For those wolves whose sex could be determined, males vocalized more often than did females ($p < 0.001$). Occurrences of vocalization were more common early in the breeding season (Oct–Nov) than later in the breeding season (Dec) suggesting that vocalization was more common during proestrus and sexual receptivity than during gestation.

On five occasions a wolf inside a den exchanged vocalizations with its mate outside the den. In three cases a wolf's vocalization outside a den apparently caused its mate to leave the den, and in two cases vocalization in one enclosure apparently caused a wolf in an adjacent enclosure to leave its den. These observations support the hypothesis that during the breeding

season the long-distance call functions primarily in communication between pair-mates.

### *Use of Space*

Results (Figure 24) show a high coefficient of mutual use of space (p. 30) by females during proestrus. Combining information from studies in the field and in captivity it appears that the essentially solitary existences maintained during anestrus are terminated by encroachment of males into areas formerly used mainly by females. Levels of mutual use of space by both sexes remained high, at least until late gestation.

### *Precedence in Feeding*

The results of this survey were not homogeneous with respect to initiating feeding by sex. In two breeding pairs, the females were predictably first to feed (97 and 80 percent of all recorded feedings). In the third breeding pair the male fed first in 87 percent of recorded observations. Instances of male and female beginning feeding simultaneously were rare (3, 3, and 10 percent in breeding pairs), and precedence did not appear to vary as a function of breeding stage. In two of three nonbreeding pairs the male fed first (86, 69 percent), and in the third pair priority to feed was relatively evenly split (male = 42 percent; female = 49 percent). Finally, in one pair of hand-raised siblings one year of age at the beginning of this survey, both male and female initiated feeding together in 100 percent of recorded feedings.

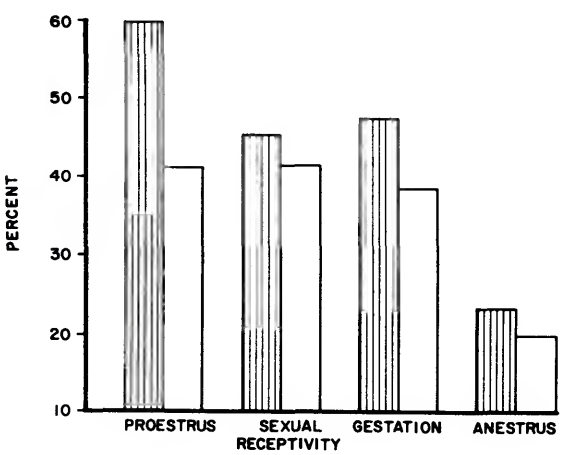


FIGURE 24.—Frequency of shared use of enclosure quadrats by three breeding pairs of maned wolves (striped bars = females; solid bars = males).

Caching of food has been described for female maned wolves prior to parturition (Encke et al., 1970; Brady and Ditton, 1979). During the present study caching by both sexes was observed for two breeding pairs late in gestation. The behavior pattern was similar for both pair-members: one pair-member carried a food item for several minutes, buried it in a shallow depression excavated with forepaws and nose, and moved a few meters away. Occasionally, the same wolf then dug up its cached food and repeated the sequence. In several cases, however, the wolf's mate retrieved the cache, carried it for several minutes and buried it again. This food sharing, although accompanied by aggressive gaping, piloerection, and short chases, represents a significant reversal in the otherwise highly defensive attitude concerning food possessed by maned wolves.

## Discussion

### *Evolution of Sociality in a Grassland Habitat*

Generalized representatives of the dog family arriving in South America were exposed to a variety of selective pressures in their new environment. One of these would have been the necessity of locomotion through the tall grass prairies covering much of the continent. There were two evolutionary options open to cursorial mammals living in this type of habitat: travel through the grass at ground level or travel high enough above ground level that resistance due to body contact with stiff plant stems were reduced. Apparently, the maned wolf was the only South American canid to evolve the latter specialization.

Long legs necessitate a relatively large body

size which in turn places increased energy demands on the individual (Brown and Lasiewski, 1972). During the late Pleistocene, when the maned wolf was dispersing across the savannas of central South America, most of the large native herbivores became extinct and were replaced ecologically by highly successful cricetid rodents (Webb, 1969, 1978; Simpson, 1980). Foraging on this dispersed trophic resource base would not have been conducive to social living. The fact that a perennial bond persists between members of a pair of maned wolves supports the assertion of Kleiman and Eisenberg (1973) that the pair bond is a phylogenetically old trait within the Canidae.

I suggest that the monogamy and strict territoriality (sensu Burt, 1943) displayed by the maned wolf are the results of long-term ecological and genetic constraints. The energetic demands imposed by the large body size of the maned wolf and its morphological and physiological dependence on a food source that is scarce, dispersed, and relatively dependable may have favored the selection of a social organization based on solitary and mutually exclusive foraging. Because of the lack of exposure to factors promoting sociality, this social structure may now be relatively inflexible. That is, the genome of the maned wolf may limit the extent of cooperative social interaction among individuals.

