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DISSERTATION

**SOLITARY, REPRODUCTIVE, AND PARENTAL BEHAVIOR OF MANED
WOLVES (*CHRYSOCYON BRACHYURUS*)**

Submitted by

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Department of Biology

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2000

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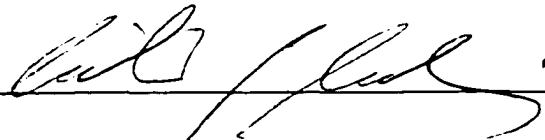
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6 December 1999

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY STEPHANIE V. BESTELMEYER ENTITLED SOLITARY, REPRODUCTIVE, AND PARENTAL BEHAVIOR OF MANED WOLVES (*CHRYSOCYON BRACHYURUS*) BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

SOLITARY, REPRODUCTIVE, AND PARENTAL BEHAVIOR IN MANED WOLVES (*CHRYSOCYON BRACHYURUS*)

The maned wolf is an endangered species native to central South America. Efforts to preserve the species in the wild and through captive breeding programs have been hampered by a lack of information on its natural history. The maned wolf is a member of the family Canidae, which is known for extensive paternal care. Thus, the maned wolf is an interesting species for studying parental investment theory. I studied maned wolves in U.S. zoos and in Emas National Park, Brazil to gather information necessary for developing conservation plans while simultaneously testing many parental care theories. High pup mortality, often caused by females abandoning or cannibalizing newborns, plagued early captive breeding efforts. At the time, the custom at most zoos was to remove the male prior to birth for fear that he would harm pups or that his presence would stress the female, causing her to harm pups. I compared pup survival in the presence and absence of males and found that male care increased pup survival, as predicted by the paternal investment hypothesis. I observed seven pairs to test predictions arising from game theory models of parental investment and suggest that increased pup survival is due, in part, to decreased aggression by females to pups when males are

present. Furthermore, I outlined a procedure to reintroduce males to their pups if they have been removed prior to birth. Estrous timing in seasonal mammals can be triggered by a variety of cues, and I showed that maned wolf estrus is influenced more by internal factors than by temperature or latitude. During 1997, I studied the behavior of habituated, free-ranging maned wolves and provided new information on their solitary, hunting, marking, parental, and social behavior. Finally, I compared the behavior of free-ranging and captive maned wolves and showed that generalizing from captive animals to their free-ranging counterparts may not be appropriate.

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Studying maned wolf parental behavior often required that I collect data from two or more locations simultaneously. My ability to perform this feat was made possible through the help of 37 volunteers and keepers at many zoos. I am grateful for their assistance, and special mention should be made of Kim Bishop, David Cheung, Bridgette Daley, Gina Landucci, Tonya Loreman, Greg McCumsey, Mary Jo Stearns, Joanie Steinhaus, and Karen Zeigler who videotaped maned wolves for many hours, keeping steady hands even in the presence of biting insects.

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TABLE OF CONTENTS

Chapter I. Introduction.....	1
Literature Cited	5
Chapter II. Effect of the Father's Presence on Pup Survival and Growth in Captive Maned Wolves (<i>Chrysocyon brachyurus</i>)	
Introduction	9
Methods	13
Data Collection	13
Data Analysis	15
Results	17
Litter Survival	17
Pup Survival	18
Litter Weight Gain	19
Discussion	20
Literature Cited	27
Chapter III. Maternal and Paternal Care in Captive Maned Wolves (<i>Chrysocyon brachyurus</i>): The Effect of Male Presence on Female Behavior	
Introduction	42
Methods	46

Subjects	46
Data Collection	47
Data Analysis	48
Results	49
Time Budgets and Rates of Behavior	49
Male versus Female Parental Care Patterns	49
Correlation of Male and Female Behavior Within a Pair	50
Effects of Male Presence	51
Discussion	52
Literature Cited	56
 Chapter IV. Behavioral Changes Associated with Introductions of Male Maned	
Wolves (<i>Chrysocyon brachyurus</i>) to Females with Pups	
Introduction	71
Methods	73
Subjects and Housing	73
Introduction Procedure	74
Behavioral Observations	75
Data Analysis	75
Results	76
Introduction Procedure	76
Behavioral Changes	78
Discussion	79
Literature Cited	81

Chapter V. Timing and Behavioral Patterns of Estrus in Maned Wolves

(Chrysocyon brachyurus)

Introduction90

Methods94

 Estrous Timing94

 Breeding Behavior95

 Data Analysis96

Results97

 Estrous Dates97

 Breeding Behavior98

Discussion99

Literature Cited103

Chapter VI. Maned Wolf (*Chrysocyon brachyurus*) Behavior and Ecology in Emas

National Park, Brazil

Introduction116

Study Area.....120

Methods.....122

 Behavioral Observations122

 Vegetation Measurements123

 Data Analysis124

Results125

 Activity Cycle and Time Budgets125

 Solitary Behaviors126

Diet and Hunting Behaviors	127
Marking Behaviors	130
Den Site Characteristics and Parental Behaviors	131
Social Behavior	133
Habitat Use	133
Discussion	133
Literature Cited	142
Chapter VII. Captive and Free-Ranging Maned Wolves' Behavior: A Quantitative	
Comparison	
Introduction	160
Methods	164
Subjects and Study Sites	164
Behavioral Observations	164
Data Analysis	166
Results	167
Number and Form of Behaviors	167
Activity Cycles	168
Time Budgets	168
Rates of Behavioral Events	169
Discussion	170
Literature Cited	174
Chapter VIII. Conclusions	188
Literature Cited	191

CHAPTER I

INTRODUCTION

With the rapid loss of biodiversity, conservation biology has become an increasingly important discipline. The challenging, multifaceted nature of conservation issues attracts scientists from diverse backgrounds, including population genetics, ecology, sociology, and political science. Scientists studying animal behavior and behavioral ecology have been noticeably absent from the development of conservation biology, resulting in little communication between scientists in these disciplines. For example, the 1996 volume of *Animal Behaviour* contained no papers directly relating to conservation (Sutherland 1998). This lack of influence of animal behavior and behavioral ecology on conservation biology has become the subject of numerous papers (Curio 1996; Ulfstrand 1996; Sutherland 1998) and books recently (Clemmons and Buchholz 1997; Caro 1998).

