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ECOLOGY AND SOCIAL ORGANIZATION OF THE MANED WOLF (*CHRYSOCYON BRACHYURUS*)

by

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ABSTRACT

ECOLOGY AND SOCIAL ORGANIZATION OF
THE MANED WOLF (CHRYSOCYON BRACHYURUS)

By

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The maned wolf is the largest and most distinct member of the South American Canidae. Its distribution is limited to the grasslands and savannas of central South America. Although prized by zoological gardens and classified by conservation agencies as endangered with extinction, relatively little is known about the natural history of this species. Therefore, the objectives of this study included quantification and description of the following aspects of the ecology and social organization of the maned wolf: relative use of available habitat types, circadian and seasonal activity patterns, social organization, reproduction, mortality and other limiting factors, and relations with humans. The results of this study are based on two years of field work conducted in and around Serra da Canastra National Park in southeastern Brazil.

Nine adult maned wolves were captured in large wooden box traps using live chickens as bait. Observations were

also recorded on the behavior of two captive pups. Captured adults were immobilized, weighed, measured, examined for ectoparasites and fitted with radiotelemetric collars. Blood, urine and fecal specimens were collected for laboratory determinations. Individuals were located daily on a scheduled basis and also were periodically monitored for several hours at a time. Availability of trophic resources was estimated by monthly censuses of small mammals and fruits. Scat analysis was used to determine food habits of resident maned wolves.

Results suggest that maned wolves used grassland significantly less than the proportion of occurrence of that habitat. During the day, wolves most commonly rested in cerrado habitat; at night, they were most often found in forest habitat. Wolves were largely nocturnal with the majority of circadian activity occurring from dusk to midnight. No significant differences in activity patterns were noted between bonded pairs, but males were significantly more active than females.

The most important components of the diet of these maned wolves, as determined by relative volume and occurrence in scats, were the fruit Solanum lycocarpum, small mammals and miscellaneous fruits. Consumption of these three items was consistent with their seasonal availability suggesting that maned wolves were opportunistic and flexible in their feeding habits.

Feces were nonrandomly deposited along trails and were replaced after I collected them. Locus-specific defecation was practiced near dens and resting places.

Maned wolves of the Serra da Canastra displayed facultative monogamy characterized by a long-term pair bond between male and female. The male and female, as a pair, had completely overlapping ranges, yet individuals were rarely located in close association except during the breeding season. Each bonded pair defended a territory averaging 27 km^2. Territorial boundaries were apparently inflexible except when an adjacent territory was vacated by the death of a resident wolf. Under those circumstances, territorial invasion by the male of the adjacent pair was observed on three occasions. In three cases, vacancies created by the deaths of resident wolves were quickly filled by wolves that were presumably unlanded nomads.

The greatest source of mortality of maned wolves appeared to be the result of reprisals by local ranchers for depredation on domestic fowl. In addition, six of eight examined wolves tested positive for cystinuria, an inherited metabolic disease occasionally fatal in captive wolves. Suggestions based on the available literature and on the results of this study are presented concerning the conservation and management of this endangered species.

ACKNOWLEDGEMENTS

The Maned Wolf Project, as this research was denominated in Brazil, was the result of the combined efforts of many people in several countries. It is with pleasure that I acknowledge the contributions of the following individuals who made this study possible. To Rollin H. Baker, chairman of my Advisory Committee, I extend my warmest thanks for participation in every aspect of this project. Similar thanks are also due present members of my Advisory Committee: S. C. Bromley, R. W. Hill, and G. A. Petrides; and past members of my Advisory Committee: J. H. Fitch and L. Gysel.

Coordination of this research at the federal level in Brazil was not an easy task, but was handled smoothly and efficiently by Dra. Maria Teresa Pádua and her competent team of professionals at IBDF, Brasilia. I thank her and Renato Petry Leal, José Carlos Duarte and Eduardo Kunze Bastos for their support during my two years in Brazil. 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

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Life in the Serra da Canastra would have been difficult without the assistance of the IBDF staff in the park. I am indebted to Oliveiro A. Soares, park Director, and to members of his staff: Antónia, Amadeu, Jean-Pierre, Delmo, and Adaniel; to Hélio Lasmar and his work crew; to Guilherme and the park guards.

All of the people of the small city of São Roque de Minas were supportive of my study and contributed directly and indirectly to its success. To these wonderful people, I extend my thanks. Particularly helpful were Aldivino and Fiinha Fregúgia and their 14 sons and daughters. I also wish to thank Vicente Candido, his family and his ranch hand Sebastião for loaning us supplies, housing and horses, and for teaching us to use the latter.

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Dra. Rosa Vieira, director of the Clinical Laboratory, School of Veterinary Medicine, Federal University of Minas Gerais gratuitously performed the laboratory analyses during the course of this research. I also thank J. O. Whitaker and N. Wilson for identification of ectoparasites, and D. O. Straney, P. Meyers, and R. Pine for identification of small mammals. R. Ramalho and J. Carlos identified botanical specimens. P. C. Dietz, L. A. Dietz, and R. Krasnoborski deserve thanks for their translations of literature in various languages into English. The latter two friends were also kind enough to read and edit the manuscript for this dissertation.

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Finally, I would like to acknowledge the contribution and participation of my wife, Lou Ann, in this study. It was she who gave up two years of her career to cook on a wood-burning stove, wash clothes in a creek, and chase maned wolves in the Serra da Canastra. It is to her that I dedicate this dissertation.

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INTRODUCTION

The maned wolf (Chrysocyon brachyurus Illiger, 1815; Figure 1) is the largest and most distinct member of the South American Canidae. The first detailed description of the species 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 Tupí-Guaraní Indians and has been shortened to guara. Rengger (1830) suggested that the name Aguara-guazu 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. Within this context, classification at the generic level of the South American forms has been the most unstable (see Cabrera, 1931, and Clutton-Brock, 1976, for reviews). Fortunately the maned wolf has largely escaped these problems of "vexatious

FIGURE 1. Adult maned wolf in the Serra da Canastra National Park, Brazil.

Figure 1.

technical nomenclature of the canids" (Simpson, 1941) 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 question which canid groups constitute the maned wolf's nearest relatives still remains unanswered: 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 Schmidt, 1970) but a relatively low incidence of polymorphic loci has generally limited the effectiveness of this technique in the Canoidea (Seal, 1975).

Morphological data collected from free-living maned wolves are relatively rare. Recently-published measurements can often be traced back through the literature to Azara (1801), who recorded the dimensions of only one captive wolf. Detailed morphological information will be presented later in this dissertation; therefore, only a

brief description will be presented here. The adult maned wolf weighs about 23.3 kg, stands nearly 90 cm at the shoulder, and has a total length of about 147 cm, of which approximately 45 cm is contributed by the tail. The pelage is long and buff-red over most of the body. The legs are black as is part of the dorsal erectile mane. White markings are found on the pinnae, under the chin and on the tip of the tail. Pocock (1927) and Langguth (1969) have described respectively the external characters and the morphology of the maned wolf and have compared these data with those from other South American canids. Studer (1904) made similar comparisons using cranial measurements. Two additional facts concerning the anatomy of the maned wolf are of interest: first, 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 three species of Brazilian canids occupying forest habitats: the bush dog (Speothos venaticus), the crab-eating fox (Cerdocyon thous) and the short-eared dog (Atelocynus microtis) (Langguth, 1969). Second, the long legs of the maned wolf make it one of the tallest members of the Canidae. Sokolowsky (1927), speculating on the adaptive significance of these long legs, surmised that maned wolves are not adapted for swift running, as stated by Stains (1975), but rather for efficient travel and vision in tall vegetation.

That the maned wolf, as well as the other South American canids, evolved from one or more North American prototypes is now generally accepted (Simpson, 1980). 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). However, the question of when this radiation took place is still a matter of some contention. Simpson (1980) believes that all South American canids evolved from North American forms that arrived during the faunal exchange brought about by the closing of the Panamanian land bridge at the beginning of the Pleistocene Epoch. Langguth (1969) argues that the maned wolf and the three Brazilian forest foxes descended from a common ancestor that must have been in Brazil well before the Pleistocene. The present species 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 (Breyer, in prep.; Cabrera, 1958; Cabrera and Yepes, 1960; Hofmann et al., 1975-1976; Paiva, 1973; Schaller, 1975; Schaller and Vasconcelos, 1976).

Because the maned wolf is a species highly valued by zoological gardens, the management and breeding of these animals in captivity is relatively well documented.

Acosta (1972) described hand-rearing a litter of maned wolf pups. These data were used by Bekoff and Jamieson (1975) to compare their 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 to maintain maned wolves successfully in captivity has been summarized by Brady and Ditton (1979), Carvalho (1976), and by Crandall (1964). The longevity of maned wolves in captivity has been estimated at from 12 to 15 years (Silveira, 1969).

Reproduction by maned wolves in captivity is rarely successful. In most cases the neonates are killed by one of their parents. This, perhaps, has led to the publishing of several articles concerning the reproductive behavior of this species in captivity. Female maned wolves are monoestrous and may copulate several times during an estrus period of about five days (Kuhme, 1975; Lippert, 1973). 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 (Altmann, 1972; Encke, 1971), 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 gestation period of about 65 days (Faust and Scherpner, 1968). A record of seven pups in one litter was recorded in the São Paulo Zoo

(Carvalho, 1976). Parturition has been described by Hammerling and Lippert (1975), and the studbook record for the species has been published by Roeben (1975).

Another problem associated with the breeding and raising of maned wolves in captivity is that of parasites and diseases. Renal parasites in maned wolves were early described by Azara (1801) in Paraguay, and later by Magalhães (1939) for maned wolves in Brazil. The nematode described by these authors was later identified as the giant kidney worm (Dioctophyma renale) (Giovannoni and Molfi, 1960; Lamina and Black, 1966; Matera et al., 1968), 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 questioned by Carvalho (1976). Other endoparasites found in maned wolves are mentioned by Carvalho (1976), and by Encke et al. (1970). Bush (in press) reviewed the diseases and medical management of maned wolves in captivity.

Maned wolves in captivity lead essentially solitary existences except during the reproductive period. Pairs composed of animals of opposite sexes are apparently easier to house in the same enclosure than like-sexed animals. Individuals maintain separate preferred resting sites and do not usually rest in close association (Altmann, 1972; Encke, 1971; Kuhme, 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 (in prep.), and the behavior of pups by Encke et al. (1970).

Information concerning the ecology and natural history of free-living maned wolves is scarce and often anecdotal. The wolf feeds mainly on small vertebrate animals and on fruits (Azara, 1801; Cabrera and Yepes, 1960; Carvalho, 1976). Dennler de la Tour (1968) and Miller (1930) 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 and 1948) refers to the wolf as the "savanna stroller" and comments on its solitary nature. Dennler de la Tour (1968) also noted 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, 1976), and classified by agencies of the Brazilian government as "endangered" (Carvalho, 1968; Coimbra Filho and Magnanini, 1968). Silveira (1968) estimated that only 1,500-2,200 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.

In consideration of the above, the general objective of the present study was to obtain sufficient data about the ecology and social organization of the maned wolf so that rational decisions could be made with respect to the conservation and management of this endangered species in its natural range. Within this context I attempted to achieve the following specific objectives: (1) measure quantitatively the relative use by maned wolves of available habitat types in the Serra da Canastra National Park, Brazil; (2) describe diurnal and seasonal activity patterns; (3) describe the social organization of the wolves of the Serra da Canastra and the behavioral mechanisms by which social relationships are maintained or reinforced; (4) quantify seasonal food habits, including the exploitation of domestic stock; (5) make observations on the reproduction of maned wolves in the Serra da Canastra; (6) identify direct sources of mortality of wolves, and also factors such as diseases and parasites that may limit population expansion; and (7) portray the relations between humans and maned wolves residing in the Serra da Canastra.

METHODS

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 1,500 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 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.

Approximately 35 percent of the area was composed of cerrado vegetation. This habitat type is typified by well-spaced, thick-barked trees (see Table 21, Appendix) less than about 7 m in height. Trees of the cerrado are

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


Manaus
Brazil
Brasilia
Minas
Gerais
São Paulo
Rio de Janeiro
SERRA DA CANASTRA
NATIONAL PARK

Figure 2.

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 (Table 22, Appendix). 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. 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 1,300 to 1,700 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) is locatd in the Serra da Canastra National Park. The park was created by Brazilian federal decree in 1972, but at the time of my study had not been paid for and was still being used for cattle grazing by local ranchers. 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, with help from workmen of the Brazilian Forest Service (IBDF), rebuilt a stone house originally occupied by slaves during the 1800s. We lived in this house in the park from July 1978, through May 1980. Our living conditions were pleasant, and by maintaining a large flock of chickens and a garden, we were largely self-sufficient. We soon became friends with several rural families living outside the park and relied

on them for help in collecting much of the information presented in this dissertation.

Capture Procedure

The first critical problem faced during this field research was that of devising a noninjurious method to capture maned wolves in the Serra da Canastra. Political considerations as well as the likelihood of breaking the long and apparently fragile limb bones of captured maned wolves precluded the use of steel leg-hold traps. Extensive interviews with area residents produced several models of live-traps purported to have been successful in capturing wolves. From these suggestions, I designed a wooden live-trap (Figure 3), and hired a local carpenter to build seven to my specifications.

The traps were constructed of durable native hardwoods and weighed about 110 kg assembled. The sides of the trap were held in place by bolts to permit 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. A live chicken supported on a platform above the treadle was used as bait. The chicken was provided with a four-day supply of corn and water in liter cans and was separated from the inside of the trap by a wall of light chicken-wire.

A second critical problem was trap placement. Since initial attempts using random distribution of traps within

FIGURE 3. Wooden live-trap used to capture maned wolves. Trap is baited with a live chicken.

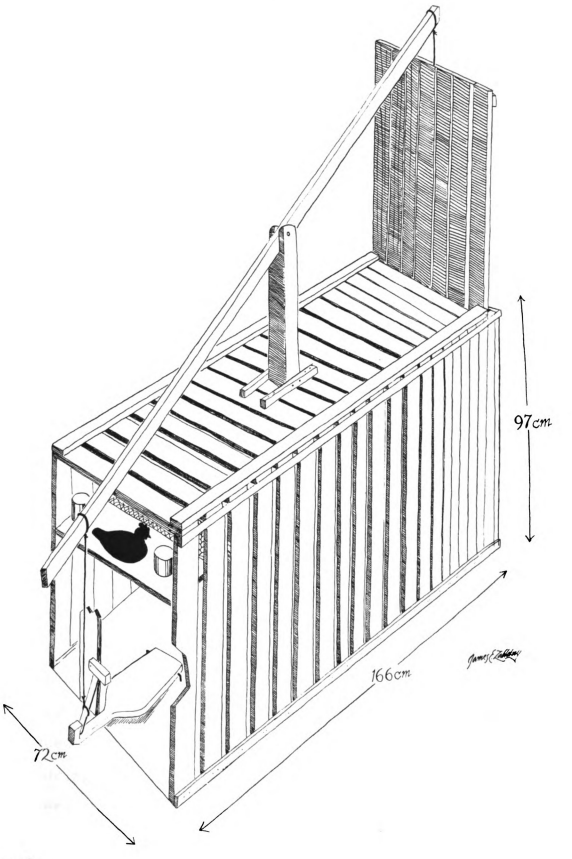

Figure 3.

the study area produced no captures, I again interviewed area residents and determined the exact locations where maned wolves had recently been observed. At these areas, I estimated quantities of urine, feces and tracks to determine which trails were currently being used by maned wolves. All traps set within a few meters of these major trails 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 particular trap repeatedly captured the same wolves, that trap was temporarily closed or was moved to a new area of wolf activity.

A third critical problem was daily trap inspection. Because the objective of trapping was to capture and place radiotransmitters on all resident maned wolves in the study area, sign of wolf activity and not an area grid design selected a priori was used to determine trap placement. When traps were in place, the size and topographical irregularity of the area, and the general lack of roads absolutely disallowed my examination of all traps in a single day. Therefore it became necessary to enlist the help of interested area residents in this respect. Each trap was assigned to a resident of the study area and was placed such that he could check that trap from a distance during the course of his daily activities. These volunteers informed me immediately when a wolf was discovered in a trap. For this service, I paid one day's

wages (approximately US$2.00) for the capture of a wolf with a radiocollar, and eight days' wages for each wolf captured for the first time.

Handling Procedure

The information collected from a trapped maned wolf usually depended on whether that wolf had been captured previously. Recaptures of wolves were relatively common, and the associated handling procedure was not complex. While the wolf was still in the trap, I tested its transmitter for proper functioning and examined the wolf for signs of external injuries. Attempts were made to photograph the wolf before and after it left the trap. In every case the captured wolf tore a hole in the chicken wire and consumed the chicken used for bait.

The handling procedure associated with the first capture of any wolf was more complex and involved the collection of information and biological materials according to a standardized chronological outline (Table 1). The first step in this procedure was collection of a urine sample for use in testing that wolf for cystinuria. I noticed that trapped maned wolves urinated when first approached and I capitalized on this to collect fresh urine samples from eight wolves. I used one stick to distract the wolf and simultaneously inserted a second stick, with a piece of filter paper attached, between the legs of the wolf and collected the urine as it was voided. The urine absorbed

TABLE 1. Chronological outline of procedures performed during handling of maned wolves captured for the first time.

Activity
Assign name to wolf
Record date
Trap type, bait and person in charge
Note location and habitat description
Collect urine sample
Apply immobilizing drugs and note doses
Record time to immobilization
Sex of captured wolf
Apply ear tags and record numbers
Note identifying marks
Affix transmitter and record frequency
Start transmitter
Collect whole blood and mix half with anticoagulant
Apply antibiotic injection and note dose
Record other treatment
Describe tooth wear
incisors
canines
cheek teeth
Measure length of canines
upper
lower
Note reproductive condition
testes
vulva
lactating
nipples
gravid
Record condition and color of pelage
Measure the following
weight
total length
tail
ear
right hind foot
forefoot to scapula
hindfoot to ilium
white on tail
black on front foot
black on hind foot
black on mane

TABLE 1 (continued)

Activity
Determine heart rate
Determine respiration rate
Collect all ectoparasites
Note time elapsed before wolf is alert
Collect fresh feces from the trap
Photograph captured wolf
Record names of field personnel present

onto the filter paper was stored for future analysis by paper chromatography.

The following combination of immobilizing drugs was injected intramuscularly by means of a syringe recessed into a hole bored down the end of a broomstick: 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. No permanent adverse effects were noted with this combination of immobilizing drugs, and 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. Blood samples and feces from the trap 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. Any breaks in the skin 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.

Transmitters (Wildlife Materials) measured 4 cm by 11 cm, were equipped with external whip antennae 26 cm in length, weighed about 250 g and operated in the 151 MHz frequency range. These transmitters were equipped with bimodal activity-monitoring switches to constantly transmit information about the relative levels of activity of radiocollared wolves. Transmitters were fastened to collars of nylon webbing which were riveted around the necks of captured wolves. The sizes and shapes of collars were based on models of the necks of maned wolves from a zoological garden (courtesy of Dr. P. T. Robinson, San Diego Zoo). Various types of receiving antennae were tested, and a collapsible three-element yagi model (Wildlife Materials) proved most satisfactory under field conditions in the Serra da Canastra.

Location of Maned Wolves by Radiotelemetry

The objectives expedited by radiotelemetry were the determination on a year-round basis of home ranges, activity patterns, habitat preference, and the monitoring of social behavior of maned wolves residing in my study area. These objectives were achieved by locating radiocollared wolves according to a daily schedule based on four six-hour

time blocks: 0601-1200, 1201-1800, 1801-2400, and 0001-0600 hours. Temporal and economic constraints precluded the daily location of all wolves during each time block. In addition, the accentuated topographic relief in the area severely restricted my capacity to travel at night and often reduced the effective radius of transmission of a transmitter to a few hundred meters. Nonetheless, after all resident wolves were fitted with radiotransmitters, an effort was made to locate each wolf at least once in each 24-hour time period. Attempts to radiolocate particular wolves were dispersed over time so that each time-block was represented in a given month.