If territoriality promotes survival of maned wolves, natural selection should favor characteristics that emphasize the ownership of an area. Several such morphological and behavioral traits are displayed by this species. Extended-bark vocalizations are loud and far-reaching but not complex or variable between individuals. This type of signal is well suited for transmitting simple messages to all conspecifics at a long distance from the sender. The urine of maned wolves has a strong odor and is placed in a manner that would increase detection by conspecifics at a distance or long after it has been deposited. Visual cues used by the maned wolf are discernible at considerable distances: erection of the dorsal mane, broadside arching of the back, and contrasts in color of the regions of the body are used in display. In monogamous species there would be little need for sexual dimorphism, and natural selection should favor monomorphism (Kleiman, 1977) as is found in maned wolves.

### *The Pair Bond in Maned Wolves*

Canid social systems are often highly flexible in response to a number of factors, including food availability, human persecution, and population status (Macdonald, 1979, 1983). Therefore, it would be premature to state that the social organization of the maned wolves of the Serra da Canastra is "species-typical." However, based on my studies of free-living and captive maned wolves I offer the following conclusions concerning the pair bond in this species.

The majority of canids are monogamous (Kleiman, 1977) with males of most of these species assisting in provisioning of young (Wittenberger and Tilson, 1980). Such direct male parental care benefits the reproductive fitness of both sexes. Male maned wolves also occasionally provision their offspring in captivity (Kleiman and Malcolm, 1981). However, information from the Serra da Canastra indicates that females are not dependent on direct aid from their mates for the care of offspring. There is no indication that groups of maned wolves contribute to the welfare of the offspring of a single female as in certain other canid species (Macdonald, 1980; Moehlman, 1979). In only two instances during the field study did local observers see two adult wolves accompanying pups. All observations of defense of pups by adults involved only a single adult. In all cases in which it was possible to determine the sex of an adult accompanying pups, the adults were females.

The facultative monogamy (Kleiman, 1977) seen in maned wolves apparently evolved as a result of indirect selective factors, such as (1) the mutual defense of an area large enough to support parents and offspring prior to dispersal of the latter; (2) mutual defense of young from conspecifics or other predators; and (3) reduced

levels of intersexual aggression, especially during the breeding season. Higher rates of vocalization, scant marking, and initiation of activity by captive males, and territory acquisition by males of the Serra da Canastra, indicate that males play a more prominent role in territorial defense than do females. Because of the high level of intraspecific aggression, male territorial defense is probably important in the indirect defense of pups as they begin to travel farther from the female parent.

In summary, territoriality in maned wolves is associated with foraging on a dispersed but relatively predictable trophic resource base. Male and female share the same territory because social interactions, especially those during the breeding season, are less costly in established pairs. The amount of intrapair aggression would be expected to decrease from year to year in permanent pairs (Ewer, 1973). Facultative monogamy may have evolved under circumstances in which the reproductive fitness of both parents benefitted more from male territorial defense than from direct male care of offspring. In addition, the association of a resident male with his mate and her litter may increase his reproductive fitness by decreasing the probability of another male copulating with that female (Niewold, 1980).

Although the social organization of the maned wolf appears relatively unflexible, the nature of the pair bond changes with reproductive stages, and allows female choice in the extent to which males directly participate in parental care. Anestrus in captive females was characterized by mutual avoidance by pair-members and by reduced mutual use of space. The frequency of scent marking, as well as the frequency, duration, and synchrony of vocalization were at minimum levels for both sexes. Males maintained maximum levels of distance-increasing behavior and initiated rest more often than did females. Data on vocalization and movements of wolves in the Serra da Canastra are consistent with these conclusions.

During proestrus, urine-marking reached maximum frequencies for both sexes, suggesting increased exchange of information between sexes and/or increased territorial defense. As the females become more olfactorily attractive, males exhibited a high level of distance-decreasing behavior, and the coefficient of mutual use of space increased to a maximum for females. Thus, proestrus is a period of social approximation reversing the avoidance characterizing anestrus. Because of the important role of this extended courtship, I would expect cuckoldry to be rare in free-living maned wolves.

As expected, sexual receptivity features a reduction in individual distance and in distance-decreasing behavior. However, although urine markings by males continued at a relatively high rate, frequency of urination by females dropped to a minimum level. Because in a monogamous canid with a short estrus the male presumably accompanies the female, her scent marking is perhaps less useful than other more overt behaviors. In addition, a female's advertisement of sexual receptivity to more than one male risks intermale combat and potentially reduces the likelihood of her conception.

Gestation shows marked changes in relations between the pair. Individual distance is maximized and distance-decreasing behavior drops to a minimum. However, food sharing occurs and the mutual use of space remains high for both sexes. The extent to which a female allows her mate to care for offspring may depend on the persistence of these traits after parturition.