A primary barrier to connecting these disciplines is the persistent belief by scientists studying animal behavior and behavioral ecology that conservation biology, as an inherently applied science, is not as intellectually stimulating as 'pure' research (Sutherland 1998). The roots of this problem were realized and contested over 20 years ago by Niko Tinbergen, one of the fathers of ethology. He stated, "I realize full well that I am advocating a swing of animal ethology towards a more applied course. But it must be

now be clear to many scientists that ‘applied’ science can be intellectually just as stimulating as ‘pure’ exploratory research” (Tinbergen 1976, p. 524). Nonetheless, this bias against applied science continues today, and is probably nowhere more apparent than in a recent paper that is otherwise a passionate call for the use of behavior in conservation biology (Sutherland 1998). Sutherland (1998, p. 802) states, “If most animal behaviour research were directed at applied problems, such as conservation biology, the subject could well be less exciting and develop more slowly conceptually.”

Despite this bias, animal behavior and behavioral ecology have tremendous potential for solving conservation problems, in both captive breeding programs and the wild (Curio 1996; Ulfstrand 1996; Clemmons and Buchholz 1997; Caro 1998; Sutherland 1998). It is therefore important to convince scientists studying animal behavior that working on conservation issues can be both exciting and useful. One way to achieve this goal is to show examples of behavioral studies that simultaneously address issues of great interest in animal behavior and provide valuable information for conservation issues.

In this dissertation, I test hypotheses about parental behavior while simultaneously providing information useful for the preservation of the endangered maned wolf, *Chrysocyon brachyurus*. The maned wolf belongs to a mammalian order, the carnivores, with an unusually high incidence of male investment in offspring care. Only 5% of mammalian species exhibit direct male care (Clutton-Brock 1991), but paternal care is common in the carnivores (Kleiman and Malcolm 1981; Woodroffe and Vincent 1994) and has been confirmed in every well-studied member of the family Canidae (Malcolm 1985). One of the primary explanations for the rare cases of mammalian paternal behavior is the ‘paternal investment hypothesis,’ which postulates that paternal care may be

avored when a male's care greatly increases offspring survival (Woodroffe and Vincent 1994). This hypothesis has been tested in rodents and primates, the other mammalian orders with a high incidence of paternal care, but little is known about paternal care in carnivores. My work provides one of the first tests of the paternal investment hypothesis in a carnivore and compares parental behaviors of male and female maned wolves.

My research has broad applications for the conservation of the maned wolf, especially in captive breeding programs. Loss of the maned wolf's primary habitat, the cerrado (Ratter et al. 1997), prompted the establishment of a captive breeding program in the United States in 1985. Throughout the first years of the captive breeding program, maned wolves sustained low reproductive rates and high pup mortality, often caused by dams abandoning or cannibalizing their pups shortly after birth. At this time, most zoos removed the male prior to parturition for fear that he would harm pups directly or that his presence would stress the female, causing her to abandon or cannibalize pups (Bartmann 1983). Given that no well-studied canid has ever been shown to lack male parental care (Malcolm 1985), I hypothesized that at least part of the high pup mortality may have been caused by removing the male. Perhaps by removing the male we were unknowingly stressing the female and thereby causing her to abandon or cannibalize young pups. Similar effects have been observed in rodents (Gubernick et al. 1993). The next three chapters examine this hypothesis while also testing the paternal investment hypothesis and several predictions from game theory analyses of parental investment.

In Chapter II, I test the effect of male presence or absence on captive maned wolf litter survival, pup survival, and pup weight gain. The results of this study provide one of the first tests of the paternal investment hypothesis in a carnivore and provide important data

for deciding whether or not to leave the male with the female and pups to maximize pup survival in the captive breeding program.

In Chapter III, I investigate patterns of male and female parental care in maned wolves. Game theory predicts that the level of parental care exhibited by an individual will depend upon the presence and behavior of the other parent (Maynard Smith 1977). I test this and other hypotheses by examining parental care patterns of seven pairs of maned wolves that raised 10 litters, either with or without the male present. Differences in care patterns dependent on male presence can be used by the captive breeding program to determine potential mechanisms underlying pup survival differences discussed in Chapter II.

Managers who remain apprehensive about leaving the male with the female and pups may prefer to remove the male before birth and reintroduce him when the pups are older and perhaps less vulnerable. In Chapter IV, I describe a procedure for carrying out such introductions and illustrate the important behavioral changes in males and females resulting from introductions.

Most mammals are seasonal breeders (Estep and Dewsbury 1996), and a variety of cues may be used to initiate breeding (Ims 1990). In Chapter V, I investigate the role of six variables potentially used by maned wolves as cues for estrous timing, and I determine if there are easily measured behavioral changes that indicate estrus. This information is interesting because very little is known about carnivore estrous timing. Furthermore, it is critical for captive breeding efforts that the five-day estrous period of female maned wolves be predicted accurately (Rodden et al. 1996).

Knowing the details of a species' behavior in its natural habitat is crucial to developing effective, long-term conservation strategies. Unfortunately, maned wolves are one of the many endangered species about which very little is known outside of captivity. In Chapter VI, I study maned wolf behavior in Emas National Park, Brazil. This study is the first comprehensive, quantitative examination of free-ranging maned wolf behavior based on direct observations of habituated individuals. It therefore provides new information on habitat use and solitary, hunting, marking, and parental behavior. These data provide a first step toward understanding why maned wolves do not live in large social groups, exhibit cooperative hunting, or have large litters like most other large canids (Moehlman and Hofer 1997).