I used triangulation based on two or more radio-telemetric vectors to determine the location of each wolf (e.g., Craighead and Craighead, 1972; Craighead et al., 1973; Seidensticker et al., 1973). For each of these locations, the time of day, level of physical activity of the wolf and habitat type were recorded. Based on 30 seconds of monitoring at the time of location, I assigned that wolf to one of three distinct classes: inactive (no activity recorded during the interval), intermittently-active (activity not continuous during the interval), or constantly-active. These activity classes were established by affixing radiocollars to domestic dogs and observing the effects of various levels of physical activity on transmitted pulse rates. The type of habitat where a wolf

was located was classified grassland, cerrado (see Description of Home Ranges, this dissertation) or forest.

Radiotelemetric triangulation also facilitated the location of maned wolves for subsequent visual monitoring of individual and social behavior. This type of observation was attempted periodically when a wolf was known to be active or in a location where visual observation was likely to be successful. However, since maned wolves were largely nocturnal, extensive visual observation of their behavior was not often possible.

If a wolf had not been visually 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 if it was in good physical condition. This activity often forced the wolf to abandon its resting place and to take flight at my approach. Observations on the behavior and physical condition of the wolf were recorded at this time. The constant movement of cattle and ranch hands throughout my study area often displaced these maned wolves in a similar manner; therefore, it is unlikely that my interference had any significant effects on their behavior or activity patterns.

Determination of Food Habits

Scat Collection

The food habits of maned wolves residing in my study area were determined by the collection and analysis of fecal droppings (scats). To reduce the possible confusion of maned wolf scats with those of other predators, only those fecal specimens 25 mm or larger in diameter were collected. This criterion was based on the measurement of scats known to have been deposited by a maned wolf and of scats known to have been deposited by other species of canids also occurring in my study area. Scats of questionable origin either were not collected or were analyzed separately from those probably deposited by maned wolves. After several months of scat collection, additional characteristics of maned wolf scats also became evident. These included odor, texture and site.

All maned wolf scats found were collected for analysis. However, 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 was achieved with varying degrees of success depending mainly upon climatic variables. The physical determination of these ranges and their mutual exclusivity was made empirically by radiotelemetric locations of resident wolves. Scats collected from the interface between two ranges were

omitted from analyses relating to home ranges but were included in other analyses.

Collected scats were placed in small paper bags and the following information recorded for each sample: date, location, freshness (moist and apparently intact; dry and apparently intact; or dry and disintegrating), elevation from surrounding ground level, substrate, and habitat type (grassland, cerrado or forest). All feces deposited in a single location (approximately 0.5 m in diameter) were classified as a single scat except when obvious differences in dates of deposition were evident. In this latter case, feces deposited at a single location were divided according to scat freshness criteria and were analyzed separately.

Scat Analysis

Scats were air-dried and then stored in paper bags until analysis. A measure of scat diameter for each sample was based on the largest diameter of a randomly chosen continuous segment. After recording all identifiable components, each scat was disassociated into the following 16 major food types: (1) reptiles and amphibians; (2) birds; (3) arthropods; (4) mollusks; (5) fish; (6) fruits except *Solanum lycocarpum*; (7) foliage; (8) small mammals; (9) armadillos; (10) rabbits; (11) *Solanum lycocarpum*; (12) soil; (13) paca (*Agouti paca*); (14) giant anteater (*Myrmecophaga tridactyla*);

(15) collared anteater (Tamandua tamandua); (16) unidentifiable material. These categories were selected a priori based on my previous experience in examining scats of maned wolves in other geographic regions of Brazil. Identification of fecal constituents was facilitated by the use of a reference collection that I assembled in the study area. I measured the volume of the major components of each scat by placing the material in a graduated cylinder and compacting it with a close-fitting dowel rod. Although I attempted to compact each component equally, I recognize the potential error attributable to differential compaction of components varying in amount and degree of compressibility.

The assumption that proportions of food items in fecal droppings accurately reflect the ingested proportions of those food items is probably as unfounded for maned wolves as it is for other canids (e.g., Murie, 1946). The quantitative problems of this method are well documented and include differential digestibility of types and sizes of food items (Floyd et al., 1978; Meriwether and Johnson, 1980). Thus, my results probably do not accurately reflect the relative proportions and relative importance of prey consumed by maned wolves. The nonmanipulative alternatives to determination of food habits by scat analysis include direct observation of feeding success (e.g., Brady, 1979; Schaller, 1972) or the examination of stomach contents (e.g., Korschgen, 1980). Unfortunately,

neither of these alternatives was feasible in the present study. The nocturnal and extraordinarily wary nature of the maned wolves at the Serra da Canastra made intensive behavioral observations largely impractical. Furthermore, the endangered status of the species precluded taking or risking the lives of wolves in my study area.

A quantitative evaluation of the relative importance of each component food item identifiable in fecal droppings is customarily expressed in one or more of three manners: relative volume of each component, calculated as

$$\frac{\text{Total Volume of Component } i}{\text{Total Volume of All Components}}; \quad (1)$$

frequency of occurrence, based on numbers of occurrences, calculated as

$$\frac{\text{Number of Scats in Which Component } i \text{ Occurred}}{\text{Total Number of Occurrences of All Components}}; \quad (2)$$

or frequency of occurrence, based on the number of scats, calculated as

$$\frac{\text{Number of Scats in Which Component } i \text{ Occurred}}{\text{Total Number of Scats}}; \quad (3)$$

The disadvantages of each method considered alone and the lack of quantitative data concerning the trophic habits of this species suggested the use of the first two of the above formulas in the enumeration of the data from this study. The third expression, frequency of occurrence

as a function of the total number of scats, can be obtained by multiplying Formula 3 by Formula 4:

$$\frac{\text{Total Number of Occurrences of All Components}}{\text{Total Number of Scats}}; \quad (4)$$

Volumetric data from scat analyses were transcribed directly onto Fortran coding forms and were subsequently punched onto computer cards. Data analyses were performed using a series of SPSS (Statistical Package for the Social Sciences, Version 8, Vogelback Computing Center, Northwestern University) programs on the Control Data Corporation Cyber 170, Model 750 computer at the Michigan State University Computer Laboratory.

To investigate seasonal changes in the food habits of the maned wolves of the Serra da Canastra, it was necessary to define the climatic seasons in that region for the two years of this study. Maximum and minimum temperature were measured daily; precipitation, actual temperature, relative humidity, cloud cover, wind speed and direction were determined at intervals of 12 hours (approximately 0630 and 1830 hours). Mean monthly minutes of sunlight were estimated from astronomical tables (World Almanac and Book of Facts, 1980, Newspaper Enterprise Association, New York). Total monthly precipitation and monthly averages for minimum temperature and minutes of sunlight were selected as criteria for determination of seasons (Figure 4). Other measured climatic variables were also seasonal

FIGURE 4. Temperature, length of day and rainfall as criteria for definition of wet and dry seasons. Curves: 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 measurable precipitation per month.

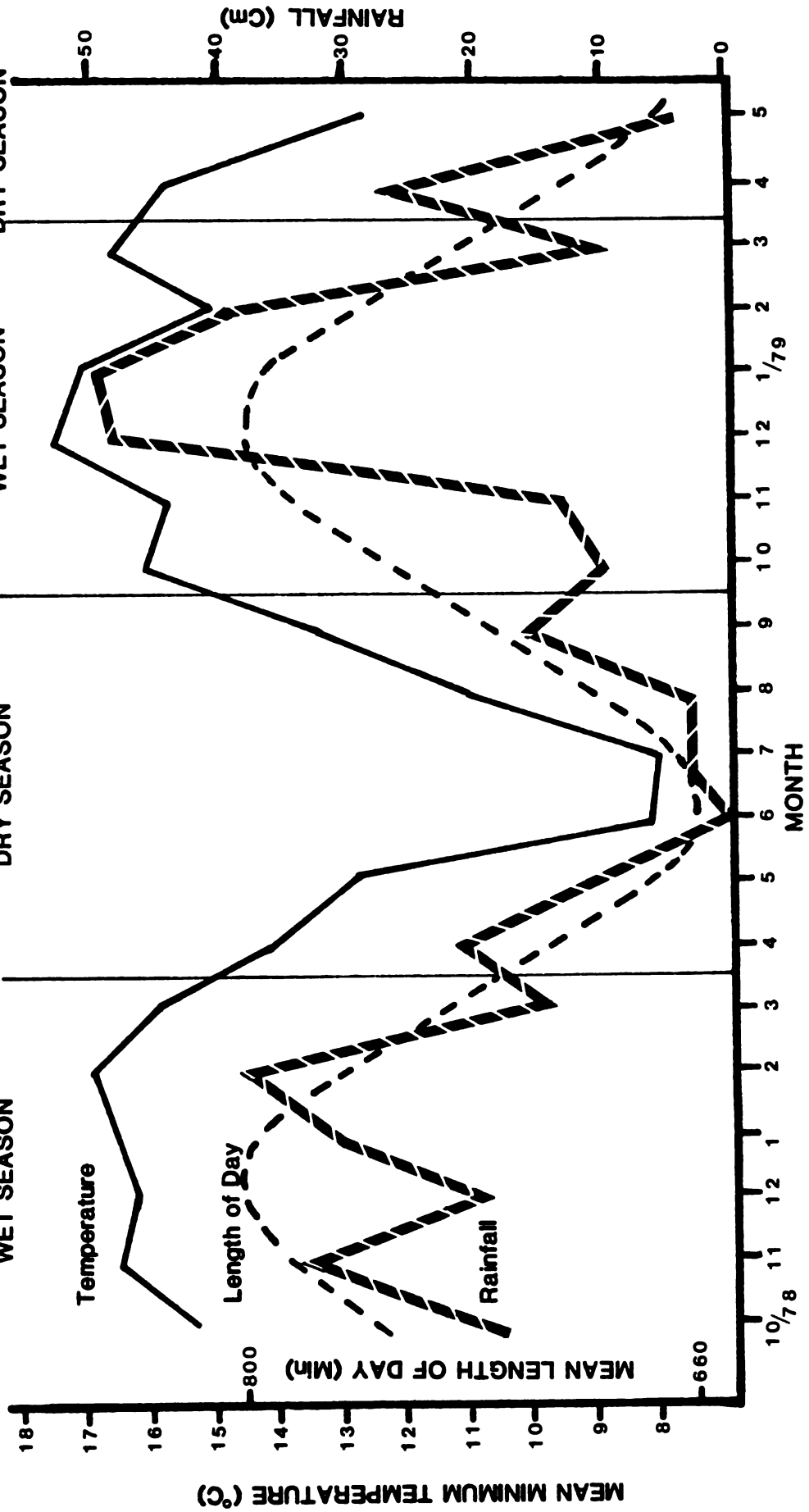
RAINFALL (Cm)
50
40
30
20
10
0
DRY SEASON
WET SEASON
DRY SEASON
WET SEASON
Temperature
Length of Day
Rainfall
MEAN MINIMUM TEMPERATURE (°C)
18
17
16
15
14
13
12
11
10
9
8
MEAN LENGTH OF DAY (Min)
800
660
10/78
11
12
1
2
3
4
5
6
7
8
9
10
11
12
1/79
2
3
4
5
MONTH

Figure 4.

but were perhaps less important in the regulation of primary productivity in the study area. Dry seasons were defined as the months of April through September and wet seasons as the months of October through March.

Census of Available Food Items

A list of the food items typically consumed by maned wolves has certain academic value, but limited practical relevance without the additional knowledge of what food items were available to choose from. More specifically, any resource-oriented management strategy would certainly benefit from knowledge of the extent to which maned wolves use available resources. A consensus taken from the 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; Carvalho, 1976). The availability of these food items was therefore selected as an indicator of the relative abundance of trophic resources available to the maned wolves in the study area. Availability of these resources was estimated on a monthly basis.

Small-mammal populations were sampled in each of the three major habitat types in the park using wooden-based rat traps. Fifty traps baited with masticated rolled oats were set for three consecutive nights during the last week of each month in each habitat type. The area to be

sampled each month within each habitat type was selected randomly from a list of candidate areas accessible from my field headquarters. To diminish the sampling problems associated with the depletion of populations in small areas, I adopted the convention of not sampling the same area twice consecutively. Traps were placed four meters apart in a straight line following a randomly chosen vector within each habitat type. Marginal areas between different habitat types were avoided. Study skins were made from the majority of captured small mammals, and the remainder were preserved in formalin. All specimens were deposited in the collections of The Museum, Michigan State University (Table 23, Appendix).

The trap lines described above were also used as transect lines for the estimation of relative diversity and abundance of fruits available to maned wolves. The 5 ha area sampled in each habitat type 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.

The above sampling scheme estimated the relative monthly diversity and abundance of all available fruits but indicated nothing of the extent to which these might be used by maned wolves. To determine which fruit species

might be eaten by maned wolves, I interviewed area residents and from their responses made a list of fruits likely to be consumed. The months when these species were in fruit were noted and examples were incorporated into a reference collection used in the analysis of scats of maned wolves. Finally, the fruits found in scats of maned wolves were recorded, and the season in which these species were in fruit was documented.

RESULTS

Physical Characteristics of Captured Maned Wolves

Various authors (e.g., Azara, 1801; Cabrera and Yepes, 1960; Langguth, 1969) have described in detail certain physical attributes of the maned wolf such as pelage, weights and measurements. My observations are in general agreement with these previously published descriptions and therefore are not stressed in this dissertation. However, as published data on the hematology and blood chemistry of this species are unavailable for free-living individuals, I have considered these aspects in greater detail.

Pelage, Weights and Measurements

Examination of close-up photographs of the nine adult maned wolves captured in the Serra da Canastra revealed almost no observable variation in pelage coloration between these individuals. 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 any of the individuals in my study area without the aid of radio-telemetry.

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 2).

Weights and selected measurements of nine captured adult wolves are also presented in Table 2. All comparisons of these values between age classes, and all but one comparison between sexes were not significantly different at the $p = .05$ level of significance. A Student's t-test for unpaired observations (Steel and Torrie, 1960) indicated that sampled male wolves had significantly longer pinnae than sampled females ($p < .05$) in this small group.

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 maned wolves (Zoo 1 and Zoo 2) recently acquired by

TABLE 2. Weights and measurements of captured maned wolves.

	WOLF NAME									
	Alpha	Beta	Gamma	Delta	Epsilon	Kappa	Lambda	Zeta	Sigma	
	Female	Male	Male	Female	Female	Female	Male	Male	Male	$\bar{x}$ ± SD
Age classification*	M	M	M	O	Y	Y	Y	M	M	
Weight (kg)	25.1	22.4	25.8	21.3	20.5	24.0	23.1	23.1	24.4	23.3 ± 1.73
Head and body length (cm)	99.0	95.0	107.0	104.0	105.0	104.0	99.0	100.0	114.0	103.0 ± 5.57
Tail length	49.0	45.0	#	43.0	38.0	46.0	45.0	43.0	47.0	44.5 ± 3.30
Ear length	16.0	17.0	17.0	16.5	17.0	15.0	18.0	17.5	17.5	16.8 ± .90
Hind foot length	29.5	29.0	30.0	30.0	29.0	30.5	28.0	27.5	32.0	29.5 ± 1.35
Forelimb length**	85.0	87.0	91.0	91.0	86.0	90.0	91.0	89.0	96.0	89.6 ± 3.32
Hindlimb length***	80.0	85.0	96.0	84.0	81.0	95.0	92.0	91.0	99.0	89.2 ± 6.92
Length of white on tail	--	--	--	--	18.0	8.0	19.0	23.0	31.0	19.8 ± 8.35
Length of black on antebrachium	--	--	--	--	34.0	50.0	46.0	44.0	47.0	44.2 ± 6.10

TABLE 2 (continued)

	WOLF NAME										
	Alpha	Beta	Gamma	Delta	Epsilon	Kappa	Lambda	Zeta	Sigma		
	Female	Male	Male	Female	Female	Female	Male	Male	Male	$\bar{x}$ ± SD	
Length of black on hindlimb	--	--	--	--	37.0	38.0	37.0	38.0	37.0	37.4	.55
Length of black stripe on mane	--	--	--	--	49.0	47.0	40.0	45.0	54.0	47.0	5.15

*Age classification: Y = young; M = middle-aged; O = old.
**Measured from the manus to the dorsal border of the scapula.
***Measured from the pes to the cranial crest of the ilium.
#Extremity missing.

that institution. One of the latter two wolves was a female; the sex of the other was not recorded.

These data (Tables 3 and 4) serve as a standard to which values from other maned wolves may be compared. However, due to factors such as small sample sizes, difficulties during collection and transportation of blood samples, and the fact that little information was available concerning the preexisting environmental or physiological conditions that may have affected these values, a degree of caution should be used when consulting them as normal standards.

The values obtained from these analyses generally fall within the ranges established for normal dogs, Canis familiaris (Brunden et al., 1970; Bulgin et al., 1970; Bulgin et al., 1971; Porter and Canaday, 1971; Schalm, 1975). Hematocrit, hemoglobin and erythrocyte values for tested wolves, however, fall toward the lower ends of the ranges for these values in normal dogs. These values are particularly low for maned wolf Zoo 2: the mean corpuscular volume (hematocrit/RBC count) calculated for this individual is 55 μ^3. A value this low in a dog would be indicative of microcytic anemia. The fact that hematocrit, hemoglobin and RBC count values for the tested wolves were generally low in comparison with standards for normal dogs may be the result of higher parasite loads and lower quality diets in these maned wolves. That environmental factors may have contributed to the lower values of

TABLE 3. Hematologic values for 10 maned wolves.*

Determination	Alpha (♀)	Delta (♀)	Epsilon (♀)	Zoo 2 (♀)	Zoo 1 (?)	Beta (♂)	Gamma (♂)	Lambda (♂)	Zeta (♂)	Sigma (♂)	$\bar{x}$	SD
Hematocrit (%)[a]	--	47.0	41.5	32.0	37.5	36.5	37.0	37.0	37.5	37.0	38.1	4.11
Hemoglobin (g/100 ml)	--	15.8	14.0	10.2	12.0	11.2	10.8	11.8	12.0	11.6	12.2	1.72
Erythrocytes (10^6)[b]	--	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)[b]	--	14.1	12.3	14.1	17.75	14.8	12.15	15.4	12.15	14.8	14.17	1.83
Myelocytes (%)[c]	0	0	0	0	0	0	0	0	0	0	0	0
Metamyelocytes (%)[c]	0	0	0	0	0	0	0	0	0	0	0	0
Band cells (%)[c]	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 (%)[c]	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 (%)[c]	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 (%)[c]	0	0	2.0	0	0	0	0	0	0	0	0.2	0.63

TABLE 3 (continued)

Determination	Alpha (♀)	Delta (♀)	Epsilon (♀)	Zoo 2 (♀)	Zoo 1 (?)	Beta (♂)	Gamma (♂)	Lambda (♂)	Zeta (♂)	Sigma (♂)	$\bar{x}$	SD
Lymphocytes (%)[c]	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 (%)[c]	2.0	0	2.0	0	3.0	1.0	3.0	2.0	2.0	3.0	1.8	1.14

*Two of the tested maned wolves, "Zoo 1" and "Zoo 2," were captive in the Belo Horizonte Zoological Garden. Other wolves were free-living in the Serra da Canastra. The sex of "Zoo 1" was not recorded.

[a]Percent of blood volume.
[b]Cells per mm^3.
[c]Percent of white blood cells.

TABLE 4. Biochemical serum values for seven maned wolves.*

Determination	Delta (♀)	Epsilon (♀)	Beta (♂)	Gamma (♂)	Lambda (♂)	Zeta (♂)	Sigma (♂)	$\bar{x}$	SD
Total Protein (g/100 ml)	--	14.0	8.8	--	7.6	6.4	7.8	7.7	.98
Albumin (%)[a]	--	22.0	26.0	--	21.0	22.0	24.0	23.3	2.22
Globulin, α_1 (%)[a]	--	7.0	12.0	--	11.0	7.0	12.0	10.5	2.38
Globulin, α_2 (%)[a]	--	10.0	13.0	--	12.0	10.0	14.0	12.3	1.71
Globulin, β (%)[a]	--	55.0	36.0	--	41.0	42.0	36.0	38.8	3.20
Globulin, γ (%)[a]	--	6.0	13.0	--	15.0	19.0	14.0	15.3	2.63
SGPT (IU/l;R-f)	51.0	--	50.0	47.0	58.0	49.0	--	51.0	4.18
SGOT (IU/l;R-f)	200.0	--	66.0	92.0	95.0	68.0	--	104.2	55.18

*The blood sample from maned wolf Epsilon hemolyzed prior to analysis and therefore was excluded from calculations of sample mean and standard deviation.