There was no evidence of a social dominance hierarchy in these captive pairs. The outcome of social conflicts between male and female was generally predictable for each pair of wolves, but was not generalizable with respect to sex. Dominance was specific to each situation and was based on norms established by each pair. For example, one member of a pair had precedence in feeding, whereas its mate had priority in the use of a favorite resting place.

### *Conservation and Management*

Most, if not all species are proceeding toward extinction at varying rates. John Terborgh

(1974:715) writes: "Our goal as conservationists is not to enforce a stasis of nature by somehow stopping the march of evolution; that is impossible. Rather, it is to prevent, over the period of transition to a steady state society the process of species loss from running too far ahead of the process of species gain." When a species rapidly approaches extinction, the cause is often a disequilibrium with environmental factors related to human activities.

### *Maned Wolves in the Wild*

Several traits have been implicated in extinction-prone species. For example, large body size and habitat specialization were proposed by Brown (1971) and Willis (1974) as detrimental to long-term survival. The maned wolf qualifies in the first category but not in the second category. The geographic distribution of the maned wolf includes a variety of habitats including grasslands, *chaco*, *pantanal*, *pampas*, several types of cerrado, as well as part of the *caatinga* of northeastern Brazil (Dietz, in press). In addition, the maned wolf has extended its range into the *Zona de Mata* of southeastern Brazil. In the last 100 years, the tropical forest that covered the latter region has been cut and replaced by farms, ranches, and commercial conifer and *Eucalyptus* plantations. Maned wolves are often observed in these commercial conifer stands where small mammals are abundant (Dietz et al., 1975).

Factors such as den sites and resting areas do not appear to be limiting population density in this species. Although seasonal variation may reduce the availability of some food items, it is likely that others would be favored and that maned wolves would take advantage of those items that are most abundant. The generalist foraging habits of this canid would tend to buffer it against population decline due to sudden changes in food resource composition.

Several authors have stressed the negative effects of human colonization on population density of the maned wolf (Dennler de la tour, 1965; Langguth, 1972, 1975). However, no evidence is presented in support of these statements. The wolves and humans of the Serra da Canastra interacted very little. With the exception of an occasional wolf killed for stealing poultry, farmers and ranchers were indifferent to wolves. Conversely, maned wolves avoided being seen, but did not avoid the areas inhabited, by humans. In a few instances, wolves were reported using abandoned human habitations and hunting small vertebrates dislodged by tractors. In general, direct human disturbance, including my activities, appeared to have little effect on the maned wolves of the Serra da Canastra.

The long-term indirect effects of human activities on maned wolves are potentially significant. Practices, such as extensive overgrazing by cattle, pasture management by annual burning, and the cutting of brush, and agricultural practices inducing erosion, probably have significantly unfavorable impact on the resource base available to these wolves. These effects would be more severe in regions where the percentage of tillable land is greater than in the Serra de Canastra. However, since agriculture has been much the same in the Serra da Canastra for at least the past 80 years and maned wolves are still present, areas such as this will probably retain populations of wolves for the present.

Populations of free-living maned wolves are apparently not in immediate jeopardy over much of their range in South America. However, this situation could change radically as a result of large-scale habitat modification taking place in the cerrado of the Brazilian Highlands. With that in mind, I recommend the following policies be adopted throughout the species range of the maned wolf.

The great majority of biological reserves, such as state and national parks, will not be large enough to support populations of maned wolves. I estimate that no more than 10 maned wolves live entirely within the confines of the Serra da Canastra National Park. However, on the order of 40 wolves may have ranges that overlap both park and private land. I recommend the establishment of buffer strips 2 km wide around the perimeter of parks and reserves within the species range of the maned wolf. Landowners within

these protected zones could be given tax incentives in return for performing prescribed habitat management practices such as controlled burning, grazing, hunting, and clearing of brush. In the case of the Serra da Canastra National Park, this action would effectively increase by one-third the area of the land protected by this park and perhaps triple its carrying capacity for maned wolves.

A campaign to increase public awareness concerning the endangered status of the wolf might significantly reduce mortality of wolves stealing poultry. A campaign of this nature is likely to succeed in Brazil for two reasons: first, the maned wolf does not have the negative public image that large canids have in the United States; second, Brazilians are nationalistic and, therefore, likely to preserve an animal that they perceive to be part of their national heritage.

### *Maned Wolves in Captivity*

Several facts indicate that the future of the maned wolf in captivity may not be entirely secure. First, fewer than 100 individuals are exhibited in 12 zoos worldwide (Bush, 1980). Since the United States Endangered Species Act of 1973, and the International Convention on Endangered Species, also in 1973, few wild-caught maned wolves have entered captive populations in countries outside South America. Second, successful reproduction by maned wolves in captivity is improving but is still relatively rare (C. Carvalho, 1976). Although 105 births were recorded in zoos during the period from 1969 to 1973 (Roeben, 1975), a high percentage of these resulted in early mortality. Third, due to the high incidence of diseases, parasitization, and problems associated with the social stress found in maned wolves in captivity, mortality of adults is also relatively high in this species. Mortality has been particularly high in some of the smaller South American zoos.