In Chapter VII, I compare free-ranging maned wolves' behavior in Emas National Park with the behavior of captive maned wolves. This comparison allows a test of whether or not generalizations about how a maned wolf behaves in its natural habitat can be made based on captive observations. It also helps determine if obvious behavioral differences indicate domestication in captivity, as has been predicted for other species (Snyder et al. 1996). Finally, in Chapter VIII, I examine the implications of these studies and recommend avenues for further research.

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Here is an animal which has to be seen to be believed, and even then it is hard to be sure it is real. It appears to be assembled by mistake from assorted parts of other canines, for the legs are far too long, the neck too short, the ears too big and the fur a sort of hit-or-miss affair. This is the maned wolf, which is found in the dense forests and small clearings of the southern edge of the Amazonian Basin, Paraguay, and northern Argentina. It is about the most ungainly canine ever to chase a dinner.

(Colby, C. B. 1965. *Wild Dogs*. New York: Duell, Sloan, and Pearce. p. 121)

CHAPTER II

EFFECT OF THE FATHER'S PRESENCE ON PUP SURVIVAL AND GROWTH IN CAPTIVE MANED WOLVES (*CHRYSOCYON BRACHYURUS*)

INTRODUCTION

Paternal care in mammals is rare, with only 5% of mammalian species exhibiting direct male care (Clutton-Brock 1991). Internal gestation and lactation predispose female mammals to care for their young and often enable females to successfully rear offspring without male assistance. These same traits emancipate male mammals from parental care and mean that males can usually maximize their fitness by searching for additional mating opportunities rather than providing paternal care (Trivers 1972). A male is therefore expected to invest in offspring care only when benefits resulting from male care are especially high or costs of care are extremely low.

The “paternal investment hypothesis,” the most common explanation for the evolution of paternal care, focuses on high benefits of male care (Woodroffe and Vincent 1994; Paul et al. 1996). According to this hypothesis, if male care increases offspring survival, a male may maximize his fitness by caring for young rather than searching for additional

mates. This explains why paternal care is widespread in birds (Clutton-Brock 1991); due to external incubation of fertilized eggs and the absence of lactation, male birds can provide all forms of parental care, and a pair of birds can often raise more offspring than a solitary female. Although male mammals cannot incubate or feed newborns, they can provide direct care by huddling with, carrying, and grooming young or indirect care by constructing a shelter for the young and feeding the lactating female (Kleiman and Malcolm 1981). Males can also provide food for their offspring during and after weaning. Even slight increases in offspring survival due to these paternal contributions may be favored when costs of paternal care are low, such as when additional mating opportunities are scarce (Maynard Smith 1977).

Testing the paternal investment hypothesis requires a comparison of survival and growth rates of offspring raised by both parents versus those raised by only the female. If the paternal investment hypothesis is correct, the survival and/or growth rate of offspring raised by the female and male together will be higher than the survival rate of offspring raised by the female alone. Finding no such increase rules out the paternal investment hypothesis and necessitates testing alternative hypotheses for the evolution of paternal care (Woodroffe and Vincent 1994).

Although few studies have attempted to measure the effects of male care in mammals (Clutton-Brock 1991), empirical evidence supports the paternal investment hypothesis for some captive rodents (Dewsbury 1985) and some primates (Wright 1990). Male care leads to increases in the survival and/or growth of California mice (Gubernick et al 1993), Mongolian gerbils (Elwood and Broom 1978; but see Gerling and Yahr 1979), and Djungarian hamsters (Wynne-Edwards 1987; Walton and Wynne-Edwards 1998).

Paternal care is also pronounced in several primate groups (e.g. owl monkeys: Dixson and Fleming 1981; titi monkeys: Fragaszy et al. 1982; cotton-top tamarins: Tardif et al. 1990), but fewer tests of the effects of male care have been done in primates. One exception is a study by Anderson (1992) demonstrating that infant carrying by male chacma baboons increases infant survival.

Few tests of the effects of male presence have been done on carnivores, a mammalian order with extensive paternal care (Kleiman and Malcolm 1981; Woodroffe and Vincent 1994). I set out to fill this gap by testing the paternal investment hypothesis in captive maned wolves, *Chrysocyon brachyurus*. In captivity, male maned wolves groom and guard pups (Bartmann and Nordhoff 1984; Uka 1986), regurgitate to pups (Rasmussen and Tilson 1984), and regurgitate to the female (Bestelmeyer, unpublished data).

Although paternal care has not yet been studied in wild maned wolves, I suspect that males play a similar role in the wild because (1) they are monogamous (Dietz 1984), and monogamy is often associated with paternal care in mammals (Kleiman 1977; Clutton-Brock 1991), (2) paternal care is widespread within the family Canidae (Malcolm 1985), and (3) many captive male maned wolves under a wide variety of conditions have exhibited paternal behavior (Bartmann 1983).

Rapid loss of the maned wolf's primary habitat, the cerrado (Ratter et al. 1997), prompted its listing as an endangered species (USFWS 1989) and the establishment of a coordinated North American captive breeding program, the Maned Wolf Species Survival Plan (MWSSP), in 1985. Until recently, zoo personnel routinely removed the male one to three weeks before birth due to erroneous early reports that maned wolves are solitary in the wild and males therefore probably do not care for pups (Bartmann 1983). There are

therefore numerous cases of females attempting to rear their young without male assistance. These cases provide an opportunity to compare the survival of litters reared by the female and litters reared by both parents.

Conducting this test of the paternal care hypothesis on the maned wolf has the added benefit of showing how behavioral research can be applied to conservation biology, an application that has received much attention recently (Curio 1996; Clemmons and Buchholz 1997; Caro 1998; Sutherland 1998). Despite many studies on diet (Barboza et al. 1994), endocrinology (Gross et al. 1991; Wasser et al. 1995; Velloso et al. 1998), and medical management (Montali and Kelly 1989; Munson and Montali 1991), the MWSSP was still plagued by a high rate of pup mortality in 1994, caused in part by females abandoning or cannibalizing their litters shortly after birth. Between 1984 and 1993, 33-100% of the litters born each year were affected by abandonment or cannibalization (Bestelmeyer et al. 1996). Aggression from the mother has also led to the death of older pups. For example, in 1994 a mother-reared 7.5-week-old pup died from a head wound caused by an attack from the female. High captive pup mortality caused me to question the custom of removing the male prior to the birth of pups. If male maned wolves usually help females care for pups, removing the male before birth may stress the female, eliciting cannibalization, abandonment, or aggression toward pups. Gubernick et al. (1993) found such an effect in California mice (*Peromyscus californicus*) where many females cannibalized their pups after the male was removed.