[a]Percent of total protein.

hematocrit and erythrocyte count for wolves of the Serra da Canastra is corroborated by the fact that similar determinations from wolves in the National Zoological Park, Washington (Bush, in press), resulted in mean corpuscular volumes above the mean for normal dogs.

Numbers of mature and immature neutrophils were within limits for normal dogs for all tested wolves except Delta. The relatively high percentages of band and segmented cells in the blood of this individual may indicate that an inflammation or suppurating wound was present at the time the blood sample was collected. In fact, Delta was suffering at that time from severe fly strike in one inner ear and surrounding tissues. This infestation, perhaps accompanied by a secondary bacterial infection, was possibly responsible for the elevated neutrophil count.

With the exception of maned wolf Beta, eosinophil counts were normal, as judged by dog standards, for all tested wolves. The phagocytic role of eosinophils is often involved in antigen-antibody reactions to parasitic infestation or re-exposure to a foreign protein (Rich, 1974). The fact that four species of nematode larvae were found in the feces of Beta lends some support to an allergic reaction to endoparasites as the explanation of this eosinophilia. Parasitization by the giant kidney worm, common in maned wolves, might also have contributed to an elevated eosinophil count if that parasite were present in this wolf. The presence of this parasite could not have

been determined by the diagnostic technique used in this study.

Lymphocyte counts were above normal levels for dogs only for the two wolves residing in the Belo Horizonte Zoological Garden. Lymphocyte function is involved in chronic immune responses, and elevated counts often indicate lymphosarcoma or recovery from an infection. I have no indication as to what may have caused the elevated counts in these zoo animals. However, it is interesting to note that the lymphocyte counts for the captive maned wolves tested by Bush are also higher than values for normal dogs.

With the exception of maned wolf Epsilon, total protein in blood serum samples from wolves tested in this study was within established limits for normal dogs. The cellular component of the blood sample from Epsilon had apparently hemolyzed prior to removal of the serum fraction and was therefore not considered in calculation of group means.

The α_1, α_2, and γ globulin components of the serum protein from tested wolves were within the ranges for normal dogs. However, although the normal values of albumin and β globulin are respectively about 50 percent and 25 percent in dogs, these values in tested wolves averaged about 23 percent and 39 percent. If these values are not artifactual, then either the normal values for these serum proteins in maned wolves are different from those of the

normal values in dogs, or an extrinsic factor such as chronic infection caused a mobilization of protein from albumin to β globulin in all tested maned wolves. However, the consistency of these values, as indicated by the small standard deviations for these proteins (2.22 and 3.20, respectively), tends to refute the latter explanation.

Serum glutamic pyruvic transaminase (SGPT) and serum glutamic oxalacetic transaminase (SGOT) were measured by the Reitman-Frankel procedure in each of five wolves. Although SGPT values from tested wolves were higher than those for normal dogs, the consistency of the values from tested wolves (SD = 4.18), and the fact that the values for these enzymes often vary significantly among the laboratories performing the analysis suggests that this difference may be an artifact of laboratory procedure. In normal dogs, SGPT and SGOT values are of about equal magnitude. Maned wolves Gamma and Lambda showed SGOT values moderately greater (45 and 37 percent, respectively) than SGPT values; the SGOT value for Delta was 149 percent greater than the SGPT value. Myositis associated with capture and restraint could have contributed to the elevated SGOT in these wolves. The very high SGOT value for Delta could be associated with muscle damage resulting from the fly strike in her inner ear and surrounding tissues.

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. 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

The West Range was located northwest of my field headquarters and east of the village of São João Batista (Figure 5). Connecting peripheral points on a map of plotted radiotelemetric locations yields a polygon with an area of 21.7 km^2. This estimate, however, is probably smaller than the area actually used by the resident pair of wolves. This is because one series of ridges and valleys, measuring about 4 km^2, was so difficult to reach from my field headquarters that I never obtained more than one radiotelemetric vector from a wolf in that area. Thus, I was unable to quantify the extent to which that area was used by wolves of the West Range.

FIGURE 5. Locations of home ranges of maned wolves in the study area.

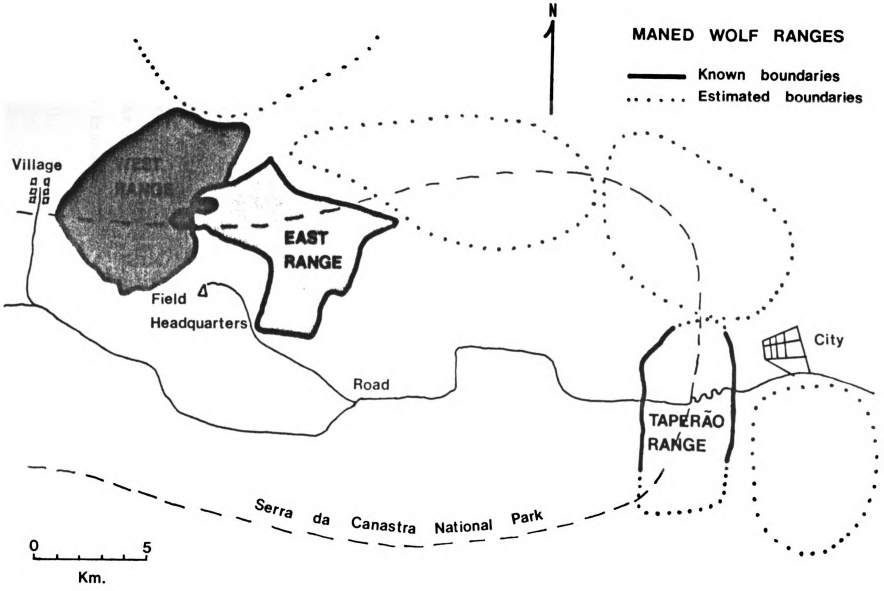
N
MANED WOLF RANGES
Known boundaries
Estimated boundaries
Village
WEST RANGE
EAST RANGE
Field Headquarters
Road
City
TAPERÃO RANGE
Serra da Canastra National Park
0
5
Km.

Figure 5.

East Range

Directly northeast of my field headquarters and adjacent to the West Range was the East Range (Figure 5). The pairs of wolves that successively used this range were more easily located than the wolves of the other two ranges. Therefore, my estimate of the area of this range, as based on radiotelemetric locations, is perhaps the most accurate of the three under consideration. Connection of the peripheral points on a map of radiotelemetric locations for wolves using this area show that the total occupied area was 30.0 km^2.

Taperão Range

The Taperão Range (Figure 5) 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 were particularly knowledgeable about the movements of the maned wolves in the Taperao Range and declared that the extent of the movements of the resident wolves had remained unchanged for many years. With the help of these farmers, I easily located paths frequently used by wolves and trapped male maned wolf Beta on 10 September 1978. On many occasions, Beta was seen in the company of a small female wolf. Although Beta was recaptured six times during the course of the study, I was never able to trap and put a transmitter on his mate.

The region of 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 signal from Beta's transmitter. Therefore, the area of his home range, 12 km^2 as calculated from radiotelemetric data, underestimates the area actually used by this wolf. A more realistic estimate, based on single radiotelemetric vectors and visual sightings is about 24 km^2 for the Taperão Range. The problems with radio reception in this area, the long distance from my field headquarters, and the fact that I never succeeded in capturing a female wolf there combined to make the Taperão Range unsuitable for attaining several of the objectives of my study. I therefore elected to spend the majority of my limited temporal and financial resources in the West and East Ranges. With the exception of scat collection, data were collected only occasionally or opportunistically in the Taperão Range.

Other Ranges

In addition to the three home ranges previously mentioned, I was also aware of several other ranges in the region (Figure 5). 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. Because of the problems associated with access to these additional ranges, I made no attempts to capture their resident maned wolves. I have little information on how many wolves occupied these ranges other than the facts that pairs of wolves were sighted in three of the four 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 probably occupied each of these additional ranges.

Use of Available Habitat Types by Maned Wolves

I determined the extent to which available habitat types were used by the maned wolves of the Serra da Canastra by first establishing criteria to distinguish functionally between the various vegetation types in my study area. Overstory density, composition and height were used to classify habitats either as grassland, cerrado or forest. I defined grassland habitat as areas dominated by annual grass species up to 1 m in height, and with only occasional trees or shrubs. Cerrado was characterized by an open, woody overstory up to 5 m in height and composed of small, tortuous trees or shrubs. I defined forest habitat by the presence of a closed overstory composed largely of trees greater than 5 m in height. The relative percentages of these habitat types in the

study area as previously mentioned, were 50, 35 and 15 respectively.

The following questions of interest were addressed: (1) What are the relative frequencies with which maned wolves use these available habitat types? (2) Do these frequencies differ between sexes of wolves? (3) Do these frequencies differ between pairs of wolves? (4) Do these percentages vary with seasonal change? (5) Are habitat types used in proportion to their occurrence?

Tabulation of 458 radiotelemetric locations (Table 5) for which habitat types were known indicated that maned wolves spent approximately 34 percent of their time in grassland, 43 percent in cerrado and 24 percent in forest. These data were transformed to reflect equal sample sizes for both sexes, and a chi-square test of goodness of fit was applied to test for differences between sexes in the use of each habitat type. Results of these tests suggest that male maned wolves used grassland habitat significantly more than did females ($p < .05$), and that females used cerrado habitat significantly more than did males ($p < .025$). No significant difference between sexes was found in use by maned wolves of forest habitat.

Sufficient radiotelemetric observations ($n = 458$) were made to allow the comparison of habitat use between three bonded pairs of maned wolves (Table 6). G-tests of independence (Sokal and Rohlf, 1969) were performed for each habitat type. Results indicated that these three

TABLE 5. Use of three habitat types by maned wolves.

Habitat Type	MALES		FEMALES		ALL WOLVES	
	Radio-locations (n)	Percent	Radio-locations (n)	Percent	Radio-locations (n)	Percent
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 6. Use of habitat types by maned wolves grouped by bonded pairs.

Habitat Type	PAIR 1		PAIR 2		PAIR 3	
	Radio-locations (n)	Percent	Radio-locations (n)	Percent	Radio-locations (n)	Percent
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

male-female pairs were not independent of the use of cerrado ($p < .005$) or of forest habitat ($p < .005$).

Seasonal differences in habitat use were determined by dividing the radiolocations for which habitat type was known into those occurring during the wet and dry seasons (Table 7). Chi-square tests were used to test the null hypothesis that there was no seasonal difference in the use of each habitat type of these wolves. Results of these tests indicate that grasslands were used more often during the wet season ($p < .025$), and forest habitat was used more often during the dry season ($p < .025$). A possible biological significance of these data is that grassland habitat may support a lower relative abundance of prey species during the dry season when pastures are burned by local ranchers.

The preceding analyses are biased to some extent in two ways: first, the majority of the radiolocations made during this study occurred during the day. Thus, because these wolves were largely nocturnal (see the following section of this dissertation), habitat types associated with daytime rest sites would tend to 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 analyses. In an attempt to compensate for these biases,

TABLE 7. Seasonal use of three habitat types by maned wolves.

Habitat Type	WET SEASONS		DRY SEASONS		ALL SEASONS	
	Radio-locations (n)	Percent	Radio-locations (n)	Percent	Radio-locations (n)	Percent
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

I divided those radiolocations for which habitat type was known, into those recorded during the day (1601-1800 hours), and those observations made by night (1801-0600). 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 type to test the hypotheses that habitat types were used in direct proportion to their occurrence (Table 8). Results of this analysis suggest 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 in Activity

The daily and seasonal patterns of temporal activity of the maned wolves of the Serra da Canastra were determined in two manners: (1) classification by time block and activity level of daily locations of radiocollared wolves; and (2) periodic monitoring of the activity levels of one or more wolves over periods of several hours. Results of the first method include 763 radiotelemetric observations on eight maned wolves over a period of 20 months (Figure 6). I reduced the bias

TABLE 8. Use of available habitat types with respect to their relative occurrence.

Time Block	Habitat Type	Proportion of Habitat Type in Area*	Number of Radiotelemetric Observations	Proportion of Total Observations	Confidence Interval on Proportion of Occurrence**	Significant Deviation from Expected Proportion
0601-1800						
	Grassland	.50	108	.30	$.22 \leq P \leq .38$	Less
	Cerrado	.35	172	.48	$.39 \leq P \leq .57$	Greater
	Forest	.15	80	.22	$.15 \leq P \leq .29$	N.S.
1801-0600						
	Grassland	.50	21	.28	$.20 \leq P \leq .36$	Less
	Cerrado	.35	21	.28	$.20 \leq P \leq .36$	N.S.
	Forest	.15	33	.44	$.35 \leq P \leq .53$	Greater

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

**Confidence intervals are based on the Bonferroni normal statistics (Miller, 1966); p = .01.

FIGURE 6. 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 (inactive, intermittently-active or active).

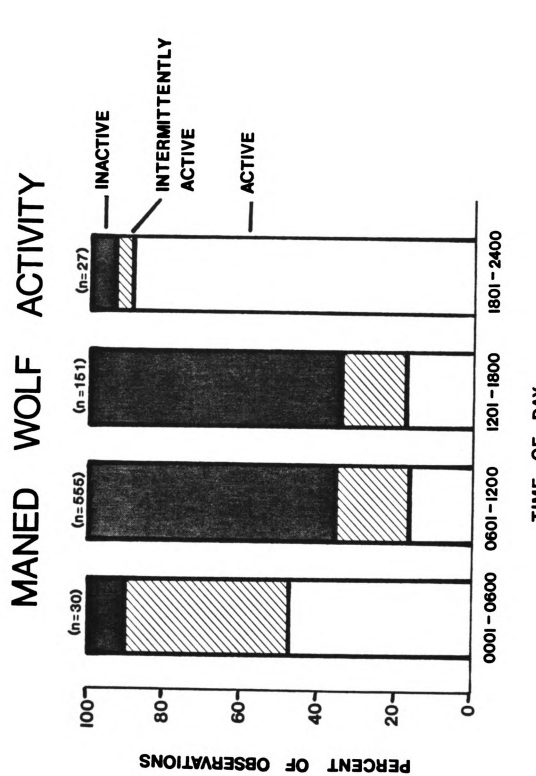
MANED WOLF ACTIVITY
INACTIVE
INTERMITTENTLY ACTIVE
ACTIVE
(n=30)
(n=555)
(n=161)
(n=27)
PERCENT OF OBSERVATIONS
100
80
60
40
20
0
0001-0600
0601-1200
1201-1800
1801-2400
TIME OF DAY

Figure 6.

contributed by many consecutive locations of the same wolf during a single time period by randomly selecting a maximum of two locations per wolf per time block for inclusion in this analysis.

The activity-monitoring devices incorporated into the transmitters worn by maned wolves in the study area consisted of glass tubes each containing a drop of mercury. When the mercury was stationary at one end of the tube, the transmitted pulse rate was about 50 signals per minute. Alternatively, when the mercury closed the circuit at the opposite end of the tube, the transmitted signal rate was approximately doubled. The high and low pulse rates differed between collars and were therefore useful in identifying individual wolves. When wolves were physically active, the drop of mercury vacillated between contact points thereby producing a syncopated pulse rate highly distinct from that of a transmitter on an inactive wolf. In most cases, the two activity classes mentioned above were distinguishable from intermittent activity, the activity class in which wolves made only occasional postural changes or other erratic movements.

Radiotelemetric data collected during the hours of daylight (0601-1800) indicate that radiocollared wolves were active during 34.7 percent of this time period, 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 observations of wolves active during the

day 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 the hours of daylight.

The maned wolves of the Serra da Canastra were considerably more active at night than during the day. Ninety-one percent of the radiotelemetric observations made between 1801 and 0600 hours were of constantly- or intermittently-active wolves. Between the hours of 1801 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. In other words, wolves of the Serra da Canastra 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 ($p = .33$; Table 9), the same test did suggest a possible relation between activity and sex ($p = .012$; Table 10). Further, when numbers of intermittently-active, and of constantly-active observations were pooled to form a single class for each sex, a G-test of independence indicated a significant level of dependence between activity and the sex of these wolves ($p < .01$). Again, using combined numbers of observations

TABLE 9. Levels of activity of eight maned wolves grouped by bonded pairs.*

Activity Level	PAIR 1		PAIR 2		PAIR 3		PAIR 4	
	Radio-locations (n)	Percent	Radio-locations (n)	Percent	Radio-locations (n)	Percent	Radio-locations (n)	Percent
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

*Chi-square value = 6.91, 6 d.f., p = .33.

TABLE 10. Levels of activity of eight maned wolves grouped by sex.*

Activity Level	FEMALES		MALES		ALL WOLVES	
	Radio-locations (n)	Percent	Radio-locations (n)	Percent	Radio-locations (n)	Percent
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

*Chi-square test value = 8.80, 2 d.f., p = .012. When intermittently-active and constantly-active observations are combined, G-test value = 7.35, 1 d.f., p < .01.

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

In addition to radiotelemetric observations across blocks of time, 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 a small stream. 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. Although I never saw a wolf perform these brief movements, 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. On some occasions, observed wolves travelled from one extreme to another of a home range with only brief stops.

Alternatively, 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. Although I did not statistically test the relationship between weather conditions and the activity patterns of maned wolves, 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

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 invested in close association. According to local observers, family groups were rarely seen. It is noteworthy to mention that of the three percent of mammal species described as monogamous, only 13 species demonstrate facultative monogamy (Kleiman, 1977). This type of monogamy has not previously been described for any species of the Carnivora.

The above findings are based on 1,537 trap-nights, 828 precise radiotelemetric locations, nearly as many single directional vectors, and approximately 50 visual sightings of eight maned wolves in the Serra da Canastra study area. Traps placed in locations featuring an

abundance of spoor resulted in the capture of eight wolves on a total of 47 occasions (Table 11) in the Serra da Canastra. One female and her two pups were taken in another area and will be discussed separately. Using daily radiotelemetry, I was able to estimate the boundaries of home ranges of the wolves in the Serra da Canastra. As estimates improved with increased numbers of observations, they are therefore likely to underestimate the areas used by wolves tracked for a short period of time. Trapping efforts were initiated in September 1978. By May 1979, at least one wolf from each of three home ranges had been captured and fitted with a radiocollar.

Beta

This wolf, a middle-aged male, was captured in the Taperão Range on 10 September 1978 (Figure 7). He was observed on numerous occasions in the company of a small female wolf that apparently shared that range. Due to previously discussed problems intrinsic to that geographic area, trapping efforts there were discontinued shortly after Beta was captured and radiotelemetric location of that wolf was attempted only occasionally. Little can be said about these wolves other than that they shared part if not all of the same home range. I estimate the area of this home range to be about 24 km^2. During the 20 months that Beta carried a transmitter, he was observed either alone or with the same female wolf.

TABLE 11. Capture dates for maned wolves in three home ranges.

Home Range	Wolf Name	Sex	Date of Initial Capture	Date of Last Location or of Death	Number of Captures
Taperão	Beta	Male	10 Sept. 1978	24 May 1980	7
East	Gamma	Male	15 Dec. 1978	25 June 1979*	4
East	Delta	Female	18 Jan. 1979	28 Feb. 1979**	2
East	Epsilon	Female	22 Apr. 1979	25 May 1980	5
East	Lambda	Male	15 June 1979	25 May 1980	22
West	Kappa	Female	15 May 1979	25 May 1980	4
West	Zeta	Male	5 July 1979	17 Oct. 1979 to 26 Nov. 1979***	1
West	Sigma	Male	18 Nov. 1979	25 May 1980	2

*Radiotelemetric contact was lost with this wolf on this date. It was assumed that the animal left the study area.
**This wolf died as a result of suffering a broken leg.
***This wolf was killed by a local farmer sometime during this time period.