I suggest that increased numbers of zoos attempt to breed maned wolves in captivity using techniques recommended by Brady and Ditton (1979). The registration and cooperative exchange of maned wolves, especially in South America, should be encouraged. A monitored, low-level introduction of wild-caught individuals into the captive population would aid in maintaining genetic diversity and would not at present be detrimental to free-living populations. It has been suggested that introduction of as few as one or two individuals per generation into a small population can counter the effects of genetic drift (Avery, 1978; Franklin, 1980). Finally, the prevalence and potentially fatal nature of cystinuria in captive maned wolves (Bovée et al., 1981) make this disease a possible serious threat to this species in captivity. Whenever possible, breeding wolves should be selected from among noncystinuric individuals. I also recommend additional research on the genetic basis, treatment and frequency of occurrence of this disease in free-living populations.

# Appendix

TABLE 1.—Hematologic values for 10 maned wolves (see p. 10; dashes indicate no data).

| Determination | Alpha (♀) | Delta (♀) | Epsilon (♀) | Zoo 2 (♀) | Zoo 1 (?) | Beta (♂) | Gamma (♂) | Lambda (♂) | Zeta (♂) | Sigma (♂) | $\bar{x}$ | SD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | PERCENT OF BLOOD VOLUME | | | | | | | |
| Hematocrit | – | 47.0 | 41.5 | 32.0 | 37.5 | 36.5 | 37.0 | 37.0 | 37.5 | 37.0 | 38.1 | 4.11 |
| | | | | | GRAMS PER 100 MILLILITERS | | | | | | | |
| Hemoglobin | – | 15.8 | 14.0 | 10.2 | 12.0 | 11.2 | 10.8 | 11.8 | 12.0 | 11.6 | 12.2 | 1.72 |
| | | | | | CELLS PER CUBIC MILLIMETER | | | | | | | |
| Erythrocytes ($10^6$) | – | 8.61 | 6.60 | 5.78 | 6.87 | 5.83 | 6.04 | 6.14 | 5.06 | 5.90 | 6.3 | 1.00 |
| Leucocytes ($10^3$) | – | 14.1 | 12.3 | 14.1 | 17.75 | 14.8 | 12.15 | 15.4 | 12.15 | 14.8 | 14.17 | 1.83 |
| | | | | | PERCENT OF WHITE BLOOD CELLS | | | | | | | |
| Myelocytes | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Metamyelocytes | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Band cells | 2.0 | 6.0 | 5.0 | 1.0 | 3.0 | 2.0 | 5.0 | 3.0 | 1.0 | 2.0 | 3.0 | 1.76 |
| Segmented cells | 74.0 | 77.0 | 74.0 | 49.0 | 53.0 | 74.0 | 70.0 | 66.0 | 78.0 | 66.0 | 68.1 | 9.93 |
| Eosinophils | 3.0 | 3.0 | 7.0 | 8.0 | 6.0 | 14.0 | 2.0 | 7.0 | 2.0 | 8.0 | 6.0 | 3.71 |
| Basophils | 0 | 0 | 2.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0.63 |
| Lymphocytes | 19.0 | 14.0 | 12.0 | 42.0 | 35.0 | 9.0 | 20.0 | 22.0 | 17.0 | 21.0 | 21.1 | 10.18 |
| Monocytes | 2.0 | 0 | 2.0 | 0 | 3.0 | 1.0 | 3.0 | 2.0 | 2.0 | 3.0 | 1.8 | 1.14 |

TABLE 2.—Biochemical serum values for seven maned wolves (the blood sample for maned wolf Epsilon hemolyzed prior to analysis and therefore was excluded from calculations of sample mean and standard deviation; dashes indicate no data).

| Determination | Delta (♀) | Epsilon (♀) | Beta (♂) | Gamma (♂) | Lambda (♂) | Zeta (♂) | Sigma (♂) | $\bar{x}$ | SD |
|---|---|---|---|---|---|---|---|---|---|
| | | | | GRAMS PER 100 MILLILITERS | | | | | |
| Total Protein | – | 14.0 | 8.8 | – | 7.6 | 6.4 | 7.8 | 7.7 | 0.98 |
| | | | | PERCENT OF TOTAL PROTEIN | | | | | |
| Albumin | – | 22.0 | 26.0 | – | 21.0 | 22.0 | 24.0 | 23.3 | 2.22 |
| Globulin, $\alpha_1$ | – | 7.0 | 12.0 | – | 11.0 | 7.0 | 12.0 | 10.5 | 2.38 |
| Globulin, $\alpha_2$ | – | 10.0 | 13.0 | – | 12.0 | 10.0 | 14.0 | 12.3 | 1.71 |
| Globulin, $\beta$ | – | 55.0 | 36.0 | – | 41.0 | 42.0 | 36.0 | 38.8 | 3.20 |
| Globulin, $\gamma$ | – | 6.0 | 13.0 | – | 15.0 | 19.0 | 14.0 | 15.3 | 2.63 |
| SGPT (1U/1;R-f)* | 51.0 | – | 50.0 | 47.0 | 58.0 | 49.0 | – | 51.0 | 4.18 |
| SGOT (1U/1;R-f)* | 200.0 | – | 66.0 | 92.0 | 95.0 | 68.0 | – | 104.2 | 55.18 |

* Reitman-Frankel procedure.