Given these considerations, I designed this study to simultaneously test the general paternal investment hypothesis and to test for a link between pup mortality and the practice of removing males prior to parturition. Using records from 77 captive maned

wolf litters, I examined the effects of male presence/absence on litter survival, pup survival, and pup weight gain. I then compared the effects of male presence with the effects of other variables that could influence reproductive success, including pair compatibility, ages of the sire and dam, and the dam's own rearing history.

METHODS

Data Collection

I used records maintained since the inception of the MWSSP to generate a list of all births between the 1984/85 and 1997/98 breeding seasons. During this time, 81 litters were born to 37 pairs at 20 institutions (Table 2.1). Litter sizes ranged from 1-6 pups with a mean of 2.62 ± 0.14 s.e. I interviewed personnel at each institution to determine the rearing condition (male present, male absent, or reared in a zoo nursery [hand-reared]) and circumstances (e.g., hand-reared due to a management decision or hand-reared due to the female harming the pups) of each pup. I did not include stillborn pups, one pup born with hydrocephaly, one litter that was not provided a den box, and two unconfirmed births listed as "possible" births in the records. Because I excluded one pair that only had one stillborn pup and six pairs that only had litters that were hand-reared due to a management decision, all analyses on rearing condition included 30 of the 37 pairs. In seven litters, the male was initially absent but was reintroduced when pups were 3-12 weeks old; these litters were excluded from analysis after the male's reintroduction to avoid biasing the analyses (since males could only be reintroduced to surviving litters).

Captive population records suggest that a pair's success in rearing pups is not independent from year to year. so I considered a pair as the independent unit rather than the litter. Litter and pup survival values were therefore averages across all years for the pairs that reproduced more than once. Three males and three females reproduced with two different mates, but I considered each pairing an independent observation.

I evaluated several dependent variables, including litter survival, pup survival, and litter weight gain. Two measures of "litter survival" were the number of entire litters surviving to 1 mo (when pups first emerge from the den) and the number surviving to 6 mo. Litters that were hand-reared due to the female neglecting or harming the pups were counted as not surviving, since they likely would have died without intervention. Two measures of "pup survival" were the average proportion of pups in each pair's litter(s) that survived to 1 mo and 6 mo. Pups pulled for hand-rearing due to illness or death of a sibling were excluded from analysis because it is impossible to determine if the adult(s) would have successfully raised the remaining pups without the intervention. Weights of 29 litters from 13 institutions were gathered from zoo records (Table 2.1). I calculated average weekly weights of the pups in a litter from birth until they reached 24 weeks, whenever possible.

I also collected information on five independent variables:

Rearing: This variable had two categories for analyses of litter and pup survival: male present and male absent. For the analysis of pup weight, there were three categories: male present, male absent, and hand-reared. Rearing data were collected for all 77 litters from 30 pairs.

Dam History: Reproductive females had been reared under four conditions: by the female only (n=5), by the male and female (n=3), by hand in a zoo nursery (n=10), and in the wild before transfer to captivity (n=2). These data were unavailable for 10 of the 30 pairs.

Pair Compatibility: I used questionnaires completed by the primary maned wolf keeper or curator at each institution to assess the compatibility of each pair. Pairs were considered to have good compatibility (n=22) when they had aggressive interactions (e.g., growling, biting, chasing) less than once a month, rested within 3 m of each other at least once a month, and did not require separating for feeding of preferred food items. Pairs with poor compatibility (n=6) were aggressive at least once a month and rested within 3 m of each other less than once a month. All 28 pairs for which these data were available were successfully classified into one compatibility category based on these traits.

Dam and Sire Ages: The dams' and sires' ages during the birth of each litter were assigned to three classes: young (2-4 yr), middle (5-7 yr), and old (8 yr or more). Because the pair was the independent unit for analyses, individuals that reproduced multiple times were assigned to the age category representing their age class during the majority of their litters' births. Ages were collected for all 30 pairs.

Data Analysis

Litter and pup survival data were collected for general management purposes rather than specifically for my study. While I recognize that statistical inference in the purest sense may not be appropriate for this type of study, I analyzed the results using statistical tests

and urge appropriate caution when results are interpreted. Although using previously collected data introduces problems of inference, this practice has the virtue of eliminating potential observer bias in data collection.

The proportion of litters surviving for each pair was transformed using the equation $p^* = 0.5[\arcsine (X/n+1)^{0.5} + \arcsine ((X+1)/(n+1))^{0.5}]$ where X=the number of surviving litters and n=the total number of litters born to each pair. This transformation converts proportions into a nearly normal distribution and is preferable to a normal arcsine square root transformation when there are many small and large proportions (Zar 1996). This transformation also weights litter survival values according to the number of litters born (n). I compared litter survival and pup survival in seven pairs that reproduced at least once when the male was both present and absent using binomial tests and Wilcoxon signed-rank tests. To compare survival in all pairs, I first randomly eliminated one rearing condition for the seven pairs that reproduced under both conditions to make the observations independent. I then jackknifed the data (Sokal and Rohlf 1995) because the underlying distribution of survival values was unknown. The resulting jackknifed values were compared with equal or unequal variance t-tests. The effects of pair compatibility, dam age, sire age, and dam history on litter and pup survival were analyzed using t-tests or ANOVA, depending on the number of classes. Weight differences between hand-reared, female-reared, and female- and male-reared litters were compared with repeated measures ANOVA. All transformed data were checked for normality prior to analysis.