FIGURE 7. A chronological representation of the relationship among wolves inhabiting the East, West and Taperão Ranges. Symbols: C = the date of the initial capture of a maned wolf; D = the date by which a wolf was known to have died. Maned wolf Zeta died some time during the period indicated by the dotted line.

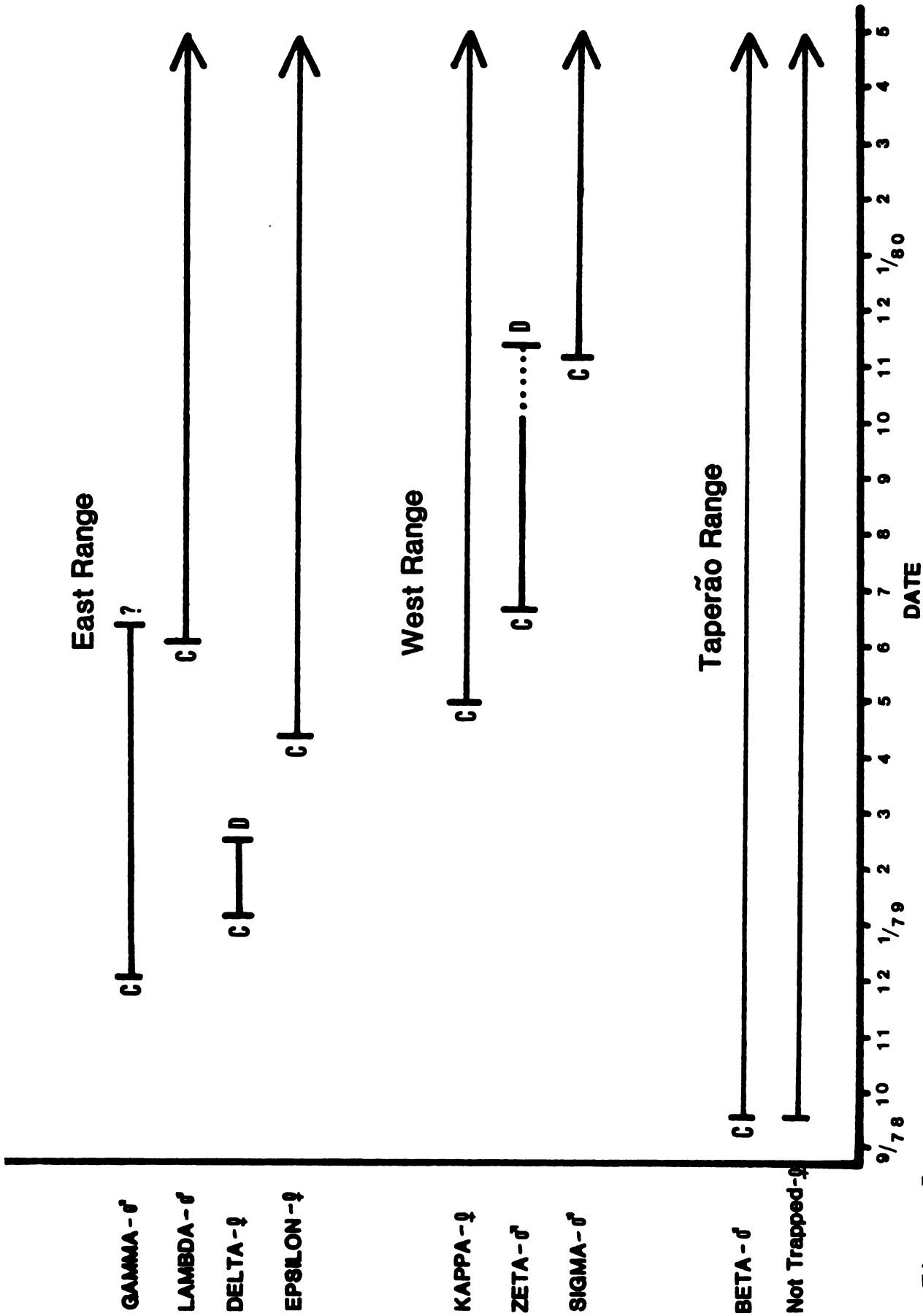
East Range
West Range
Taperão Range
GAMMA-♂
LAMBDA-♂
DELTA-♀
EPSILON-♀
KAPPA-♀
ZETA-♂
SIGMA-♂
BETA-♂
Not Trapped-♀
C
D
?
9/78
10
11
12
1/79
2
3
4
5
6
7
8
9
10
11
12
1/80
2
3
4
5
6
DATE

Figure 7.

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. I discovered at that time that the external antenna of his original antenna 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. It is probable that this damage was done during a social interaction between Beta and another wolf.

Gamma and Delta

Gamma, a male maned wolf classified as middle-aged, was first captured on 15 December 1978 in the East Range (Figure 7). Because this wolf was trapped during the height of the seasonal rains, my initial attempts to follow him by radiotelemetry were often thwarted by technical problems related to the radio equipment or by transportation difficulties. From the few precise radiolocations of this wolf, however, I learned the general outline of the East Range, plus the facts that the perimeter was well-defined and that it was stable (Figure 8).

An old female wolf, Delta, was taken in the same trap as was Gamma, but about one month later. At the time of her capture, she appeared weak and disoriented, often shaking her head from side to side. Closer examination

FIGURE 8. East Range occupied sequentially by maned wolves Delta (dotted line; n = 18 total radiolocations; female) and Gamma (striped line; n = 20 radiolocations; male); Epsilon (dashed line; n = 220 radiolocations; female) and Lambda (solid line; n = 225 radiolocations; male). Polygons represent the connected peripheral locations for each wolf.

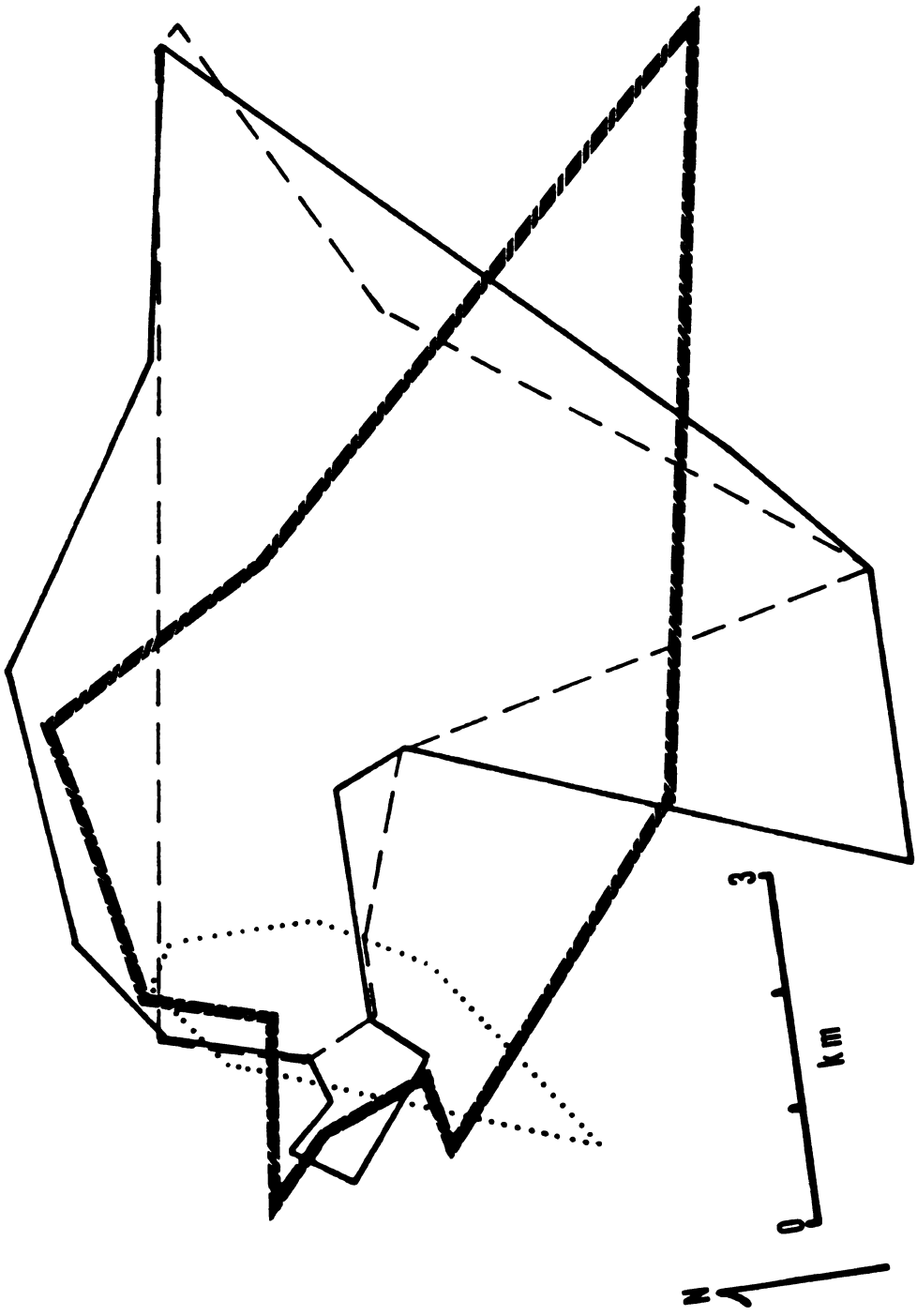

Figure 8.

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 subsequent capture on 4 February. Unfortunately, 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 on about 25 February. A subsequent necropsy revealed that the screw-worm infestation had caused considerable erosion of the left tympanic bulla and surrounding temporal bone. I speculate that her broken leg was an indirect consequence of an impaired sense of equilibrium caused by damage to the inner ear.

The number of radiolocations for Delta were few (n = 18). In addition, during three of the six weeks that this wolf carried a radiocollar, her locomotion was severely hampered by her broken leg. Nevertheless, the portion of her range that I was able to identify nearly completely overlapped that of Gamma (Figure 8), 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 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 then 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, he was located for the last time. I believe that 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. During the course of this research, I captured Lambda an additional 21 times and radiolocated him 225 times in the East Range (Figure 8). 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. He either left the range or died about two months after her capture. However, 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. I speculate, based on this circumstantial evidence, that Lambda was directly 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

Reports by area residents of 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 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 9) for about 14 weeks. On 17 October 1979, Zeta was located for the last time. Nearly six weeks later, I received a signal from his

FIGURE 9. 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.

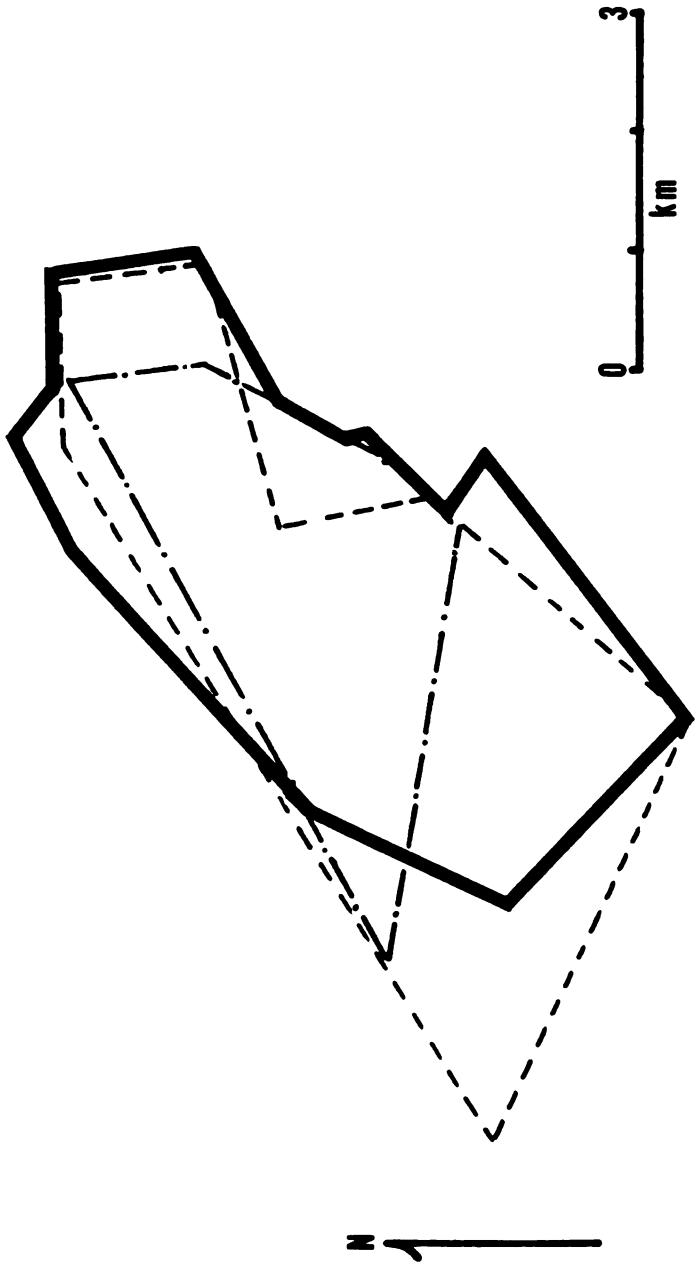

Figure 9.

transmitter, and, following the signal to its source, I found the transmitter on the bank of a swollen stream. The nylon collar had obviously been cut with a sharp instrument. It is probable that Zeta had been killed by an area farmer and the removed transmitter thrown into a deep pond. A flash flood washed the transmitter up onto the shore on the day that I received the final radio-signal.

On 18 November, a male middle-aged wolf, Sigma, was trapped in the West Range. Sigma took over the range formerly occupied by the missing Zeta (Figure 9), and on several occasions was observed in close association with Kappa.

During this study, 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 10). Because of small numbers of observations and because sampling was not randomized, the deviations in these frequencies may not represent actual monthly differences in the relative amount of time these wolves spent in close association. Other data such as the distribution of wolf feces and tracks, however, indicated to me that social activities involving

FIGURE 10. Percent of radiotelemetric locations per month in which Lambda and Epsilon were found in close association (n = the number of observations during which these wolves were located in close association during each calendar month).

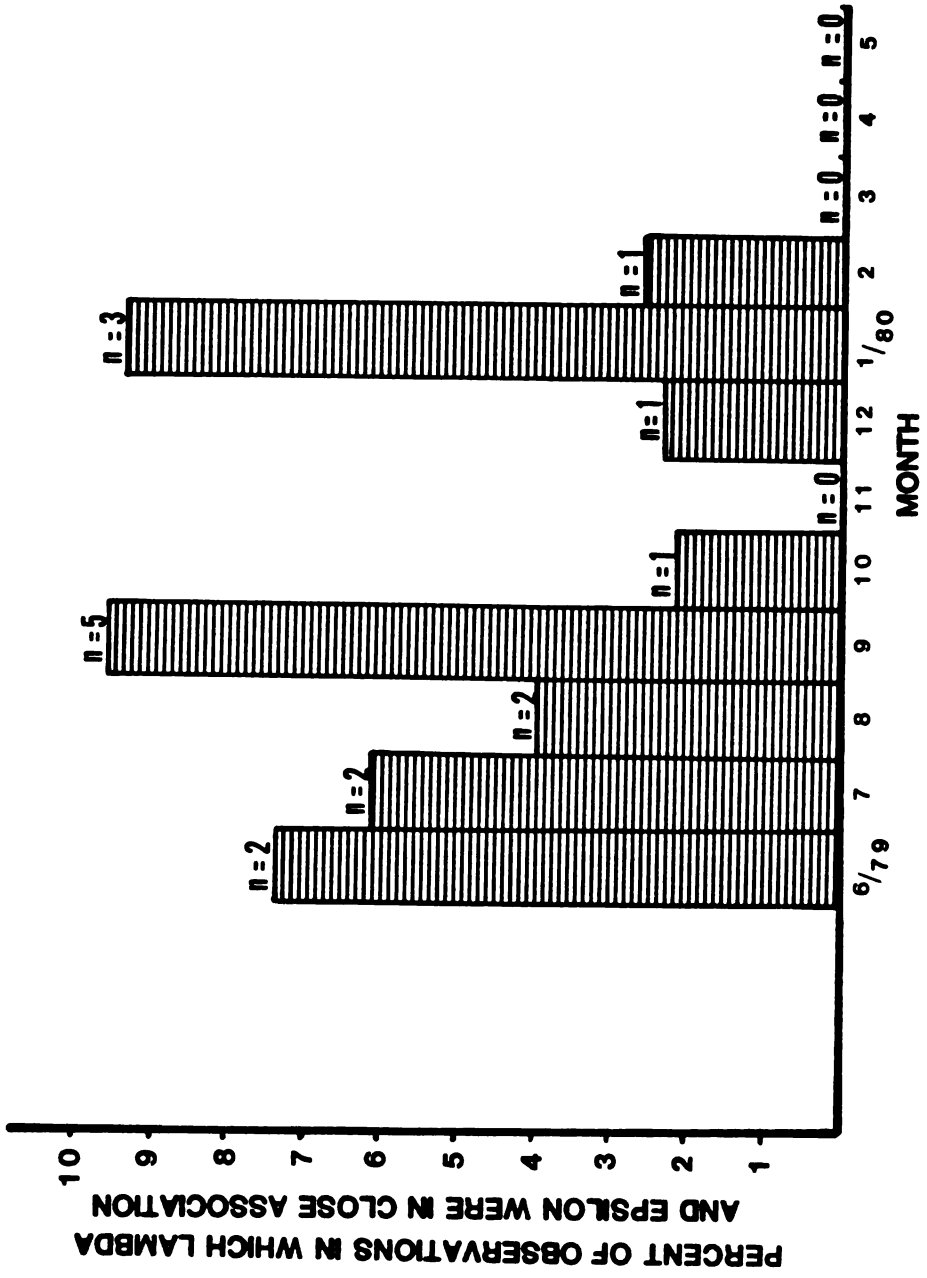
PERCENT OF OBSERVATIONS IN WHICH LAMBDA
AND EPSILON WERE IN CLOSE ASSOCIATION
10
9
8
7
6
5
4
3
2
1
n=2
n=2
n=2
n=5
n=1
n=0
n=1
n=3
n=1
n=0, n=0, n=0
6/79
7
8
9
10
11
12
1/80
2
3
4
5
MONTH

Figure 10.

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 diad were not often in close association, the location of one maned wolf did not appear to be independent of that of its mate. Both individuals used the same trails and resting places, but not simultaneously. In all but the Taperão Range, both members of a pair also were taken in the same trap. Often capturing one wolf seemed to facilitate the prompt capture of its mate in the same trap. Although traps and favorite areas were used by both members of a pair, I was unable to distinguish a pattern of alternation based on gender. That is, wolves of one sex did not generally appear to follow wolves of the opposite sex in the use of a particular locus within a home range.

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 produced by the maned wolves of the Serra da Canastra more resembled an extended variation of the bark of a large domestic dog. Each howl lasted approximately 0.7 second, was repeated at regular intervals of from two to four seconds, and sounded something like "oo-wáhh." Howling wolves repeated this call

from two to 23 times in succession with an average of about 9 repetitions. Both male and female wolves were heard vocalizing. However, because of the lack of discernable variation between the calls of different animals, I was unable to use vocalization alone to identify individual wolves. Occasionally as many as three wolves were heard howling simultaneously, and in at least two instances, wolves of two adjacent home ranges were heard exchanging vocalizations.

Wolves were heard vocalizing on 46 occasions in the study area (Figure 11). Twenty-nine of these occasions occurred in the East Range. Although sampling was not random, these data do suggest that maned wolves vocalized at any time of year, and that a peak in frequency occurred during the months of June through August, 1979. I speculate that 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.

In addition to the extended bark, the only vocalization that I heard uttered by adult maned wolves was a low-volume growl. This sound was produced when a trapped wolf was first approached by a human. As I came closer, the trapped wolf invariably began a series of extended barks. I was unable to distinguish differences in amplitude or frequency between the extended barks of captive and noncaptive wolves. Artificial predator calls and

FIGURE 11. 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).