TABLE 3.—Weights and measurements of captured maned wolves (M = middle-aged, O = old, Y = young; dashes = no data).

| Character | Alpha (M♀) | Beta (M♂) | Gamma (M♂) | Delta (O♀) | Epsilon (Y♀) | Kappa (Y♀) | Lambda (Y♂) | Zeta (M♂) | Sigma (M♂) | $\bar{x} \pm SD$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Weight (kg) | 25.1 | 22.4 | 25.8 | 21.3 | 20.5 | 24.0 | 23.1 | 23.1 | 24.4 | 23.3 ± 1.73 |
| Length (cm) | | | | | | | | | | |
| Head and body | 99.0 | 95.0 | 107.0 | 104.0 | 105.0 | 104.0 | 99.0 | 100.0 | 114.0 | 103.0 ± 5.57 |
| Tail | 49.0 | 45.0 | –[3] | 43.0 | 38.0 | 46.0 | 45.0 | 43.0 | 47.0 | 44.5 ± 3.30 |
| Ear | 16.0 | 17.0 | 17.0 | 16.5 | 17.0 | 15.0 | 18.0 | 17.5 | 17.5 | 16.8 ± 0.90 |
| Hindfoot | 29.5 | 29.0 | 30.0 | 30.0 | 29.0 | 30.5 | 28.0 | 27.5 | 32.0 | 29.5 ± 1.35 |
| Forelimb[1] | 85.0 | 87.0 | 91.0 | 91.0 | 86.0 | 90.0 | 91.0 | 89.0 | 96.0 | 89.6 ± 3.32 |
| Hindlimb[2] | 80.0 | 85.0 | 96.0 | 84.0 | 81.0 | 95.0 | 92.0 | 91.0 | 99.0 | 89.2 ± 6.92 |
| White on tail | – | – | – | – | 18.0 | 8.0 | 19.0 | 23.0 | 31.0 | 19.8 ± 8.35 |
| Black on antebrachium | – | – | – | – | 34.0 | 50.0 | 46.0 | 44.0 | 47.0 | 44.2 ± 6.10 |
| Black on hindlimb | – | – | – | – | 37.0 | 38.0 | 37.0 | 38.0 | 37.0 | 37.4 ± 0.55 |
| Black stripe on mane | – | – | – | – | 49.0 | 47.0 | 40.0 | 45.0 | 54.0 | 47.0 ± 5.15 |

[1] Measured from the manus to the dorsal border of the scapula.
[2] Measured from the pes to the cranial crest of the ilium.
[3] Extremity missing.

TABLE 4.—Use (%) of three habitats by maned wolves as determined by number (N) of radiolocations.

| Habitat | Males | | Females | | All wolves | |
|---|---|---|---|---|---|---|
| | N | % | N | % | N | % |
| Grassland | 97 | 39.1 | 66 | 28.3 | 163 | 33.9 |
| Cerrado | 89 | 35.9 | 116 | 49.8 | 205 | 42.6 |
| Forest | 62 | 25.0 | 51 | 21.9 | 113 | 23.5 |
| Total | 248 | 100.0 | 233 | 100.0 | 481 | 100.0 |

TABLE 5.—Use (%) of three habitats by bonded pairs of maned wolves as determined by number (N) of radiolocations.

| Habitat | Pair 1 | | Pair 2 | | Pair 3 | |
|---|---|---|---|---|---|---|
| | N | % | N | % | N | % |
| Grassland | 104 | 31.6 | 17 | 29.3 | 27 | 38.0 |
| Cerrado | 163 | 49.5 | 11 | 19.0 | 24 | 33.8 |
| Forest | 62 | 18.8 | 30 | 51.7 | 20 | 28.2 |
| Total | 329 | 99.9 | 58 | 100.0 | 71 | 100.0 |

TABLE 6.—Seasonal use (%) of three habitats by maned wolves as determined by number (N) of radiolocations.

| Habitat | Wet seasons | | Dry seasons | | All seasons | |
|---|---|---|---|---|---|---|
| | N | % | N | % | N | % |
| Grassland | 66 | 27.6 | 97 | 40.1 | 163 | 33.9 |
| Cerrado | 104 | 43.5 | 101 | 41.7 | 205 | 42.6 |
| Forest | 69 | 28.9 | 44 | 18.2 | 113 | 23.5 |
| Total | 239 | 100.0 | 242 | 100.0 | 481 | 100.0 |