The best approximating models for 6 mo litter survival and 6 mo pup survival were chosen from a set of 6 *a priori* candidate models using Akaike's Information Criterion with a correction for small sample size (AIC_c; Burnham and Anderson 1998). I only

included the 18 pairs for which complete data were available for all variables. The candidate models were selected prior to analysis based on independent variables found to be important in previous studies of large, captive vertebrates (e.g. Beck and Power 1988; Carlstead et al. 1999). Models evaluated included: (1) rearing, (2) rearing and dam history, (3) compatibility, (4) dam age, (5) dam age and dam history, and (6) rearing and pair compatibility, as defined above.

Because the sample size (30 pairs) and power were relatively low, I considered statistical tests significant at $P < 0.10$. All tests comparing survival when males were present or absent were one-tailed due to the *a-priori* expectation that survival would be higher with males present. All other tests were two-tailed.

RESULTS

Litter Survival

All seven pairs that reproduced at least once with the male removed and at least once with the male present had an equal or higher litter survival rate with the male present (binomial: $N=7$, $P=0.01$). When the three pairs with equal litter survival under both rearing conditions were removed, litter survival to 1 and 6 mo was still significantly higher when the male was present than when the male was removed prior to birth (Wilcoxon signed-rank test: $T_+=10$; $N=4$, $P=0.06$). This result cannot be explained by females simply becoming better parents with experience since two of these seven pairs reproduced first with the male present.

Across all pairs, there was no difference between litter survival to 1 mo when the male was present or not present (Fig. 2.1; $t_{28}=-1.06$, $P=0.15$). However, litter survival to 6 mo was higher when the male was present than when the male was absent (Fig. 2.1; $t_{25}=-2.17$, $P=0.02$). Litter survival was not affected by pair compatibility, sire age, dam age, or dam history (Table 2.2). For the 18 pairs with information on all five independent variables, the global model including rearing, compatibility, sire age, dam age, and dam history explained 65% ($R^2=0.65$) of the variation in 6 mo litter survival rates. This high percentage of explained variance justifies the use of AIC (Burnham and Anderson 1998). However, most of these explanatory variables were not necessary because the best approximating model for these 18 pairs included only two variables: dam history and dam age (Table 2.3; $F_{5,12}=2.06$; $P=0.14$; $R^2=0.46$). The distributions of females in dam history and age classes were not dependent (Chi-square test of independence: $X^2=4.18$; $df=6$; $P>0.10$). No other candidate model had strong support ($AIC_c < 2.0$; Burnham and Anderson 1998; Table 2.3).

Pup Survival

For the seven pairs that reproduced under both rearing conditions, there was no difference in pup survival at 1 mo (binomial: $N=7$, $P=0.16$) or 6 mo (binomial: $N=5$, $P=0.16$) depending on whether or not the male was present. Across all pairs, there was no difference between the average proportion of each pair's pups surviving to 1 mo when the male was present and when the male was absent (Fig. 2.2; $t_{28}=-0.75$, $P=0.23$). However, the proportion of pups in a litter surviving to 6 mo was higher when the male was present (Fig. 2.2; $t_{16,2}=-2.28$, $P=0.02$).

Pup survival was not affected by pair compatibility, sire age, or dam age (Table 2.4). The dam's own rearing condition had no effect on pup survival to 1 mo, but had a significant effect on 6 mo pup survival (Table 2.4). Dams raised by both of their parents had a higher proportion of their pups survive than dams raised by only their mother, by hand, or in the wild (Fig. 2.3; Fisher's least significant difference test: $P < 0.05$). There was no difference between the pup survival rates of hand-reared, mother-reared, or wild-caught dams (Fisher's least significant difference test: $P > 0.10$). Including all independent variables (rearing, dam history, compatibility, sire age, and dam age) to explain 6 mo pup survival for the 18 pairs with complete data resulted in an R^2 value of 0.59, thus justifying the use of AIC. Two models were supported with AIC (Table 2.2): (1) dam history and rearing ($F_{4,13}=3.17$; $P=0.05$; $R^2=0.49$) and (2) dam history and dam age ($F_{5,12}=1.86$; $P=0.18$; $R^2=0.44$); no other model had strong support.

Litter Weight Gain

From birth until 24 weeks, there was no difference in the rate of weight gain of litters reared by hand, by the female, or by the male and female together (Fig. 2.4; $F_{24,255}=0.34$; $P=0.99$). There was also no difference in the rate of weight gain of all parent-reared pups (female only or male and female) and hand-reared pups ($F_{17,262}=0.36$, $P=0.99$). Pup survival to 6 months was not correlated with the average litter weight at birth ($r=0.38$; $N=19$; $P=0.11$), 1 mo ($r=0.20$; $N=17$; $P=0.44$), 3 mo ($r=-0.26$; $N=15$; $P=0.35$), or 6 mo ($r=-0.46$; $N=4$; $P=0.54$).

DISCUSSION

These results support the paternal investment hypothesis by showing that the sire's presence enhanced litter and pup survival to 6 months. There are two alternative hypotheses often proposed for the evolution of male parental care (Woodroffe and Vincent 1994): (1) males gain future access to females by providing care to current offspring (Freeman Gallant 1998) and (2) males use offspring to buffer agonistic encounters with other individuals (Paul et al. 1996). While I did not test these hypotheses, the maned wolf's natural history makes these alternatives unlikely. Female maned wolves enter estrus only once per year (Brady and Ditton 1979), so caring for pups is unlikely to increase the male's access to the female when she enters the next estrous period ten months later. It is even more unlikely that males care for pups to regulate interactions with other adults because maned wolves live in solitary pairs rather than larger social groups (Chapter VI; Dietz 1984).

I believe that this is one of the first studies to test the paternal investment hypothesis in a carnivore, and generalizations will require studies on a wide range of carnivore species. These studies will likely be time-consuming and may also require the use of zoo animals because (1) many carnivores are intractable for laboratory studies due to their often large body sizes and (2) carnivores are notoriously difficult to study in the wild (Schaller 1994). Carnivore studies are also difficult because carnivores have relatively long gestation periods, long periods of offspring care, and (in most canids) only one estrus period per year (Asa and Valdespino 1998). Nonetheless, understanding the evolution of

paternal care in mammals requires that these difficulties be overcome and that data be collected on a wider range of mammalian species with paternal care.