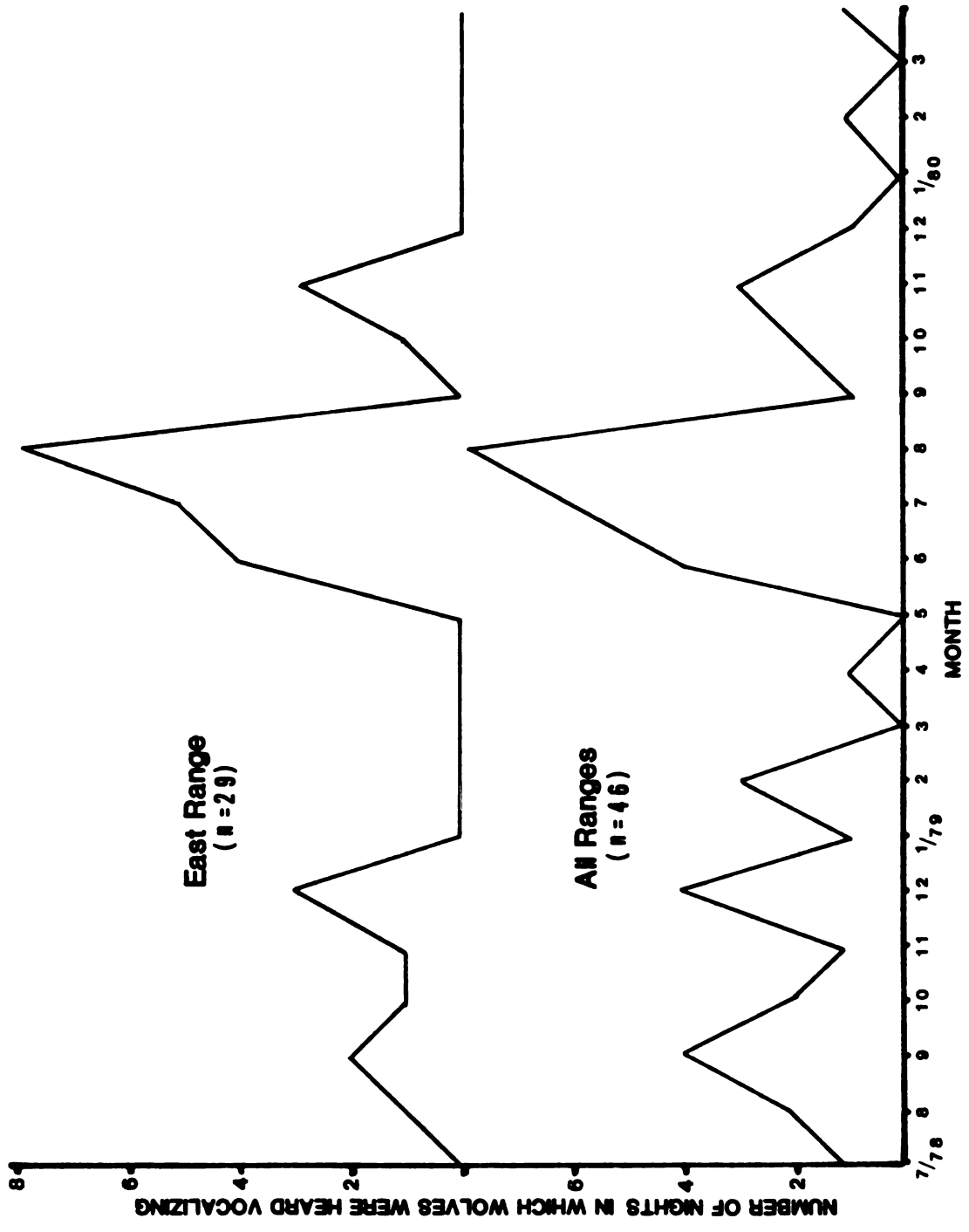
East Range
(n=29)
All Ranges
(n=46)
NUMBER OF NIGHTS IN WHICH WOLVES WERE HEARD VOCALIZING
MONTH
7/78
1/79
1/80

Figure 11.

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

The geographic locations used for deposition of feces by maned wolves did not appear to be random within home ranges. 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, intersections of trails, or termite mounds. The manner in which scats were grouped, their elevations above surrounding ground level, and the substrates on which they were deposited often differed between these location types. The variation within these parameters perhaps was related to communication between conspecifics.

I examined three den sites recently used by maned wolves (see section on Reproduction). At one of these, scats deposited by one or more adults and by two pups were present. 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. It is perhaps significant that all scats presumably 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. It has been suggested that maned wolves are locus-specific defecators (Kleiman, 1972). That is, feces are concentrated at certain loci within the home range of an individual. This was the case with the maned wolves of the Serra da Canastra to a limited extent. In the immediate vicinities of frequently-used resting places, I often found one, and occasionally two or three concentrations of scats. 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. My observations suggest that these latrines were probably used by both paired wolves residing in a home range.

After several months of collecting scats in the Serra da Canastra, I became proficient at assaying from a distance a section of home range and predicting where scats probably would be located. Scats thus 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 resisistance. For example, often-used trails were customarily located along open ridge tops rather than in valley bottoms. Scats along these important routes were not concentrated but were deposited individually at intervals along the 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.

The substrates upon which scats were deposited were also not randomly selected by maned wolves (Table 12). Sixty-five percent of the 740 collected scats were found on rocks, dirt piles, or termite mounds elevated above the surrounding ground level. 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 may perhaps be useful in interpreting any communicatory function of defecation in maned wolves. When startled or confronted at close quarters, trapped wolves approached by a member of the research team usually defecated, urinated and vocalized. Also, on two occasions when I surprised free maned wolves 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 in the trail and one vocalized. These incidents may imply that defecation by wolves serves a defensive or agonistic purpose.

With the exception of a few isolated incidents, I was able to collect very little information concerning urine-marking by maned wolves. The odor of the urine of maned

TABLE 12. Substrate used by maned wolves for the deposition of feces.

Substrate	Number of Locations	Percent
Rocks	257	34.7
Termite mounds	206	27.8
Paths or roads	202	27.3
Dirt mounds	16	2.2
Clumps of grass	4	.5
Log	1	.1
Wolf trap	1	.1
Substrate not recorded	53	7.2
TOTAL	740	99.9

wolves was characteristic and prevalent along frequently-used trails indicating that scent-marking may have been employed in the same context as the strategic deposition of feces. No scratching at the site was observed with recently-excreted urine, or for that matter with feces. In addition to urination by all wolves within traps, two individuals urinated immediately after being released from traps -- again suggesting a parallel between the agonistic or defensive function of deposition of feces and that of urine. All trapped wolves and a free female wolf were observed to use a squatting posture during urination. One free male was observed on two occasions to cock a hind leg when urinating. The urination postures used by captive maned wolves have been described by Kleiman (1972).

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 favorite locations for resting were used by both occupants of a 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 in a defensive or agonistic manner and may have aided in the indirect

defense of territories. Reduced dispersal of scats in the area of the den site perhaps drew less attention to potentially vulnerable offspring. Likewise, locus-specific defecation near resting-sites may function to reduce the likelihood of discovery of that location by unfriendly conspecifics or other predators.

Relationships Between Adjacent Pairs of Wolves

The maned wolves studied in the Serra da Canastra maintained strict territoriality during this research. That is, boundaries of the ranges of each bonded pair were fixed and were almost never transgressed by wolves of an adjacent range. Although many radiotelemetric locations were necessary to delineate the boundaries of a territory, once these limits were discovered, it became clear that they were known and respected by the resident wolves. 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 side opposite their own range. Scats were liberally deposited along trails on either side of the road, and wolves were occasionally heard vocalizing back and forth across this boundary.

For the most part, boundaries of home ranges appeared to remain constant over time. The two observed exceptions concerned cases in which wolves either died, or in one case, perhaps left the area. These two observations are of particular interest in that they give some insight into the type of territoriality maintained by the maned wolves of the Serra da Canastra. Unfortunately, in both cases the numbers of observations are small and therefore only the most general conclusions are warranted.

When Delta (female) died and Gamma (male) abandoned the west portion of the East Range, the interface between the West Range and the East Range (the Gameleira Road) was as indicated in Figure 12. 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 António'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 António'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, António's Area remained vacant for about four weeks before being repossessed by Lambda, male of the East Range. He was the only wolf known to use this area for the remaining five months of the study.

FIGURE 12. Areas of dispute between maned wolves residing in the West Range and in the East Range. António's Area was successively occupied by maned wolves of the East Range, West Range and then 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.

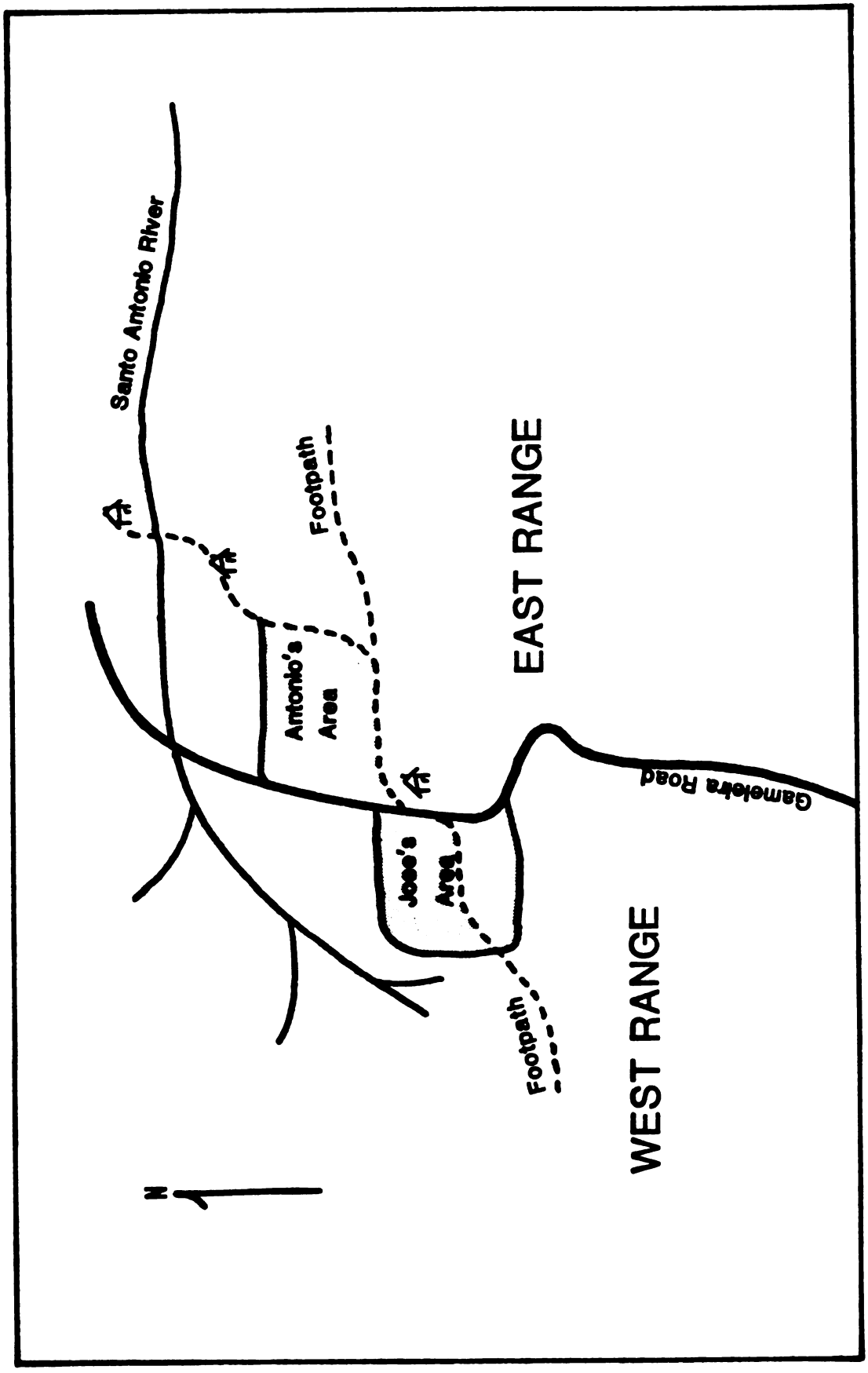
Santo Antonio River
Footpath
Antonio's Area
EAST RANGE
Gamelara Road
Footpath
WEST RANGE
N

Figure 12.

A second region of contention along the border of the West and East Ranges was a 0.75 km^2 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 expropriation, the only wolf observed in this area was Lambda. José's Area had apparently also been added to the East Range.

Perhaps the most significant conclusion that can be drawn from these observations is that 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. Whether it is significant that all successful expropriations were accomplished by male wolves, and that female wolves were not subsequently observed in these areas is open to speculation. However, these data suggest a system in which males competed to secure territory rather than mates. It is possible that these new additions to the territories of males were also acquired by their mates during periods of decreased social distance associated with the breeding season. Whether female maned wolves routinely made range extensions or territorial expropriations cannot be determined from these data.

Floaters, 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 conceivably have been floaters 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-aged male) as a group. I have no information that suggests a social tie between floating wolves and resident wolves, nor do I have information as to whether these nomadic wolves remain in close association with a few ranges or travel incessantly from range to range until a vacant area of suitable habitat is found. Based simply

on the negligible amount of area between established ranges, the latter alternative is intuitively more appealing.

Feeding Ecology

Seasonal Availability of Trophic Resources

To determine the extent to which maned wolves of the Serra da Canastra use existing food resources it was first necessary to have some a priori knowledge of what maned wolves eat. Although literature is scarce and not quantitative, authors are in general agreement that the diet of the maned wolf consists mainly of small vertebrates and of fruits, particularly lobeira (Solanum lycocarpum; Figure 13). Given this assumption, a correlation of scat contents with indices of relative abundance for fruits and for small vertebrates across seasons gives an indication of the flexibility of the foraging patterns of these maned wolves.

Interviews with at least 50 area residents produced a list of 43 fruits which might be eaten by the maned wolves of the Serra da Canastra, and the months during which these plants are in fruit. I was able to verify the months when most of these fruits were available and found that information from the area residents was reliable. In general, these people believe that maned wolves eat any fruit suitable for human consumption plus several fruits not normally eaten by the people of this area.

FIGURE 13. Solanum lycocarpum, "fruit of the maned wolf."

Figure 13.

Therefore, their responses to my queries regarding fruits eaten by wolves usually consisted of a list of the wild and domestic species of fruits that those people ate plus the fruits whose seeds they had observed in feces of maned wolves.

To determine the seasonality of fruit resources, the numbers of available species as determined by questionnaires were graphed against the months in which these are in fruit (Figure 14, Curve A). A second estimation of the seasonality of fruit resources was given by the number of species in fruit encountered in monthly transect-lines (Figure 14, Curve C). Although neither of these curves gives any indication of the extent to which a particular fruit might be used by maned wolves, they both show more species in fruit during the wet season than the dry season. Further, the similarity of the graph of seasonality of available fruits with that of the seasonality of 14 species of fruits identified in maned wolf scats (Curve B in Figure 14) suggests a similar seasonal fruiting pattern between the fruits available to and consumed by maned wolves.

Because of the importance of the fruit lobeira in the diet of the maned wolves of the Serra da Canastra, its distribution and relative abundance in my study area will be considered apart from those of other fruits. This species is common in the Serra da Canastra but is not ubiquitous. The fact that lobeira was never counted in

FIGURE 14. 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 of fruits known to be consumed by maned wolves; C = the estimated total number of species fruiting per month as determined by transect-lines.

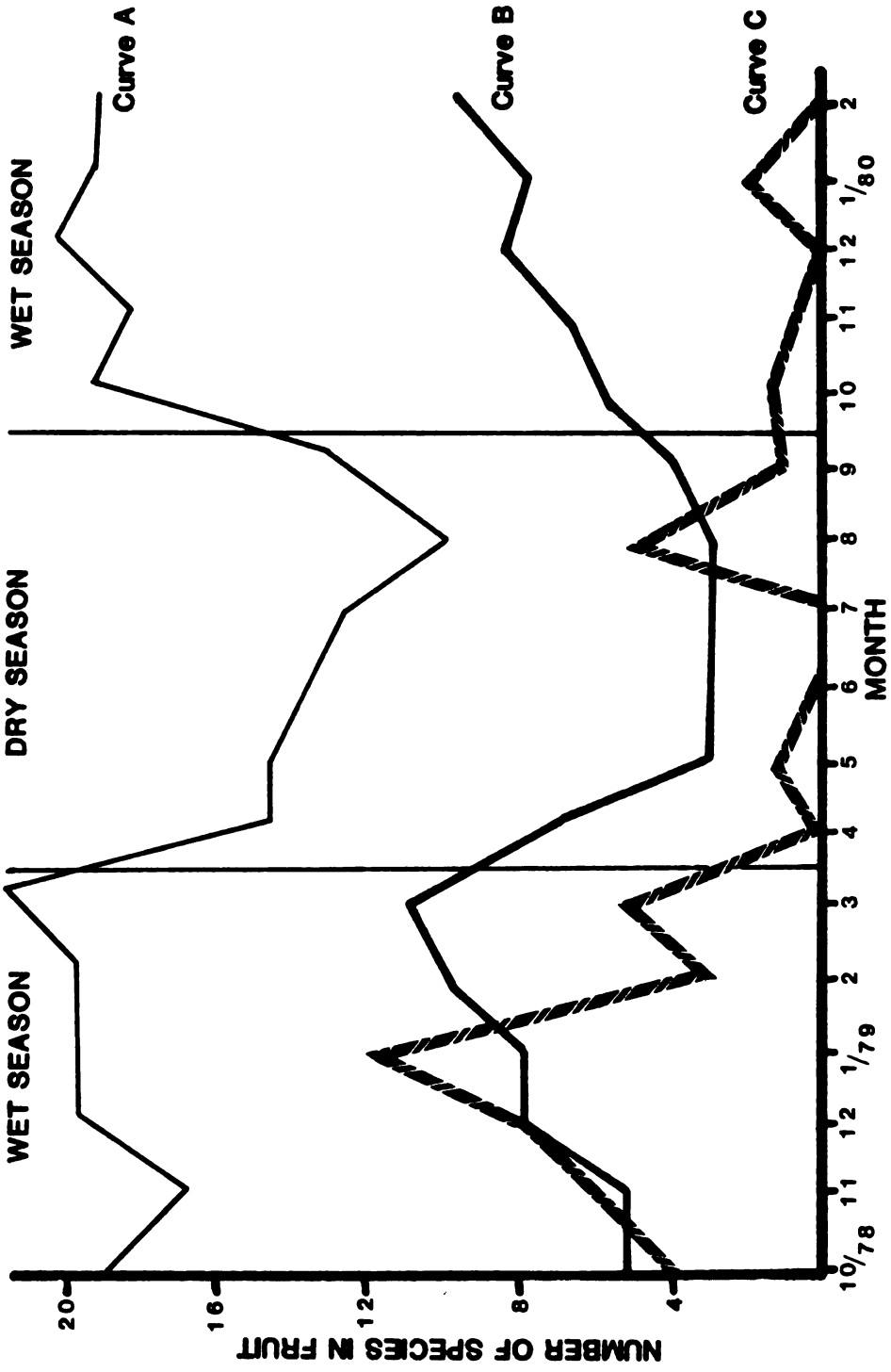
WET SEASON
DRY SEASON
WET SEASON
Curve A
Curve B
Curve C
NUMBER OF SPECIES IN FRUIT
20
16
12
8
4
10/78
11
12
1/79
2
3
4
5
6
7
8
9
10
11
12
1/80
2
MONTH

Figure 14.

monthly transect-line fruit censuses is attributable to the preference of this species for more organic soils than were prevalent in much of the national park where I conducted fruit censuses. Lobeira in this region is commonly located in richer soils and along horse-trails and near corrals. The species is everbearing, but I was unable to note quantitative differences in fruit production between seasons.

Small animals that could be trapped in wooden-base rat traps were selected to represent the small vertebrate component of the diet of maned wolves and were sampled during a 17-month trapping study conducted in the park. The results from this study (Figure 15) strongly suggest that small mammals were more abundant, or at least were more readily caught, during the dry season than during the wet season (chi-square value = 46.5, 2 d.f., $p < .005$).