TABLE 7.—Use of available habitats with respect to their relative proportions in the study area (ns = not significant).

| Habitat (Proportion of study area)[1] | Number of radiotelemetric observations | Proportion of total observations | Confidence interval on proportion of occurrence[2] | Significant deviation from expected proportion |
|---|---|---|---|---|
| | | 0601–1800 HOURS | | |
| Grassland (0.50) | 108 | 0.30 | $0.22 \leq p \leq 0.38$ | less |
| Cerrado (0.35) | 172 | 0.48 | $0.39 \leq p \leq 0.57$ | greater |
| Forest (0.15) | 80 | 0.22 | $0.15 \leq p \leq 0.29$ | ns |
| | | 1801–0600 HOURS | | |
| Grassland (0.50) | 21 | 0.28 | $0.20 \leq p \leq 0.36$ | less |
| Cerrado (0.35) | 21 | 0.28 | $0.20 \leq p \leq 0.36$ | ns |
| Forest (0.15) | 33 | 0.44 | $0.35 \leq p \leq 0.53$ | greater |

[1] Proportions of habitat types in the study area also represent expected proportions of use by maned wolves of those habitats. The proportions are tested against confidence intervals placed on observed proportions of occurrence.

[2] Confidence intervals are based on the Bonferroni normal statistics (Miller, 1966); $p = 0.01$.

TABLE 8.—Levels of activity (%) of eight maned wolves grouped by bonded pairs as determined by number (N) of radiolocations.[1]

| Activity level | Pair 1 | | Pair 2 | | Pair 3 | | Pair 4 | |
|---|---|---|---|---|---|---|---|---|
| | N | % | N | % | N | % | N | % |
| Inactive | 302 | 61.6 | 28 | 56.0 | 101 | 60.8 | 36 | 62.1 |
| Intermittent | 99 | 20.2 | 7 | 14.0 | 27 | 16.3 | 13 | 22.4 |
| Constant | 89 | 18.2 | 15 | 30.0 | 38 | 22.9 | 9 | 15.5 |
| Total | 490 | 100.0 | 50 | 100.0 | 166 | 100.0 | 58 | 100.0 |

[1] Chi-square value = 6.91, 6 d.f., p = 0.33.

TABLE 9.—Levels of activity (%) of eight maned wolves (grouped by sex) as determined by number (N) of radiolocations.[1]

| Activity level | Females | | Males | | All wolves | |
|---|---|---|---|---|---|---|
| | N | % | N | % | N | % |
| Inactive | 267 | 65.6 | 200 | 56.0 | 467 | 61.1 |
| Intermittent | 74 | 18.2 | 72 | 20.2 | 146 | 19.1 |
| Constant | 66 | 16.2 | 85 | 23.8 | 151 | 19.8 |
| Total | 407 | 100.0 | 357 | 100.0 | 764 | 100.0 |

[1] Chi-square test value = 8.80, 2 d.f., p = 0.012. When intermittently active and constantly active observations are combined, G-test value = 7.35, 1 d.f., p < 0.01.

TABLE 10.—Capture dates for maned wolves in three home ranges of the Serra da Canastra.

| Wolf (sex) | Initial capture | Last location or date of death | Number of captures |
|---|---|---|---|
| | TAPERÃO RANGE | | |
| Beta (♂) | 10 Sep 1978 | 24 May 1980 | 7 |
| | EAST RANGE | | |
| Gamma (♂) | 15 Dec 1978 | 25 Jun 1979[1] | 4 |
| Delta (♀) | 18 Jan 1979 | 25 Feb 1979[2] | 2 |
| Epsilon (♀) | 22 Apr 1979 | 25 May 1980 | 5 |
| Lambda (♂) | 15 Jun 1979 | 25 May 1980 | 22 |
| | WEST RANGE | | |
| Kappa (♀) | 15 May 1979 | 25 May 1980 | 4 |
| Zeta (♂) | 5 Jul 1979 | 17 Oct 1979 to 26 Nov 1979[3] | 1 |
| Sigma (♂) | 18 Nov 1979 | 25 May 1980 | 2 |

[1] Radiotelemetric contact was lost with this wolf on this date. It was assumed that the animal left the study area.

[2] This wolf died as a result of suffering a broken leg.

[3] This wolf was killed by a local farmer sometime during this period.