The males' presence had substantial effects on offspring survival in this study, suggesting that paternal care may be favored in this species. Even a much smaller increase in offspring survival might favor paternal care if the costs of care are low. One cost of paternal care is the lost opportunity to breed with other females, but this cost may be substantially reduced if males have little chance of mating with more than one female because females are widely dispersed or have highly synchronous estrous periods (Chapter V). Both characteristics are likely in maned wolves. Free-ranging females and males share large territories of approximately 27 km² (Dietz 1984); such wide spacing of females makes it difficult for a male to encounter another female. In addition, some evidence suggests that the timing of maned wolf estrous periods is affected slightly by photoperiod (Chapter V), so females in one area probably have synchronous estrous periods. Therefore, even small increases in offspring survival due to male care may select for paternal care in maned wolves.

While this study suggests that the male's presence has a positive effect on captive maned wolf reproductive success, it is unclear what proximate mechanism underlies this effect. Male presence did not increase the rate of pup weight gain, probably because food is provided *ad libitum* to adults and developing pups (Allen 1995). Lack of increased offspring weight gain in the presence of males has been documented in other species in captivity (Elwood and Broom 1978; Shilton and Brooks 1989; Gubernick et al. 1993; Wang and Novak 1994). Also, although the data indicate a trend, the male's presence did not consistently affect litter or pup survival to 1 mo, suggesting no significant effect on

the female's abandoning or cannibalizing tendencies, which usually appear within the first 3 days (Rodden and Rosenthal 1995).

Finding no difference in litter or pup survival at 1 mo but higher survival at 6 mo when the male is present corresponds with observed patterns of parental care. Females provide the majority of care when pups are confined to the den box, but males show high rates of interactions with pups once pups start emerging from the den at 4-5 wk (Chapter IV; Bestelmeyer 1999). In addition, when males are reintroduced to their mates and pups, the activity level of females declines, leading to better health (Chapter IV; Bestelmeyer 1999). These patterns suggest that longer-term (6 mo) survival differences may be due to increased care for pups and decreased female stress when the male is present. In Chapter III, I will describe the sires' behavior toward pups and examine differences in dams' parental behavior depending on whether or not the male is present.

Increased pup survival when the male is present in captive individuals suggests that an even greater effect may be seen in the wild. Wild maned wolves lack *ad libitum* food and therefore spend more time away from the den, as confirmed in the field (Bestelmeyer 1998). Increased foraging time means that males may be necessary to protect pups when females are away from the den and/or to bring food to pups, especially once pups begin to eat regurgitated food at approximately 4 weeks (Brady and Ditton 1979). Several studies of the paternal investment hypothesis in rodents support the contention that a male's effect on offspring survival may be more dramatic outside of the mild conditions found in captivity. For example, Dudley (1974) found that male California mice enhance pup weight gain and development when the female is experimentally removed for 12 hours per day, but not when the female is continuously housed with pups. In a separate study,

California mice stressed by cold temperatures or the need to forage for food have higher pup survival when the male is present, but there is no effect under mild temperatures with free access to food (Gubernick et al. 1993).

Effects of the male's presence on offspring appear to last beyond the first generation, since dams reared by both of their parents had more pups surviving than other dams (Fig. 2.3). Additionally, for the 18 pairs with complete data, dam history appeared in the top two models for both litter survival and pup survival (Table 2.3). Thus, although it is still unclear how males increase pup survival, the effect persists until at least the second generation.

There are both benefits and drawbacks to studying paternal behavior in a captive setting. Perhaps most importantly, behavioral research that is directly relevant to zoo management decisions emphasizes its value to captive breeding programs, one component of conservation biology (Schaaf 1984; Kleiman 1992). Studies like mine can test questions of interest to many animal behaviorists while simultaneously providing information that may increase success in captive breeding programs for threatened and endangered species. Additionally, because males and females are housed together continually before and during the breeding season in captive situations, a male's certainty of paternity is high. Although there is considerable debate about the necessity of paternity certainty for paternal behavior (e.g. Møller and Birkhead 1993; Kempnaers and Sheldon 1997), removing this potentially confounding factor simplifies data interpretation. Captive carnivores, especially wide-ranging species like maned wolves, are also much easier to study than their wild counterparts.

These benefits are countered by the drawbacks of studying captive animals, including the fact that some species show paternal behavior in small enclosures in labs but not in larger enclosures or presumably in the wild. For example, Xia and Millar (1988) saw no signs of paternal behavior in *Peromyscus leucopus* housed in large enclosures, although this species shows paternal care in smaller enclosures (Hartung and Dewsbury 1979). Confirmation of the male maned wolf's role in rearing pups requires parental behavior studies of wild maned wolves that have not yet been done, but paternal care in captivity is unlikely to be an artifact of captivity because paternal care seems universal in the Canidae (Malcolm 1985). Furthermore, enclosures at several institutions in the MWSSP are quite large (approximately 2500 m² at the White Oak Conservation Center), casting additional doubt on the argument that male care may be due only to the males' close proximity to pups.

A more serious drawback to studying zoo animals is the lack of control over potentially confounding factors. It is unlikely for one institution to house enough individuals to adequately test hypotheses, especially for large carnivores (Mellen 1994). It was only by using records of every birth in North America since 1984 that I was able to gain enough power to test each variable. Maned wolf enclosures at SSP institutions vary in size (Werle et al. 1995), and there is likely a large difference in the amount of external disturbance from visitors and zoo personnel across the zoos represented in this study. These variables affect the behavior and reproductive success of other species (Roberts 1987; Mellen 1991; Carlstead et al. 1999) and may also affect maned wolves. Some confounding factors may be mitigated in species like the maned wolf for which extensive husbandry manuals (e.g., Fletchall et al. 1995) have been written. These manuals

recommend husbandry standards, thereby making some conditions more uniform across zoos. While I recognize these problems as important for my data, it is striking that 32.6% of the variation in 6 mo litter survival and 49.4% of the variation in 6 mo pup survival is explained by just dam history and male presence. Thus, although caution should be exercised when using data such as mine, robust conclusions can still be drawn.