Certain insects also showed seasonality in their relative abundance. 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

Unlike Africa, and to a lesser degree North America, the continent of South America lacks large concentrations of available protein afforded by dense populations of ungulates. Fruits and other plant materials, however, are quite abundant and relatively evenly distributed. We

FIGURE 15. Monthly captures of individual small mammals.

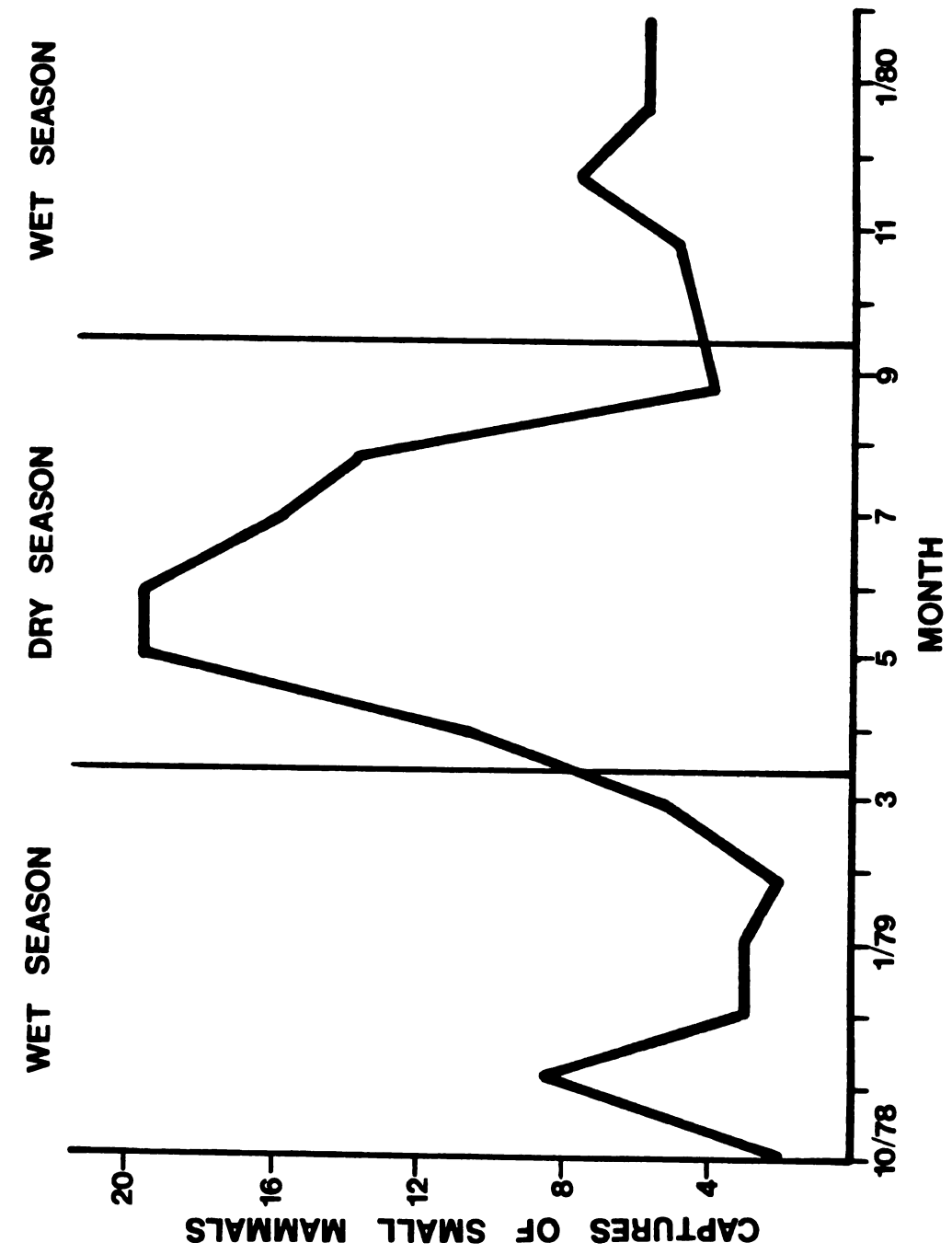
WET SEASON
DRY SEASON
WET SEASON
CAPTURES OF SMALL MAMMALS
20
16
12
8
4
10/78
1/79
3
5
7
9
11
1/80
MONTH

Figure 15.

would expect, therefore, that of the larger South American Carnivora, obligate meat-eaters would be relatively rare in comparison with generalist omnivores. The diet of maned wolves of the Serra da Canastra, based on a complete list of food items identified in scats (Tables 13 and 14), is typical of the latter category; of 41 identifiable items, 20 were animal in origin, 20 were of plant materials and 1 was inorganic. Approximately 49 percent of the 2,056 occurrences of food items in the analyzed scats were animal material and 51 percent were plant material.

The components of the exhaustive 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. These categories were quantified in analyzed scats using percent relative volume and frequency of occurrence -- number of occurrences of a specific food item divided by the number of occurrences of all food items (Table 15).

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." Although common in pastures and around corrals, lobeira was relatively scarce in less disturbed areas of the Serra

TABLE 13. Animal material identified in 740 scats of maned wolves.

Food Item Category	N	Proportion of Occurrence*
Small mammals	524	.255
Bird, bones and feathers	230	.112
Armadillos	63	.031
Miscellaneous insects	43	.021
Beetles (Coleoptera)	31	.015
Grasshoppers	28	.014
Rabbits (S. brasiliensis)	23	.011
Ants	10	.005
Chickens (Gallus gallus)	10	.005
Bird, egg shells	7	.003
Snakes	6	.003
Giant anteaters	6	.003
Maned wolf, hair	5	.002
Fish	3	.002
Bee or wasps	2	.001
Collared anteaters	2	.001
Pacas	1	.001
Ticks	1	.001
Spiders	1	.001
Termites	1	.001
Unidentified	7	.003
TOTAL	997	.491

*Expressed as a function of total occurrences (2,056) in all examined scats.

TABLE 14. Plant material identified in 740 scats of maned wolves.

Food Item Category	N	Proportion of Occurrence*
Lobeira (Solanum lycocarpum, Solanaceae)	670	.326
Miscellaneous grass (Gramineae)	228	.111
Gravatá (Bromelia anthiacantha, Bromeliaceae)	44	.021
Coquinho (Astrocaryum sp., Palmaceae)	25	.012
Casaco (Unidentified, Myrtaceae)	16	.008
Melancia do campo (Unidentified, Cucurbitaceae?)	12	.006
Goiaba (Psidium sp., Myrtaceae)	10	.005
Mángue (Callophylum brasiliense, Guttiferae)	6	.003
Articum rasteiro (Annona sp., Annonaceae)	6	.003
Gabiroba (Campomanesia sp., Myrtaceae)	5	.002
Corn (Zea mays, Panicoideae)	5	.002
Araçá (Psidium sp., Myrtaceae)	4	.002
Aperta-mão (Unidentified, Melastomaceae or Piperaceae?)	3	.002
Limãozinho (Unidentified, Rutaceae)	2	.001
Amouriçí (Byrsonima sp., Malpighiaceae?)	2	.001
Amora (Morus sp., Moraceae)	2	.001
Cega olho (Unidentified)	1	.001
Pitanga (Eugenia uniflora, Myrtaceae)	1	.001
Araçá grande (Psidium sp., Myrtaceae)	1	.001
Articum grande (Annona sp., Annonaceae)	1	.001
Unidentified	20	.010
TOTAL	1,044	.510

*Expressed as a function of total occurrences (2,056) in all examined scats.

TABLE 15. Volume and occurrence of selected food items in 740 scats of maned wolves.

Food Item Category	Proportion of Total Volume	Proportion of Occurrence*
Solanum lycocarpum	.576	.338
Small mammals	.281	.254
Birds	.023	.122
Foliage	.013	.108
Miscellaneous fruit	.068	.063
Insects	.003	.052
Armadillos	.016	.032
Rabbits	.009	.011
Unidentified material	.004	.007
Soil	.006	.005
Amphibians, reptiles	.000	.003
Giant anteaters	.001	.002
Fish	.000	.001
Collared anteaters	.001	.001
Pacas	.000	.000

*Expressed as a function of total occurrences (2,056) in all examined scats.

da Canastra. 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 of the study area. This, I assume, was due to domestic and wild fauna feeding on the fruits 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.

The remains of small vertebrates were common in the scats of maned wolves: 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 generally 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 (Brady and Ditton, 1979; Kuhme, 1975), and 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. 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. I suspect that ingestion of grass may be

related to olfactory communication between maned wolves. 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 quite common in my study area, and four were found in 8.6 percent of examined scats. Consumed armadillos were identified by their dermal scutes in wolf scats. The 740 examined scats contained the remains of the following armadillo species: 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 armadillos 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

did not forage as intensively for insects as did these smaller canids.

Small amounts of the hair of giant anteaters were found in 0.7 percent of the maned wolf scats that I analyzed. 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. It is possible that 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.

The above descriptive information regarding the food habits of maned wolves can be further analyzed with respect to seasonal resource partitioning and to variation of food resource use between the maned wolves of nonoverlapping home ranges. This approach allows a crude estimation of the breadth and flexibility of the trophic utilization function for maned wolves of the Serra da Canastra.

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 (April through September) or wet season (October through March). 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.

The seven selected food items most important in terms of volume and of occurrence in scats were tested by chi-square analysis for significant variation in occurrence from expected equal proportions for each season (Table 16). Lobeira, the main staple in the diet of these maned wolves, was consumed consistently across seasons ($p < .90$) whereas small mammal remains and foliage were encountered more often in dry-season scats. Conversely, fruits (except lobeira) and insect remains were more prevalent in scats collected in the wet season.

Given the methods that were feasible in this study, it was impossible to determine the food habits of individual maned wolves. However, since adjacent home ranges were mutually exclusive (as demonstrated later in this dissertation), I assumed that scats in a particular home range were deposited by one of the two permanent residents of that range. Because nomadic wolves were only rarely observed in my study area, and never in an occupied range, scats deposited by these wolves were assumed not to affect significantly the results of this analysis.

The seven food items most important in terms of volume and of occurrence in scats were divided according to home range (Table 17). Chi-square analysis was used to test for deviation from expected equal proportions. The null hypothesis that equal proportions of that item would

TABLE 16. Seasonal occurrence of selected food items in 740 scats of maned wolves.*

Food Item Category	OCCURRENCES			
	Dry Season		Wet Season	
	N	Proportion of Total	N	Porportion of Total
Lobeira	375	.337	304	.340
Small mammal	306[a]	.275	204	.228
Bird	120	.108	124	.139
Foliage	147[b]	.132	70	.078
Miscellaneous fruit	50	.045	76[b]	.085
Insect	43	.039	61[b]	.068
Armadillo	29	.026	35	.039
TOTAL	1070	.962	874	.977

*Significantly larger frequencies are underlined, and superscripts designate: a = $P < .025$; b = $P < .005$.

TABLE 17. Occurrence of selected food items in 740 scats of maned wolves in three home ranges.

Food Item Category	OCCURRENCES					
	Western Home Range		Eastern Home Range		Taperão Home Range	
	N	Proportion of Total	N	Proportion of Total	N	Proportion of Total
Lobeira	185	.348	362	.348	92	.342
Small mammal	149	.280	268	.258	62	.230
Bird	73	.137	115	.111	32	.119
Foliage	55	.103	103	.099	35	.130
Miscellaneous fruit	30	.056	67	.064	17	.063
Insect	22	.041	57	.055	14	.052
Armadillo	9	.017	35	.034	5	.019
TOTAL	523	.982	1007	.969	257	.955

occur in scats from each of the three discrete ranges was tested. Results were consistent with this null hypothesis for each food item ($p < .05$).

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.

These conclusions suggest that maned wolves at Serra da Canastra are opportunistic generalists in their foraging habits. They appear to feed on those food types which are most abundant and are able to shift to alternative resources when those alternatives become abundant. I found no evidence to suggest differences in food resource use between pairs of wolves in 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, during this study, 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.

Several kinds of domestic stock were raised by ranchers and farmers in the regions peripheral to the Serra da Canastra National Park concurrent with this research. Cattle were allowed to graze inside the park boundaries during most of this period. Interviews with area residents suggest that maned wolves never preyed upon calves or the adults of cattle, sheep or pigs. I never interviewed a resident who had personally lost a lamb to a maned wolf, but enough positive responses were given to warrant the conclusion that maned wolves may rarely take newborn lambs in this region. Wolves occasionally prey on young pigs and frequently take domestic chickens.

The penchant of the maned wolf for chickens deserves separate mention as this unfortunate habit 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. Chickens in this area are relatively expensive but are not shut in at night. A

marauding wolf may kill one or many chickens in a single visit and often will carry one away to be consumed some distance from the farm buildings. Visits may be repeated until all chickens have been killed or until the farmer acquires a firearm. 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. On one occasion, a wolf passed within one meter of the open window of my field headquarters, entered my barn and carried off a roosting hen. Although I stood at the window with a lit flashlight, the wolf was apparently oblivious of my presence, and I could literally have reached out and touched the animal if I had desired to do so. In two years, I lost 16 chickens to predation by maned wolves. Farmers can effectively defend barnyard fowl from predation by maned wolves by enclosing the roosting birds at night and by the acquisition of reliable watch dogs. Nocturnal predation on my chicken flock was eliminated after I adopted these measures.

Radiotelemetric data suggest that not all maned wolves in my study area were prone to attacking domestic chickens, and that of those that did prey on domestic fowl, some attacked with greater frequency than others. Predation on domestic stock is also apparently more common at specific times of the year: of 23 reported incidents, 14 (61 percent) took place from September through

November. This period correlates with 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 also 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 channel or gully formed by previous water erosion and subsequently covered over by grass. 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 from the fieldwork, from interviews with informed local residents, or from the literature to indicate that maned

wolves either excavated or enlarged abandoned underground dens.

Parturition and Litter Size

Unfortunately, none of the radiocollared wolves succeeded in raising a litter during my stay in the Serra da Canastra. However, observations of Epsilon and Lambda during the last two weeks of August 1979, suggest that Epsilon may have whelped then. 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 howling from this area on five nights during this period. The area immediately surrounding the possible den site was littered with scats. In order to reduce the likelihood of Epsilon's moving or abandoning her litter, I did not examine the den site at close quarters until the animals had abandoned the site and therefore have no direct evidence that whelping took place.

Interviews with area residents produced 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 these pups was compared with a theoretical growth curve based on interviews, my own observations and published information (Acosta, 1972). Results (Figure 16) indicate that whelping may begin as

FIGURE 16. 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.

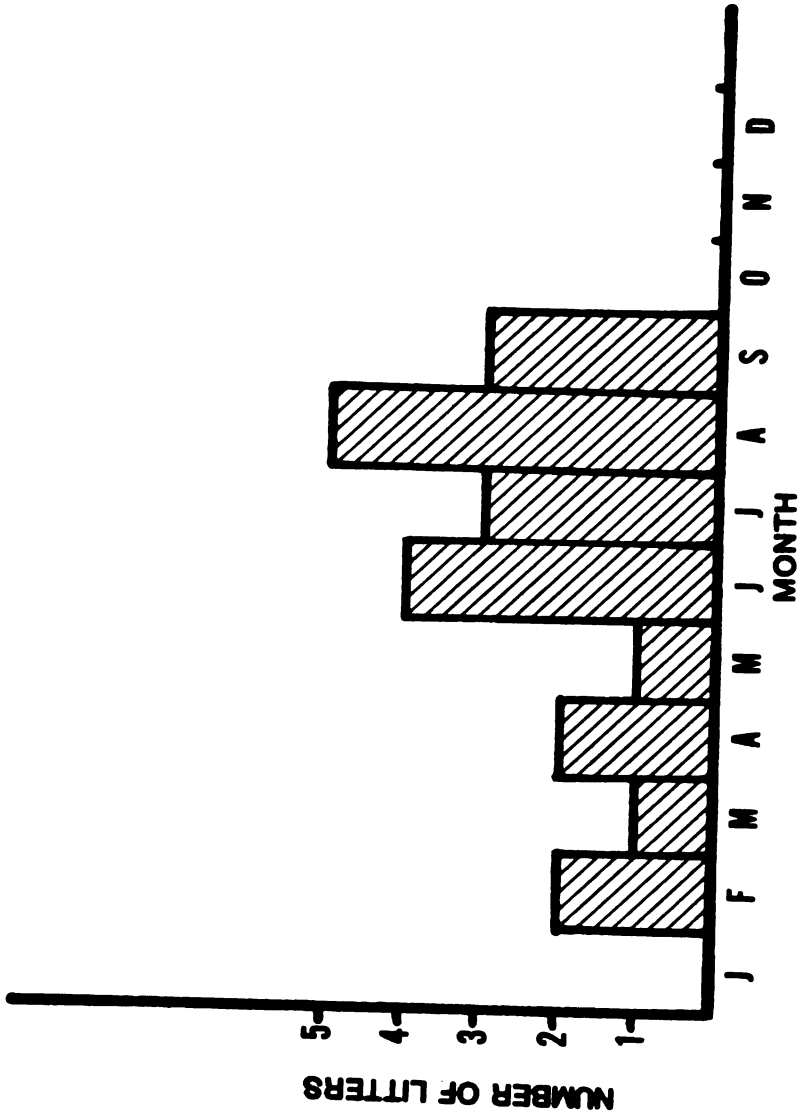

Figure 16.

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 few observations in the scientific literature generally agree on the dates of parturition by free-living maned wolves. Azara (1801) noted the birth of a litter of four pups in Paraguay in late July or early August. Rengger (1830) mentioned the finding of young maned wolf pups, also in Paraguay, toward the end of August. Carvalho (1976) wrote that births in Brazil were registered from the months of July through September. The single litter of two pups that I observed was probably born during the last two weeks of June 1978. Miller (1930) wrote that Indians in the southern part of the state of Matto Grosso considered two pups to be an average litter size for maned wolves in that region.

The observations by area residents were used to estimate the number of pups in litters born to maned wolves in the Serra da Canastra (Figure 17). The mean number of pups observed in these litters was 2.2 (n = 25), and the range was 1 to 5 pups. Given the numbers of pups in a series of litters as well as their ages at the times they were observed, it is theoretically possible to calculate the mortality rate of pups prior to dispersal. However, the correlation coefficient calculated from the above data, using stature (height at the shoulder) as an estimator of

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

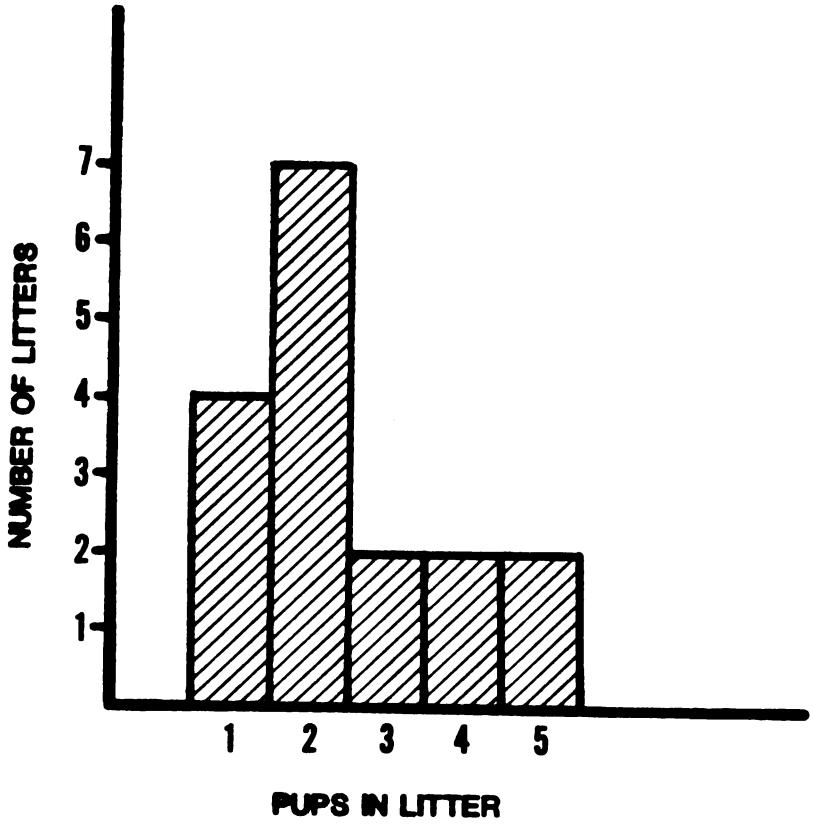

Figure 17.

age, was very low (r = 0.036). Because it is likely that survivorship does decrease as a function of time since birth, the low correlation coefficient may be explained by the small sample size and by error associated with estimating the stature of the observed pups.