TABLE 11.—Substrate used by maned wolves for the deposition of feces.

| Substrate | No. of Locations | (%) |
|---|---|---|
| Rocks | 257 | 34.7 |
| Termite mounds | 206 | 27.8 |
| Paths or roads | 202 | 27.3 |
| Dirt mounds | 16 | 2.2 |
| Clumps of grass | 4 | 0.5 |
| Log | 1 | 0.1 |
| Wolf trap | 1 | 0.1 |
| Substrate not recorded | 53 | 7.2 |
| Total | 740 | 99.9 |

TABLE 12.—Animal material identified in 740 scats of maned wolves.

| Food item | N | Proportion of occurrence[1] |
|---|---|---|
| Small mammals | 524 | 0.255 |
| Bird bones and feathers | 230 | 0.112 |
| Armadillos | 63 | 0.031 |
| Miscellaneous insects | 43 | 0.021 |
| Beetles (Coleoptera) | 31 | 0.015 |
| Grasshoppers | 28 | 0.014 |
| Rabbits (*Sylvilagus brasiliensis*) | 23 | 0.011 |
| Ants | 10 | 0.005 |
| Chickens (*Gallus gallus*) | 10 | 0.005 |
| Bird egg shells | 7 | 0.003 |
| Snakes | 6 | 0.003 |
| Giant anteaters | 6 | 0.003 |
| Maned wolf, hair | 5 | 0.002 |
| Fish | 3 | 0.002 |
| Bees or wasps | 2 | 0.001 |
| Collared anteaters | 2 | 0.001 |
| Pacas | 1 | 0.001 |
| Ticks | 1 | 0.001 |
| Spiders | 1 | 0.001 |
| Termites | 1 | 0.001 |
| Unidentified | 7 | 0.003 |
| Total | 997 | 0.491 |

[1] Expressed as a function of total occurrences of all items (2056) in all examined scats.

TABLE 13.—Plant material identified in 740 scats of maned wolves.

| Food item | N | Proportion of occurrence[1] |
|---|---|---|
| Lobeira (*Solanum lycocarpum*, Solanaceae) | 670 | 0.326 |
| Miscellaneous grass (Gramineae) | 228 | 0.111 |
| Gravatá (*Bromelia anthiacantha*, Bromeliaceae) | 44 | 0.021 |
| Coquinho (*Astrocaryum* sp., Palmaceae) | 25 | 0.012 |
| Casaco (Unidentified, Myrtaceae) | 16 | 0.008 |
| Melancia do campo (Unidentified, Cucurbitaceae?) | 12 | 0.006 |
| Goiaba (*Psidium* sp., Myrtaceae) | 10 | 0.005 |
| Mángue (*Callophylum brasiliense*, Guttiferae) | 6 | 0.003 |
| Articum rasteiro (*Annona* sp., Annonaceae) | 6 | 0.003 |
| Gabiroba (*Campomanesia* sp., Myrtaceae) | 5 | 0.002 |
| Corn (*Zea mays*, Panicoideae) | 5 | 0.002 |
| Araçá (*Psidium* sp., Myrtaceae) | 4 | 0.002 |
| Aperta-mão (Unidentified, Melastomaceae or Piperaceae?) | 3 | 0.002 |
| Limãozinho (Unidentified, Rutaceae) | 2 | 0.001 |
| Amouriçí (*Byrsonima* sp., Malpighiaceae?) | 2 | 0.001 |
| Amora (*Morus* sp., Moraceae) | 2 | 0.001 |
| Cega olho (Unidentified) | 1 | 0.001 |
| Pitanga (*Eugenia uniflora*, Myrtaceae) | 1 | 0.001 |
| Araçá grande (*Psidium* sp., Myrtaceae) | 1 | 0.001 |
| Articum grande (*Annona* sp., Annonaceae) | 1 | 0.001 |
| Unidentified | 20 | 0.010 |
| Total | 1044 | 0.510 |

[1] Expressed as a function of total occurrences of all items (2056) in all examined scats.

TABLE 14.—Proportions of volume and occurrence of selected food items in 740 scats of maned wolves.

| Food item | Proportion of total volume | Proportion of occurrence[1] |
|---|---|---|
| *Solanum lycocarpum* | 0.576 | 0.326 |
| Small mammals | 0.281 | 0.254 |
| Birds | 0.023 | 0.122 |
| Foliage | 0.013 | 0.108 |
| Miscellaneous fruit | 0.068 | 0.063 |
| Insects | 0.003 | 0.052 |
| Armadillos | 0.016 | 0.032 |
| Rabbits | 0.009 | 0.011 |
| Unidentified material | 0.004 | 0.007 |
| Soil | 0.006 | 0.005 |
| Amphibians, reptiles | 0.000 | 0.003 |
| Giant anteaters | 0.001 | 0.002 |
| Fish | 0.000 | 0.001 |
| Collared anteaters | 0.001 | 0.001 |
| Pacas | 0.000 | 0.000 |

[1] Expressed as a function of total occurrences of all items (2056) in all examined scats.