Drawbacks of captive studies must ultimately be weighed against the benefits from studies that will allow informed management decisions in captive breeding programs, which are increasingly relied upon to conserve species (Brambell 1993; Ebenhard 1995; Mallinson 1995; Mallinson and Feistner 1995; but see Balmford et al. 1995; Snyder et al. 1996). Unfortunately, animals often do not reproduce adequately in captive breeding programs (Conway 1986; Hoyt 1995; Snyder et al. 1996). This is frequently caused by a failure to provide the proper physical or social environment dictated by the species' natural history (Hediger 1964; Baker 1994; Kleiman 1994; Mallinson 1995). Significant advances in reproductive technologies like artificial insemination and *in vitro* fertilization are encouraging signs that, with enough resources, reproduction may be attained for even the most difficult individuals and species. Nonetheless, this study and other examples of reproductive problems caused by husbandry styles (Kleiman 1994) suggest that we should look for behavioral solutions before initiating more expensive technologies (Lasley and Anderson 1991; Lindburg and Fitch-Snyder 1994).

This study provides information that may be applicable to captive breeding programs where hand rearing is frequently employed. Hand rearing captive animals often affects their sexual and social behavior, leading to decreased reproductive success and abnormal reproductive behavior (Fox 1972; Beck and Power 1988; Myers et al. 1988; Mellen 1992;

King and Mellen 1994). The results of this study extend these findings and show that deciding which parent(s) should rear offspring has significant implications for future generations. Pups of dams who were reared by both of their parents had higher survival to 6 mo than pups whose dams were reared by hand, by the female, or were wild-caught. This effect is probably not the result of hand-reared animals sexually imprinting on humans because there was no significant difference between pup survival of hand-reared or female-reared females. Rather, I speculate that pups housed with both adults have increased interaction with adults, and thus may have better parenting ability in the next generation.

The effects of male presence and dam history on maned wolf pup survival outweighed the effects of pair compatibility and sire age. This result is encouraging since the former variables reflect management options rather than inherent characteristics of the pair. Pairings in most captive breeding programs are based on genetic and demographic considerations rather than mate choice (Wiese et al. 1994), and these results suggest that successful reproduction in maned wolves can be attained from genetically compatible pairs that have high rates of aggressive interactions. These results also suggest that rearing recommendations do not need to be adjusted for dams and sires of varying ages.

Reproductive failure is still possible when the male is housed with the female. For example, there was no difference in pup survival for the seven pairs that reproduced at least once when the male was present and at least once when he was not. Yet the male's presence is not detrimental to litter or pup survival; no male has ever been seen independently harming pups housed with him (Rodden, pers. obs.), and in no case was litter or pup survival higher when the male was absent. These results strongly suggest that

males should be continually housed with females during the birth of their litters to maximize reproductive success.

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Table 2.1. Locations of maned wolves that reproduced between 1984 and 1998 in the North American captive population.

Institution	Location	Number of pairs	Number of litters	Number of litters with weight data
Baton Rouge Zoo	Baton Rouge, LA	2	9	0
Center Hill	Center Hill, FL	1	1	0
Denver Zoo	Denver, CO	1	1	0
Dickerson Park Zoo	Springfield, MO	2	4	2
Fossil Rim Center	Glen Rose, TX	2	6	3
Houston Zoo	Houston, TX	1	3	1
John Ball Zoo	Grand Rapids, MI	1	3	1
Kansas City Zoo	Kansas City, MO	2	2	2
Lincoln Park Zoo	Chicago, IL	1	2	2
Little Rock Zoo	Little Rock, AR	1	3	0
Los Angeles Zoo	Los Angeles, CA	2	2	0
Louisville Zoo	Louisville, KY	2	5	0
NZP Conservation Center	Front Royal, VA	5	9	7
Oklahoma City Zoo	Oklahoma City, OK	6	12	2
Riverbanks Zoo	Columbia, SC	1	3	1
San Antonio Zoo	San Antonio, TX	1	5	2
White Oak Conservation Center	Yulee, FL	3	6	4
Wild Canid SRC	Eureka, MO	1	1	1
Wildlife World Zoo	Litchfield Park, AZ	1	3	0
Woodland Park Zoo	Seattle, WA	1	1	1
Totals		37	81	29

Table 2.2. Litter survival to 1 mo and 6 mo depending on pair compatibility (good or poor), sire age (young, middle-age, or old), dam age (young, middle age, or old), and dam history (reared by female, male and female, hand, or wild-caught).

Variable	Litter Survival to 1 mo			Litter Survival to 6 mo		
	Test Statistic	df	<i>P</i>	Test Statistic	df	<i>P</i>
Pair Compatibility	t=0.34	26	0.74	t=1.61	21.6	0.12
Sire Age	F=0.06	2,27	0.94	F=1.49	2,24	0.25
Dam Age	F=0.03	2,27	0.97	F=0.28	2,24	0.76
Dam History	F=0.51	3,16	0.68	F=1.16	3,14	0.36

Table 2.3. Number of estimated parameters (K), Akaike's information criterion values with a small sample size correction (AIC_c), and differences between each model's AIC_c and the lowest AIC_c value (Δ_i). Models with AIC_c values within 2.0 of the lowest model ($\Delta_i < 2.0$) are considered to have support.