The Behavior of Two Pups

On 23 August 1978, a rancher captured two female maned wolf pups in the third den described above, about 12 km east of São Roque de Minas. Two days later, with the help of official intervention, the pups were donated to my research project in the Serra da Canastra. I estimated the age of the pups to be eight to ten weeks at that time. Their pelage was generally fuzzy or woolly with the longer, heavier hair typical of adult wolves present only dorsally. The dentition of the two pups appeared to be entirely deciduous: incisors 3/3 and 3/2, respectively; canines 1/1; premolars 1/3. Weights and measurements are presented in Table 18.

When I received the pups, they were both suffering from severe diarrhea and were passing undigested food in their stools. One pup was very weak and had difficulty standing. It growled and cowered but showed no bite intention. The other pup was larger, more aggressive, showed bite intention and growled constantly when I was in its vicinity. The latter pup occasionally barked in a

TABLE 18. Weights and measurements of two captured maned wolf pups.

Parameter	Date	Pup A1 (♀)	Pup A2 (♀)
Weight at capture	25 Aug. 1978	4.5 kg	3.9 kg
Weight at release	10 Sept. 1978	5.9 kg	5.4 kg
Total length	"	81 cm	69 cm
Tail length	"	21 cm	19 cm
Ear length	"	14 cm	12 cm
Right hind foot length	"	17 cm	16 cm

voice higher in pitch but otherwise much like that of a vocalizing adult maned wolf.

The pups were housed in an unused wolf trap covered with a waterproof sheet and twice a day were fed a mixture of scraps of meat, bananas, milk and eggs. They were served in separate plates and ate as much of the ration as was available, often fighting for pieces of meat. The diarrhea present when I received the pups disappeared within 24 hours. On the sixth day of their captivity, I tied the legs of a small, live chicken and placed it in the cage with the wolf pups. The larger pup growled and barked at the chicken for about 10 minutes before the smaller pup walked over to the bird and began to bite it in an apparently random fashion. When the chicken flopped away, the small pup grabbed it and dragged it back to the far corner of the cage. I slit the neck of the bird and the smaller wolf drank the blood and managed to remove a piece of the chicken's head. I cut the chicken into small pieces which were immediately consumed by both wolves. A few days later, live mice thrown into the cage were pounced on and eaten by both wolves.

When not disturbed, the pups spent most of their time curled up together sleeping in one corner of their cage. I was unable to distinguish any temporal pattern in their activity periods. When I approached the cage, the larger pup stood over the smaller pup and growled and barked. When handled, the pups urinated and defecated, tucked

their tails between their legs and flattened their ears back against their heads. On one occasion, I observed what appeared to be an agonistic encounter between the two wolves. At about 1400 hours, I heard noises from the cage and observed from a distance. The pups were face to face, and at least one was making a winnowing call very similar to that produced during the ritualized encounters of two or more red foxes. Both pups displayed bite threats, and their ears were flattened against their heads.

During approximately three weeks before the pups were captured, the flock of chickens of the rancher who caught the pups was raided several times by an adult maned wolf. By 25 August, when the pups were captured, a total of 34 chickens had been removed from the barnyard. After the loss of another four chickens on 30 August, the rancher convinced me to set a live-trap to catch the marauding wolf. On September 7, the wolf took the last few chickens on the premises but was captured herself on the following night. She (Alpha) was lactating, classified as middle-aged, and was probably the mother of the two captured pups.

While she was in the live-trap, I injected immobilizing drugs, affixed a radiocollar to her neck and then transported her about 42 km by car to my study area. I eartagged the female and her pups. When she first began to awaken, I opened the door to her trap and released the pups in her vicinity. After a few seconds of apparent olfactory investigation, the pups both began suckling --

tails erect and wagging rapidly. Both pups emitted low-volume squeals similar to those used by domestic dog pups. When the adult began to show signs of alertness, I withdrew in hopes that Alpha would remain with her pups. Unfortunately, the radiocollar on the adult malfunctioned, and I was unable to obtain any subsequent radiolocations. I heard a rumor in October that a wolf with something around its neck had been killed while trying to steal chickens from a ranch about 15 km east of my study area.

On three occasions in September, individuals presumed to be the two pups were seen and/or heard by cowboys in the vicnity of my field headquarters. However, it was not until 4 November that I saw the two ear-tagged pups a final time. I had been absent from the field headquarters on the night of 3 November; when I returned, I was disconcerted to find 11 chickens missing from my flock. At 0030 hours the following morning, I was awakened by noises from within my barn. I opened a window and shone a flashlight on one of the pups, now about 18 weeks of age and of the stature of an adult coyote. For about one second, the wolf paused approximately one meter from me and it was my distinct impression that she was considering jumping through the open window and into my bedroom. Instead, she walked into the barn, grabbed a chicken and trotted off with the bird in her mouth. Immediately thereafter the second pup emerged from the barn. She too carried one of my chickens away in her mouth. I securely fastened the

door to the barn thereby thwarting further attempts by the wolves at 0100 and 0300 hours to steal additional chickens.

I never saw either pup again, but a cowboy reported seeing a small wolf with a tag in its ear on the southern border of the East Range in December. On 4 January 1980, a few bone fragments and the ear tags of the smaller pup were discovered in that same area.

Parental Care of Pups

By accepting the validity of the assumption that Epsilon produced a litter during the last two weeks of August 1979, certain 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, the explanation that I find most plausible is that Lambda carried this food item to his mate. Beginning on 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 site 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 1 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 these data indicate that at least some males associate with the female and her pups before the pups disperse.

Another aspect of parental care is the extent to which the adults are protective of their offspring. I recorded six reliable reports by area residents who experienced aggressive attacks by single adult maned wolves as the 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 burning pasture flushed and subsequently captured maned wolf pups. In two of the latter cases, these cowboys used the boughs of bushes to fend off the adult wolves. In another instance, a cowboy on horseback removed two small pups from inside a hollow termite mound. The pups vocalized but made no attempt to bite. An adult wolf, piloerected and baring its teeth,

advanced to within four meters of the cowboy. Fearing problems with his horse, the cowboy released the pups and watched as the adult wolf picked up both pups simultaneously in its mouth and carried them over a nearby hilltop. The cowboy determined the sex of the adult wolf to be female. 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 howled in the vicinity until the pup managed to escape.

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. It is likely that the female moved her litter to a new location.

Parasites, Diseases and Mortality

Ectoparasites

Because of the relatively short time during which captured maned wolves remained immobilized, it was not often possible to examine individuals carefully for external parasites. However, the lack of underfur on maned wolves facilitated this examination and on 11 occasions

(eight individual 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 (J. Whitaker per N. Wilson, in litt.). The majority were A. cajennense, but a few A. tigrinum were also found. From 10 to 50 ticks were counted on each wolf ($\tilde{x}$ = 24; SD = 12.1). Most were located in and around the ears.

One individual flea was found on each of three of the 11 examined wolves. Again, the scarcity of this parasite may be related to the lack of underfur in this host. The only other ectoparasites noted were the 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. Considering that many ticks were in the ears of Delta, it is likely that this was the case.

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 endoparasite eggs or larvae. The results of these analyses (Table 19) indicate that each examined wolf carried from two to four genera of endoparasites ($\bar{x}$ = 3, SD = 1). Six genera of endoparasites were identified: four nematodes, one cestode and one coccidian protozoan. Three nematodes, Trichuris sp., Ancylostoma sp., and Toxocara sp. were the most frequently found endoparasites 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 sedimentation method used in the above analyses. In addition, because only one fecal sample was examined from most wolves, it is probable that my results underestimated the presence of parasites whose eggs or larvae are found only intermittently in fecal samples. The fact that two more genera of parasites were found in the second sample of feces than in the first sample from maned wolf Beta (Table 20) indicates either that new infection took place between sampling dates or that two genera of parasites were overlooked during examination of the first sample.

TABLE 19. Endoparasites observed in fecal samples from eight maned wolves.*

Endoparasite	MANED WOLF NAME AND SEX								
	Alpha (♀)	Beta (♂)	Beta (2nd capture) (♂)	Gamma (♂)	Zoo 1 (?)	Zoo 2 (♀)	Epsilon (♀)	Lambda (♂)	Zeta (♂)
Trichuris sp.	+	+	+	+	+	+	+	+	++
Toxocara sp.	+	+	+				+		+
Dipylidium sp.	+								
Ancylostoma sp.			+	+	++	+++	+	++	++
Oxyuris sp.			+				+	+	+
Eimeria sp.								++	

*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 the parasitic infestation, as estimated by the relative numbers of eggs or cysts in the examined feces is represented by from one to three pluses.

TABLE 20. The results of selected laboratory examinations performed on urine samples from eight captured maned wolves.

Maned Wolf	EXAMINATION AND RESULTS*		
	Cystinuria	Dibasic Amino-Aciduria	Glucosuria
Beta	-	+	-
Gamma	-	+	-
Delta	+	+	-
Epsilon	+	+	-
Kappa	+	+	+
Lambda	+	+	-
Zeta	+	+	-
Sigma	+	-	-

*A plus indicates a positive result for the test performed. Laboratory procedures were performed by the School of Veterinary Medicine, University of Pennsylvania.

Diseases

Several diseases have been described for maned wolves in captivity. These include: Bartonella infection (Encke et al., 1970), cystinuria (Bush and Bovee, 1978; Jensen, 1977), parvovirus infection (Fletcher et al., 1979), infectious feline enteritis (Visee et al., 1974) and rabies (da Silva and Breckenfield, 1968). However, information on diseases afflicting free-living maned wolves is generally unavailable. During this study, I collected urine samples (see Handling Procedure in the Methods section of this dissertation) from eight captured wolves. Samples were sent for analysis to Dr. K. Bovee, School of Veterinary Medicine, University of Pennsylvania (Table 20).

Cystinuria is an inherited metabolic disease described only in maned wolves, in some breeds of dogs and in humans. The significance of the unexpected high incidence of this disease in maned wolves is discussed by Bovee et al. (1981). The relationship between the high incidence of cystinuria and dibasic amino-aciduria is not clearly understood. One female wolf, Kappa, showed abnormal amounts of glucose in the examined urine sample.

Mortality of Maned Wolves in the Serra da Canastra

During this research, I saw the remains of only two wolves that had died of apparently natural causes: a few bone fragments from one of Alpha's pups, and the nearly

complete skeleton of Delta. The latter wolf was examined several days after her death and points of interest were noted. First, Delta had compound fractures near the distal ends of the right radius and ulna; the right manus remained attached only by a few tendons. Second, the extremely emaciated condition of the wolf and the fact that she died curled in a natural position suggest that she died a nonviolent death -- perhaps of starvation indirectly caused by her broken leg. Third, the left tympanic bulla and surrounding temporal bone were largely eroded away due, I assume, to the fly strike present at the time of her initial capture.

Fear of police reprisal usually made local residents hesitant to admit to having killed a maned wolf. Therefore, my accounts of wolf mortality due to humans are often incomplete. I was informed of 19 adult wolves and of 4 subadults that were killed by residents of the Serra da Canastra since approximately 1970. Twenty-one of these wolves were killed in the following manners: 7 were shot, 5 were run down and killed by dogs, 4 were trapped, 2 pups were taken from a den and subsequently died of disease in captivity, 1 pup was poisoned in captivity, one adult was killed by a thrown rock and one was clubbed to death. It is of interest that 16 of these 21 deaths took place while wolves were attempting to steal chickens from the barnyards of area residents and that no mortalities were attributed to hunting for sport.

Relations of Maned Wolves with Humans

Human Disturbance Factors and Their Effects on Maned Wolves

Published accounts (e.g., Walker, 1975) are in general agreement that populations of maned wolves tend to retreat before the advancement of human colonization. My observations in the Serra da Canastra do not support this assertion. The home ranges occupied by 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 wolves. However, I noted three reports of wolf pups captured after being driven from dens by range fires.

Agriculture in the Serra da Canastra functions mainly at the subsistence level. Farms are small and are usually tilled without the aid of tractors. With the exception of three cases in which wolves were observed following tractors and capturing escaping small mammals, I noted no direct effects of 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.

Whether the nocturnal activity patterns of the maned wolves of the Serra da Canastra were an adaptation to living in an area also inhabited by farmers, ranchers and

domestic animals is unclear. Hofmann (1975-1976) states that maned wolves in the Peruvian Pampas del Heath were diurnal in an area annually burned but uninhabited by man. My observations indicated that although the wolves in my study area were apparently indifferent to the presence of cattle, they 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. Grass 30 cm in height was sufficient to conceal a wolf effectively in this position. Wolves concealed in this manner usually remained immobile until the person approached to within about 2 to 3 m. At this distance, the wolves flushed, piloerected and often vocalizing, and bounded toward the nearest cover. In most instances, retreating wolves stopped at least once, turned broadside to the human, back arched and piloerected, and displayed one or more of the following displacement activities: defecation, urination, vocalization, feigned hunting behavior, or olfactory investigation of a nearby rock or clump of grass.

It is important to note that 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

In contrast with the attitudes of residents of areas still inhabited by gray wolves (e.g., Clarke, 1971; Mech, 1970), 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. The relationship between the humans and the maned wolves sharing the Serra was usually harmonious. 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.

Maned wolves were generally thought of as timid and fearful of man. However, all area residents that I interviewed stated that female wolves will attack a human attempting to steal her pups (see Parental Care of Pups, this dissertation). My observations indicate that maned wolves without pups are wary of man but successfully coexist with him in the Serra da Canastra. Reliable reports from area residents attacked by maned wolves defending pups strongly suggest that this popular opinion is also based on fact.

Folklore

The historical roots of the people of rural central Brazil can be traced to Africa, to Portugal, and to indigenous tribes. These cultural influences, though presently mixed and diluted are still readily identifiable in the folklore, religion and folk medicine of the people of the interior of that geographical region. In the areas where I worked, the maned wolf has become an important part of the 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.

The eyes of maned wolves are often considered important in their supernatural powers. For example, several farmers reported having seen maned wolves stare at chickens roosting in trees at night thereby causing the birds to fall from their roosts. I was also informed that the stare of the maned wolf makes it invulnerable to being hit by a bullet. According to a rather bizarre legend in the Serra da Canastra, the right eye removed from a live maned wolf serves as a lucky charm for the bearer after the wolf is released.

Some of the folklore concerning maned wolves is based on fact. One legend predicts that a large snake can be found in the kidney of a freshly-killed maned wolf. However, if the kidney is not examined immediately after the

death of the wolf, the snake will have disappeared when the kidney is opened. 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.

According to tradition, maned wolves can perform a variety of tricks to fool pursuing dogs. Some people suggest that wolves jump back and forth across their own tracks in a form of a cross to cause dogs to lose the scent trail. Others maintain that dogs are confused when wolves urinate on their own tracks. On several occasions when maned wolves became aware that I was following them, they urinated or defecated before moving away from me.

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 few of the more interesting remedies follow: 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 snake-bite victim from death. Finally, a chronic cough is best cured by drinking hot tea made from the dried feces of a maned wolf.

DISCUSSION

Canid social structure has recently been described in two contexts. Fox (1975) divided the members of the family into three "types" reflected by their foraging patterns: solitary, permanently-paired and pack hunters. He characterized solitary hunters, exemplified by the red fox, by the persistence of the sexual bond only from courtship through the period when the young are weaned. Pups generally display mutual intolerance of litter mates and leave or are driven from the company of their parents before attaining one year of age. Fox classified the coyote as a permanently-paired canid. In this type of social organization, the parental pair bond persists beyond the mating to rearing season; offspring may remain with their parents for several months after weaning. Thereby, coyotes may form temporary loosely-structured hunting bands. The third social type, as defined by Fox, is the pack hunter such as the gray wolf. These animals characteristically forage in groups which display intrasexual dominance hierarchy, mate preferences, and bonds between litter mates as well as between offspring and their parents. The extent to which a canid is capable of

modifying one of the above three social organizations with changes in environmental conditions is attributed by Fox to the range of intralitter temperaments. Solitary canids are the least socially plastic and the least able to adapt socially to environmental change.

As indicated by Kleiman and Brady (1978), the above model is often misleading, in that canid social organization is not necessarily tied to foraging strategies. For example, such a species as the kit fox (Vulpes velox), as shown by Egoscue (1962, 1975), is characterized by permanent pair bonds but typically forage in a solitary manner. In addition, the classification suggested by Fox fails to predict accurately the variation in social organization found within a species. Recent detailed studies of the red fox in England (Macdonald, 1978a, 1978b, 1980; Niewold, 1980) indicate that this species, classified as solitary by Fox, may under certain circumstances show such social behavior as defense and communal feeding of offspring by both parents and by subordinate vixens.

An alternate method of describing canid social organization is based on the heterosexual pair bond and classifies species according to a greater or lesser degree of monogamy (Kleiman, 1977; Kleiman and Eisenberg, 1973; Kleiman and Brady, 1978). Monogamous species are further divided into those exhibiting either facultative or obligate monogamy. In the former type of monogamy, there is little socio-sexual contact between members of a bonded

pair outside the breeding season, and the female is potentially able to raise her offspring without help from the mate. This type of monogamy is most often found in mammals occupying habitats with thinly distributed trophic resources. Obligate monogamy, according to Kleiman, is found in species in which the female is physically unable to raise a litter without help from conspecifics. Thus Kleiman classifies 17 species of canids as displaying obligate monogamy, but describes none that displays facultative monogamy.

The concept of monogamy, although intriguing from a genetic standpoint, is somewhat impractical in describing the social organization of the Canidae. Monogamy, in the sense of mating exclusivity, is extremely difficult to test under field conditions. Continuous long-term behavioral observation of wary, nocturnal and far-ranging canids has rarely, if ever, been possible. However, electrophoretic analysis, as recently applied to determine the prevalence of monogamy in Peromyscus polionotus (Foltz, 1981), might be useful in examining monogamy in some species of canids.

In light of the fact that, in my opinion, no entirely satisfactory synthesis of canid social organization has been suggested, I will discuss the sociobiological findings of this study in a context which should be common to any treatment of this nature. I will consider group size, cohesiveness, composition, interactions, and flexibility.

It will first be necessary to reiterate pertinent points mentioned in the foregoing sections of this dissertation.

Maned wolves of the Serra da Canastra were apparently territorial (sensu Burt, 1943) and maintained ranges of about 27 km^2 per male-female pair. The boundaries shared by two pairs of wolves appeared to be nonoverlapping and inflexible. Members of a pair communicated vocally and probably olfactorially, used the same pathways and resting and foraging areas, but were rarely located in close association except during the months associated with reproduction. Although members of a pair were not often in close physical association, the bond between them appeared to be long-lasting. Available evidence suggests that maned wolves of the Serra da Canastra were monogamous. One or perhaps both members of a pair carried, provisioned and defended their offspring.

The social unit basic to the maned wolves in my study appeared to have been the bonded pair. Social distance between individuals of a pair changed predictably with time of year, but the composition of pairs remained constant. Although the months during which maned wolves were most often in close association correlated with the entire breeding season, changes in the available resource base took place concurrently. In the reproductive season, small mammals became relatively more abundant and species of fruit became less abundant. This shift in availability

of trophic resources was reflected in the diet of these wolves.

Both reproductive parameters and availability of food resources can have profound effects on social structure in carnivores (e.g., Kruuk, 1972; Lamprecht, 1978; Schaller, 1972). The extent to which each of these factors affected sociality within and between pairs of maned wolves in the present study is not entirely clear. However, a logical explanation of the unique social organization of the maned wolf in the Serra da Canastra can be derived from a combination of the two organizational models previously presented (i.e., Fox and Kleiman et al.). Of particular interest is the question of how monogamy may have evolved in a territorial and essentially solitary carnivore.