TABLE 16.—Weights and measurements of two captured female maned wolf pups.

| Character | Pup A1 | Pup A2 |
|---|---|---|
| | 25 Aug 1978 | |
| Weight (kg) at capture | 4.5 | 3.9 |
| | 10 Sep 1978 | |
| at release | 5.9 | 5.4 |
| Length (cm) | | |
| Total | 81 | 69 |
| Tail | 21 | 19 |
| Ear | 14 | 12 |
| Right hindfoot | 17 | 16 |

TABLE 15.—Seasonal occurrence of selected food items in 740 scats of maned wolves (significantly larger frequencies are underlined).

| Food item | Dry season | | Wet season | |
|---|---|---|---|---|
| | N | Proportion of total | N | Proportion of total |
| Lobeira | 375 | 0.337 | 304 | 0.340 |
| Small mammal | 306[a] | 0.275 | 204 | 0.228 |
| Bird | 120 | 0.108 | 124 | 0.139 |
| Foliage | 147[b] | 0.132 | 70 | 0.078 |
| Miscellaneous fruit | 50 | 0.045 | 76[b] | 0.085 |
| Insect | 43 | 0.039 | 61[b] | 0.068 |
| Armadillo | 29 | 0.026 | 35 | 0.039 |
| Total | 1070 | 0.962 | 874 | 0.977 |

[a] $p < 0.025$; [b] $p < 0.005$.

TABLE 17.—The results of selected laboratory examinations performed on urine samples from eight captured maned wolves (a plus indicates a positive result; minus indicates a negative result; laboratory procedures were performed by the School of Veterinary Medicine, University of Pennsylvania).

| Maned wolf | Cystinuria | Dibasic amino-aciduria | Glucosuria |
|---|---|---|---|
| Beta (♂) | − | + | − |
| Gamma (♂) | − | + | − |
| Delta (♀) | + | + | − |
| Epsilon (♀) | + | + | − |
| Kappa (♀) | + | + | + |
| Lambda (♂) | + | + | − |
| Zeta (♂) | + | + | − |
| Sigma (♂) | + | − | − |

TABLE 18.—Endoparasites observed in fecal samples from eight maned wolves (analyses were performed using a sedimentation method at the Clinical Laboratory of the School of Veterinary Medicine, Federal University of Minas Gerais; the degree of parasitic infestation, as estimated by the relative number of eggs or cysts in the examined feces, is represented by from one to three pluses).

| Endoparasite | Alpha (♀) | Beta (♂) | Beta[1] (♂) | Gamma (♂) | Zoo 1 (?) | Zoo 2 (♀) | Epsilon (♀) | Lambda (♂) | Zeta (♂) |
|---|---|---|---|---|---|---|---|---|---|
| *Trichuris* sp. | + | + | + | + | + | + | + | + | ++ |
| *Toxocara* sp. | + | + | + | | | | + | | + |
| *Dipylidium* sp. | + | | | | | | | | |
| *Ancylostoma* sp. | | | + | + | ++ | +++ | + | ++ | ++ |
| *Oxyuris* sp. | | | + | | | | + | + | + |
| *Eimeria* sp. | | | | | | | | ++ | |

[1] Second capture.

TABLE 19.—Synchrony of activity by males and females of paired maned wolves.

| Reproductive stage | Pairs (N) | Reproductive stages (N) | Observations (N) | Intervals with synchronous activity (%) |
|---|---|---|---|---|
| Breeding Pairs | | | | |
| Proestrus | 3 | 5 | 1770 | 65.0 |
| Sexual receptivity | 3 | 6 | 750 | 76.4 |
| Gestation | 3 | 6 | 3540 | 68.6 |
| Anestrus | 2 | 2 | 2490 | 75.3 |
| Nonbreeding Pairs | 2 | – | 2280 | 58.0 |

TABLE 20.—Distance between males and females of paired maned wolves.

| Reproductive stage | Pairs (N) | Reproductive stages (N) | Observation intervals (N) | Intervals when wolves within 5 body-lengths (%) | Mean distance (body-lengths) between wolves that were within 5 body-lengths |
|---|---|---|---|---|---|
| Breeding Pairs | | | | | |
| Proestrus | 3 | 5 | 1770 | 12.5 | 2.8 |
| Sexual receptivity | 3 | 6 | 750 | 21.9 | 2.5 |
| Gestation | 3 | 6 | 3540 | 9.5 | 3.7 |
| Anestrus | 2 | 2 | 2490 | 15.9 | 3.5 |
| Nonbreeding Pairs | 2 | – | 2250 | 3.8 | 2.6 |

TABLE 21.—Total rates of occurrence of extended-bark vocalization per hour of observation (numbers in parentheses indicate total number of observed occurrences).

| Character | Breeding season (N = 202 hours) | Anestrus (N = 124 hours) |
|---|---|---|
| Total instances of vocalization | 0.96 (193) | 0.06 (8) |
| Bouts with more than one wolf | 0.34 (68) | 0 (0) |
| Total barks | 10.36 (2092) | 0.43 (53) |
| Males vocalizing | 0.26 (53) | 0.01 (1) |
| Females vocalizing | 0.08 (17) | 0.01 (1) |
| Vocalizing wolves of undetermined sex | 0.61 (123) | 0.05 (6) |

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