Evolution of Sociality in a Grassland Habitat

The first canids probably arrived in South America during the Plio-Pleistocene interface, that is, during the American faunal interchange subsequent to the closure of the Panamanian land bridge (Simpson, 1980). Corridors of grassland habitat were available to the east of the Andes Mountains facilitating the dispersal of waves of Middle American canids into the savannas of central South America (Langguth, 1975; Webb, 1977, 1978). Langguth further suggests that the primitive canids successfully invading these savannas were morphologically undifferentiated and

gave rise to differentiated forms such as the maned wolf and the bush dog (Speothos venaticus).

Generalized representatives of the dog family arriving in South America would have been exposed to a variety of selective pressures imposed by their new environment. One of the most critical of these would probably have been the necessity of locomotion through the tall grass prairies covering much of the continent. I propose that 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 was significantly reduced. Apparently, the maned wolf was the only South American canid to successfully adopt the latter evolutionary strategy.

It is likely that these generalized dispersing canids were relatively solitary and that sociality evolved in response to one or more selective environmental pressures (Kleiman and Eisenberg, 1973; Wilson, 1975). The following factors have been suggested as having induced sociality in carnivores and other mammals: (1) high prey density; (2) a potential for increased foraging efficiency by group hunting; (3) defense against a common enemy or predator; (4) increased survival due to the cooperative raising of offspring (Kleiman and Eisenberg, 1973; Kruuk, 1975; Waser and Wiley, 1979; Wilson, 1975). The extent to which each of these factors may have affected the

evolution of sociality in the maned wolf will be briefly considered.

During the late Pleistocene when the maned wolf was probably spreading through the savannas of central South America, most of the large native herbivores became extinct and were replaced ecologically by highly successful cricetid rodents (see Simpson, 1980, for a review of the controversy concerning when the Cricetidae arrived in South America; Webb, 1969 and 1978). This may have meant that concentrated protein in the form of large hoofstock was relatively scarce. Relative to the plains of the East African Serengeti, for example, the Brazilian Central Highlands presently support a meager and nondiverse array of large vertebrate prey species. However, small mammals such as rodents and marsupials are abundant and diverse. Under these conditions of dispersed trophic resources, group foraging by large carnivores would not appear to be advantageous. To the contrary, concentrated concurrent foraging for small mammals by more than one individual in the same area would seem to increase the probability of overharvesting food resources in that area, thereby decreasing the total foraging success for all individuals. Trophic resource type and availability do not appear to have been conducive to social living by maned wolves.

If the maned wolf had evolved as a predator of large herbivores, it is likely that its morphology would reflect certain specializations common to other predatory canids.

This is not the case. Maned wolves do not have the robust jaws and jaw musculature present in the pack hunting canids (Langguth, 1969). With legs long and fragile, and the girdle musculature not particularly well developed, the maned wolf is not capable of running the long distances at high speeds (Langguth, 1972) that are probably necessary for pursuit of ungulate prey in open habitats. Morphologically, the maned wolf appears to be well suited to hunting small prey in tall grass.

Long legs necessitate a relatively large body size which in turn places increased energetic demands on the individual (Brown and Lasiewski, 1972). Large homeotherms must eat more than small animals to meet these energetic requirements. However, in tropical latitudes, a large body size may be advantageous in terms of the energetic cost of maintaining a stable body temperature under conditions of heat stress. Although metabolic heat production has not been examined in the maned wolf, I suggest that the increased mobility and thermoregulatory advantages conferred by long legs and associated large body size may outweigh the potential disadvantage of increased contact with direct and indirect solar radiation. In other words, the large body size of the maned wolf has perhaps not been selected for directly as an advantage in capturing large prey, but rather indirectly as a consequence of long legs useful in capturing small prey.

Congregation for defense against some mutual enemy is also not likely to have been a factor contributing to sociality in maned wolves. First, maned wolves are large enough that the great majority of South American predators would probably avoid encounters or disputes. Second, of the predators that might challenge an adult maned wolf, only the puma was commonly associated with the grassland habitats occupied by the wolf. The recent effects of man on the maned wolf will be considered later in this dissertation.

Although little information is available about parental care of pups of free-living maned wolves, my data suggest that an adult female is able to raise a litter without aid from conspecifics. Certainly, there is no indication that groups of maned wolves contribute to the welfare of the offspring of a single female. In only two instances during my study did local observers see two adult wolves accompanying pups. On all other occasions, only one adult was seen with pups. All observations of defense of pups by adults involved only a single adult. Finally, in the few cases in which it was possible to determine the sex of the adults accompanying pups, the adults were females.

In summary, none of the circumstances cited as likely to induce gregariousness appear to have greatly influenced the social organization of the maned wolf. If there is a canid that would be predicted to be solitary and

polygamous, that canid is the maned wolf. In fact, Kleiman and Brady (1978) suggest that "the maned wolf may be a solitary hunter that does not form a long-term pair bond characterized by a heterosexual association outside the breeding season." The fact that a perennial bond appears to persist between members of a pair of maned wolves supports the assertion of Kleiman and Eisenberg (loc. sit.) that the pair bond is a phylogenetically "old" trait within the Canidae.

I suggest that the monogamy and strict territoriality displayed by the maned wolves of the Serra da Canastra 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 typically scarce, dispersed and relatively dependable may have favored the selection of a social organization based on solitary and mutually-exclusive foraging. Because of the absence of socipetal factors operating on the maned wolf during its evolution in South America, 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.

Given the trophic resources historically available to the maned wolf throughout its range, two adults may have been necessary to defend an area large enough to supply themselves and their offspring with food during the period

prior to dispersal by the young. In a solitary species, this would tend to favor monogamy (Lack, 1966, 1968). Because the maned wolf is not socially labile, intraspecific interactions, particularly those associated with the transition from a solitary existence to a paired existence during the mating season, might be difficult in this species. That social interactions can be expensive for maned wolves is supported by the frequent occurrence of fighting and wounding between captive wolves (Brady and Ditton, 1979; Kleiman, 1972).

My data suggest that unlanded maned wolves may circulate outside of established territories and that they, as well as neighboring wolves, will invade undefended home ranges. The association of a resident male with his mate and her litter may serve to protect his progeny from mortality caused by these invading wolves. The association between a male and his mate during the entire breeding season may increase his reproductive fitness by decreasing the probability of another male's copulating with that female (see Niewold, 1980, for a description of similar behavior in red fox). It may also increase the likelihood of his pairing with the same female in future years. Pair bonds of this type have been described for the red fox (Vincent, 1958): although the bonds between male and female foxes apparently break down after the weaning of their young, there is a strong likelihood of the same individuals' re-pairing the following year. In

these instances, the amount of intrapair aggression prior to the establishment of companionship decreases from year to year (Ewer, 1973).

If territoriality is important to the survival of maned wolves, then natural selection would tend to favor those characteristics which emphasize the ownership of an area. Several of these morphological and behavioral traits are displayed by this species. Vocalizations are loud and far-reaching but not particularly diverse or complex. This type of communication mechanism seems well suited for transmitting simple messages to all conspecifics at a long distance from the sender. The urine of maned wolves has a particularly strong odor, even as perceived by humans, and is probably recognizable by conspecifics at a distance or long after it has been deposited. The visual behavioral cues used by the maned wolf are discernible at considerable distances. These include the erection of the dorsal mane, the broadside arching of the back, and the sharp contrasts in color of the regions of the body used in display. In addition, in monogamous species, there would be little need for sexual dimorphism and natural selection should favor monomorphism (Kleiman, 1977). My data demonstrate little, if any, sexual dimorphism in the wolves of the Serra da Canastra.

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 (e.g., Macdonald, 1979). Therefore, it would be premature to state that the social organization of the maned wolves of the Serra da Canastra is "species-typical." However, lacking additional evidence to the contrary, I offer the following tentative conclusions concerning the pair bond in this species.

The pair bond in species of canids has been characterized as long-lived, involving male defense and provisioning of young, and association between mates outside the period of reproduction (Kleiman and Eisenberg, 1973; Kleiman and Brady, 1978; Kleiman and Malcolm, 1981). These characteristics are seen in maned wolves but differ from those of more social species such as the gray wolf (Mech, 1970), and the Cape hunting dog (Estes and Goddard, 1967). Although male maned wolves will occasionally defend and provision their offspring in captivity (Kleiman and Malcolm, 1981; Porton, 1981, pers. comm.), data from my research are inconclusive about the frequency of this behavior in the Serra da Canastra. However, the role of the male in defending a territory large enough to support his offspring during rearing is an indirect but essential form of protection and provisioning. During the nonbreeding season, close physical association between

members of a pair appears rare, but the mutually beneficial activity of defense of a common territory is maintained as is vocal and probably olfactory communication. The bond between members of a pair appears to be permanent.

The preceding model of the social organization of maned wolves allows the generation of testable predictions such as the following: (1) if the social system of maned wolves is genetically constrained, then monogamy and territoriality would be expected to persist even as trophic resources vary in abundance; (2) although the size of a territory defended by a bonded pair may vary with respect to terrain, vegetation type and available resources, territorial overlap will probably take place rarely, if at all; (3) dispersal of offspring from the parental territory will probably be independent of resource availability. These predictions could be tested using quantification and/or manipulation of available trophic resources in the territories of maned wolves.

Conservation and Management

Most, if not all, species are proceeding toward extinction at varying rates. John Terborgh (1974) 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. If this disequilibrium is related to human activities, then it is our moral obligation at least to evaluate our priorities in light of the likelihood of dispatching a fellow citizen of the planet earth. In the following paragraphs, I will consider the questions of whether the maned wolf is proximately endangered with extinction, the extent to which humans are to blame, and what action should be taken.

Maned Wolves in the Wild

Several traits have been suggested as characterizing an extinction-prone species. For example, a large body size and habitat specialization were proposed by Brown (1971) and Willis (1974) as detrimental to long-term survival. The maned wolf perhaps qualified in the first category but not in the second category. The species distribution of the maned wolf includes a wide variety of habitats including grasslands, chaco, pantanal, pampas, several types of cerrado as well as part of the caatinga of northeastern Brazil. 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. It is of interest to note that maned wolves are often observed in these commercial conifer stands. This may be due to the relatively large abundance of small mammals in these plantings (Dietz et al., 1975).

Terborgh and Winter (1980) suggest rarity as a predictor of extinction. They describe three patterns of species rarity: (1) species that are near the limits of their geographical range, (2) species that specialize on patchily distributed resources, and (3) species that are "constitutively" rare, that is, that exist at low densities wherever they occur. As previously indicated, the maned wolf does not fit in the first two of these categories. However, because of the territorial nature of these animals, at least in the Serra da Canastra, they could be considered thinly distributed. Alternatively, the wary nature and nocturnal habits of the maned wolf may contribute to the underestimation of its population density.

Under certain circumstances, dependence on irregularly available resources can hasten extinction during unfavorable seasons (Terborgh and Winter, 1980). This raises the question of whether or not the resources used by the maned wolf can be considered irregularly available. 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. In other words, 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 (e.g., Dennler de la Tour, G., 1965, mimeo cited in the IUCN Red Data Book, 1976; Langguth, 1972 and 1975). However, in no case is evidence 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 paid little attention 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.

With the exception of trapping activities, my disturbance of resident wolves was minimal and of the same order of magnitude as accidental encounters between wolves and area ranchers. Traps left unset and undisturbed for long periods of time often became incorporated into the rounds of resident wolves and were routinely visited by them. This acceptance of traps by maned wolves may have been augmented by the presence of wolf scats in the traps. I attempted to make being trapped as atraumatic as possible for captured wolves. Fortunately, trapped maned

wolves generally remained alert but quiet, and did not display the physical agitation typical of North American canids in the same situation. In general, direct human disturbance, including my activities, appeared to have little effect on the activities of the maned wolves of the Serra da Canastra.

The long-term indirect effects of human activities on maned wolves were not quantitatively assessed but were 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 had significant unfavorable impact on the resource base available to these wolves. These effects would probably be more severe in regions where the percentage of tillable land is greater than in the Serra da Canastra. However, the facts that agricultural practices have been much the same in the Serra da Canastra for at least the past 80 years and that maned wolves are still present indicate that areas such as this will retain populations of wolves at least for the present.

Based on the results of this study and other available information, I tentatively conclude that populations of free-living maned wolves are not in immediate jeopardy over much of their range in South America. However, this relatively secure situation could change radically as a result of the 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. For example, if the entire Serra da Canastra National Park consisted of suitable habitat, and were saturated with maned wolves, that park would only support approximately 48 resident wolves. However, because of the irregular shape both of the park and of the ranges of maned wolves, and because much of the park appears to contain suboptimal habitat, I estimate that no more than 10 maned wolves live entirely within the confines of that national park. However, on the order of 40 wolves may have ranges that overlap both park and private land. In consideration of the above, 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.

During this study, the majority of documented mortalities of maned wolves resulted from encounters during

which wolves were stealing poultry. I suggest that a campaign of public awareness concerning the endangered status of the wolf would significantly reduce the source of mortality. This could be accomplished through local media, agricultural extension agencies, posters and instructional packets sent to schools throughout the range of the wolf. Additional information to be included in the campaign are the facts that keeping watch dogs and/or enclosing barnyard fowl at night reduces or eliminates losses due to maned wolves. 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.

Because so little recent information is available concerning this species, it is particularly important that additional studies be carried out to collect the facts necessary for the formulation of specific programs oriented toward conservation of the maned wolf. In addition to field studies, information should also be gathered from existing zoo and museum collections. Also necessary is complete documentation of past and present species distributions; critical areas of distribution attenuation must be identified and probable causes determined before remedial action can be taken.

Maned Wolves in Captivity

Several facts indicate that the future of the maned wolf may be less secure in captivity than it is in the wild. First, few maned wolves exist in captivity: fewer than 100 individuals are exhibited in 12 zoos worldwide (Bush, in press). 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 relatively rare (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.

In light of the above, 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. In my opinion, 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; Frankling, 1980). Finally, the prevalence and potentially fatal nature of cystinuria in captive maned wolves (Bovee 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.

Although the maned wolf is classified as endangered with extinction and is highly prized by zoological gardens, now valued at about $15,000 per pair, prior to this study, little information was available concerning the biology of this species in its natural environment. This deficit of information is the result of three interacting factors. First, the maned wolf is difficult to observe in the wild because it is nocturnal, thinly-distributed throughout its range, and avoids encounters with humans. Second, because of political and economic constraints, it has become increasingly difficult for foreign biologists to conduct research in South America, particularly in Brazil. Third, although the South American countries within the species range of the maned wolf have competent biologists capable of conducting this field research, the necessary

electronic equipment and technology are generally unavailable to them.

In consideration of the above, perhaps the methodology developed during my study of the maned wolf is as significant a contribution as the results of the research. The field techniques that I applied may be modified and improved and hopefully the hypotheses and conclusions herein will be tested in future studies. Finally, my research involved successful international cooperation for the achievement of a common goal: the better understanding of an endangered species. I am optimistic that this research will serve as a precedent for additional cooperative studies of this nature.

APPENDIX

TABLE 21. Woody plants identified in the grassland and cerrado habitats, Serra da Canastra National Park.

Common Name	Genus and Species	Family
Canela de ema	Vellozia sp.	Velloziaceae
Gabiroba	Campomanesia sp.	Myrtaceae
Uvaia	Eugenia sp.	Myrtaceae
Pitanga	Eugenia uniflora	Myrtaceae
Cajú	Anacardium sp.	Anacardiaceae
Arnica	Arnica montana	Compositae
Pororoca	Rapanea sp.	Myrsinaceae
Caviuna	Dalbergia violacea	Leg. Papil.
Vinhático	Plathymenia reticulata	Leg. Mimos.
Muriçí	Byrsonima sp.	Malpighiaceae

TABLE 22. Trees identified in the riparian forest habitat, Serra da Canastra National Park.

Common Name	Genus and Species	Family
Pereira	Aspidosperma sp.	Apocynaceae
Guatambú	Aspidosperma sp.	Apocynaceae
Pindaíba	Xylopia grandiflora	Anonaceae
Mangue	Callophylum brasiliense	Guttiferae
Ipê amarelo	Tabebuia ochracea	Bignoniaceae
Piuna	Buchenavia sp.	Combretaceae
Mutuqueiro	Unidentified	
Carvão	Unidentified	Rubiaceae
Erva de lagarto	Casearia sylvestris	Flacourtiaceae
Cambuatá	Cupania sp.	Sapindaceae
Taquara	Unidentified	
Gameleira	Ficus sp.	Moraceae
Sassafrás	Ocotea pretiosa	Lauraceae
Casca danta	Drimys sp.	Winteraceae
Almescla	Protium sp.	Burseraceae
Quatiguá de leite	Unidentified	
Canela rosa	Ocotea sp.	Lauraceae
Vinhático	Plathymenia reticulata	Leg. Mimos.
Bálsamo	Myroxylon balsamum	Leg. Papil.
Angazeiro	Inga sp.	Leg. Mimos.
João farinha	Callisthene major	Vochysiaceae
Cedro	Cedrela sp.	Meliaceae

TABLE 22 (continued)

Common Name	Genus and Species	Family
Gabiroba	Campomanesia sp.	Myrtaceae
Pelôto	Unidentified	
Pororoca	Rapanea sp.	Myrsinaceae
Aricanga	Unidentified	
Imbaúba	Cecropia sp.	Moraceae
Sambambaia	Unidentified	
Vermelhão	Unidentified	
Guaritá	Astronium sp.	Anacardiaceae
Peroba	Aspidosperma sp.	Apocynaceae
Moreira	Chlorophora tinctoria	Moraceae
Quaresmeira	Tibouchina sp.	Melastomaceae
Pinha do brejo	Talauma	Magnoliaceae
Palmito	Euterpe	Palmaceae
Canela preta	Nectandra reticulata	Lauraceae
Capitão-Maria preta	Vitex sp.	Verbenaceae
Jacarandá preto	Machaerium sp.	Leg. Papil.
Jacarandazinho	Platypodium elegans	Leg. Papil.
Candeia	Vanillosmopsis erythropappa	Compositae
Gabiroba	Campomanesia sp.	Myrtaceae
Folha miúda	Unidentified	

TABLE 23. Identification of small mammals captured in the Serra da Canastra National Park.*

Species Identification	Number Collected	MSU Museum Acquisition Numbers
Zygodontomys lasiurus lasiurus	47	29290, 29257, 29313, 29295, 29294, 29301, 29322, 29291, 29275, 29300, 29289, 29297, 29318, 29299, 29319, 29298, 29302, 29304, 29321, 29292, 29320, 29324, 29334, 29323, 29332, 29276, 29293, 29331, 29288, 29309, 29296, 29598 29599, 29600, 29597, 29595, 29345, 29354, 29335, 29336, 29340, 29337, 29341, 29338, 29339, 29342, 29347.
Oryzomys fornesi	31	29330, 29308, 29254, 29326, 29314, 29327, 29255, 29309, 29310, 29305, 29328, 29315, 29329, 29316, 29311, 29325, 29312, 29317, 29596, 29594, 29586, 29593, 29791, 29350, 29351, 29353, 29348, 29356 29358, 29359, 29360.
Calomys laucha tenor	15	29251, 29307, 29333, 29252, 29253, 29306, 29256, 29587, 29583, 29584, 29585, 29588, 29589, 29349, 29352.
Akodon (Thalpomys) lasiotis	15	29258, 29359, 29260, 29261, 29262, 29265, 29263, 29266, 29264, 29268, 29267, 29590, 29592, 29355, 29357.
Rhipidomys mastacalis	12	29270, 29272, 29278, 29271, 29273, 29269, 29601, 29604, 29605, 29602, 29603, 29344.
Oxymycteris roberti	7	29284, 29287, 29282, 29285, 29283, 29286, 29346.
Oryzomys subflavus	4	29287, 29277, 29281, 29343.

TABLE 23 (continued)

Species Identification	Number Collected	MSU Museum Acquisition Numbers
Nectomys squamipes	2	29279, 29280.
Marmosa agilis agilis	1	29582.
Monodelphis domestica	1	29250.
TOTAL = 10 species	135 individuals.	

*Specimens are held in the collections of The Museum, Michigan State University.

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