Model	Litter Survival to 6 mo			Pup Survival to 6 mo		
	K	AIC_c	Δ_i	K	AIC_c	Δ_i
Dam History, Rearing	4	-43.65	4.04	4	-36.77	0
Dam History, Dam Age	4	-47.69	0	4	-34.85	1.92
Rearing	3	-41.48	6.21	3	-29.52	7.25
Dam Age	3	-43.43	4.26	3	-29.17	7.60
Compatibility	3	-40.15	7.54	3	-28.03	8.74
Compatibility, Rearing	4	-38.61	9.08	4	-26.20	10.57

Table 2.4. Pup survival to 1 mo and 6 mo depending on pair compatibility (good or poor), sire age (young, middle-age, or old), dam age (young, middle age, or old), and dam history (reared by female, male and female, hand, or wild-caught).

Variable	Pup Survival to 1 mo			Pup Survival to 6 mo		
	Test Statistic	df	<i>P</i>	Test Statistic	df	<i>P</i>
Pair Compatibility	t=-0.26	26	0.78	t=-0.02	23	0.98
Sire Age	F=0.57	2,27	0.57	F=1.39	2,24	0.27
Dam Age	F=0.42	2,27	0.66	F=0.41	2,24	0.67
Dam History	F=1.15	3,16	0.36	F=2.70	3,14	0.09

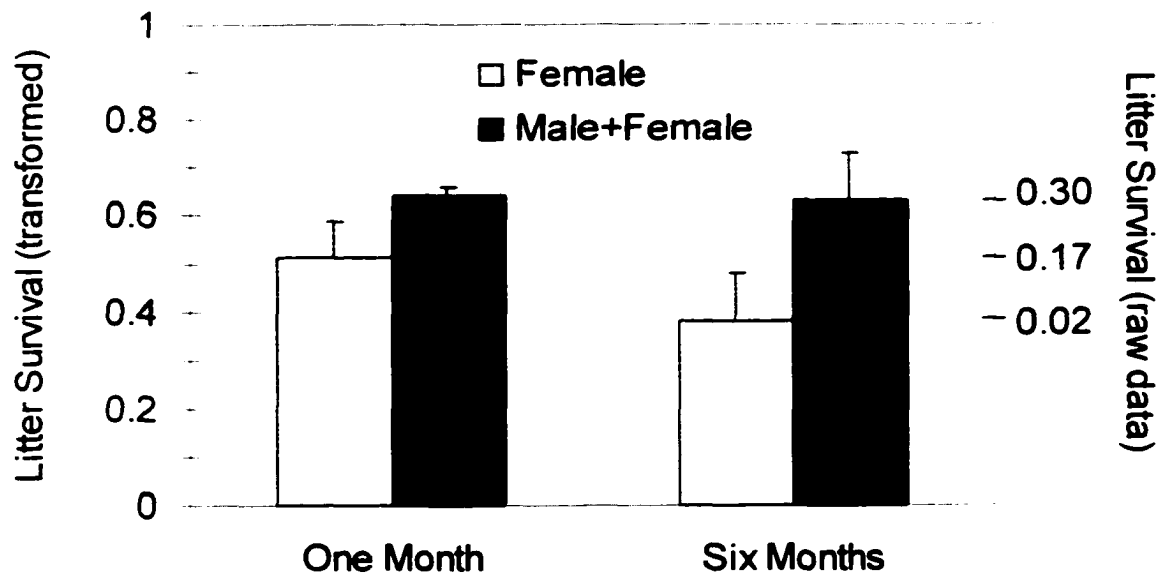


Figure 2.1. Mean (+ SE) proportions of entire litters surviving from 30 maned wolf pairs that gave birth between 1984 and 1998 in relation to whether or not the male was present during the birth and rearing of the litter. Statistical analyses were performed on transformed data (jackknifed, arcsine square-root proportions).

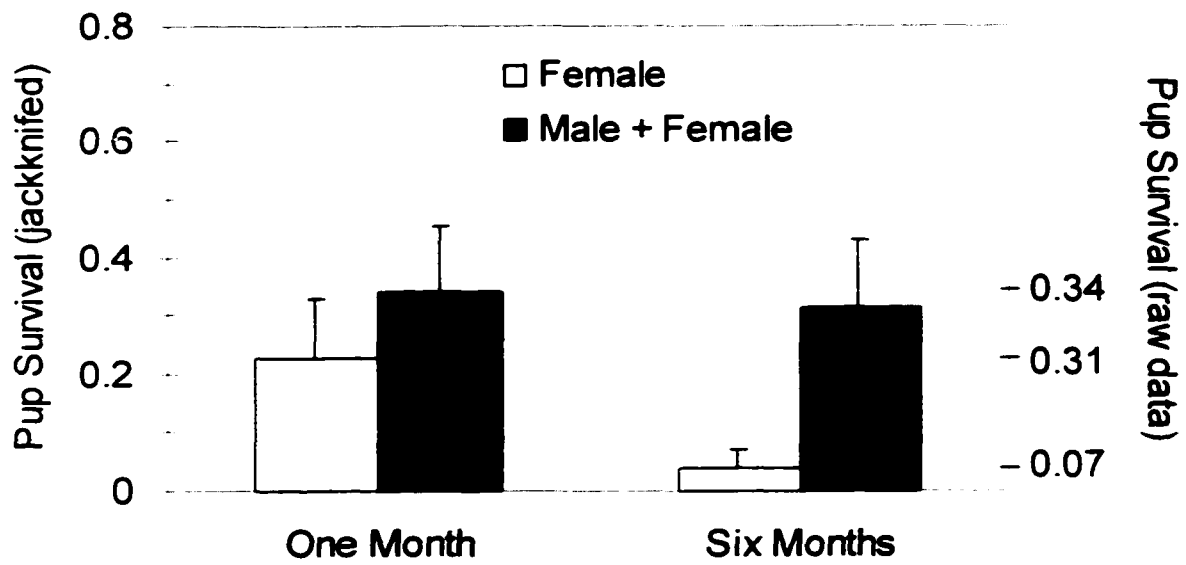


Figure 2.2. Mean (+ SE) proportion of pups surviving from 30 maned wolf pairs in relation to whether or not the male was present during the birth and rearing of the litter. Statistical analyses were performed on jackknifed data.

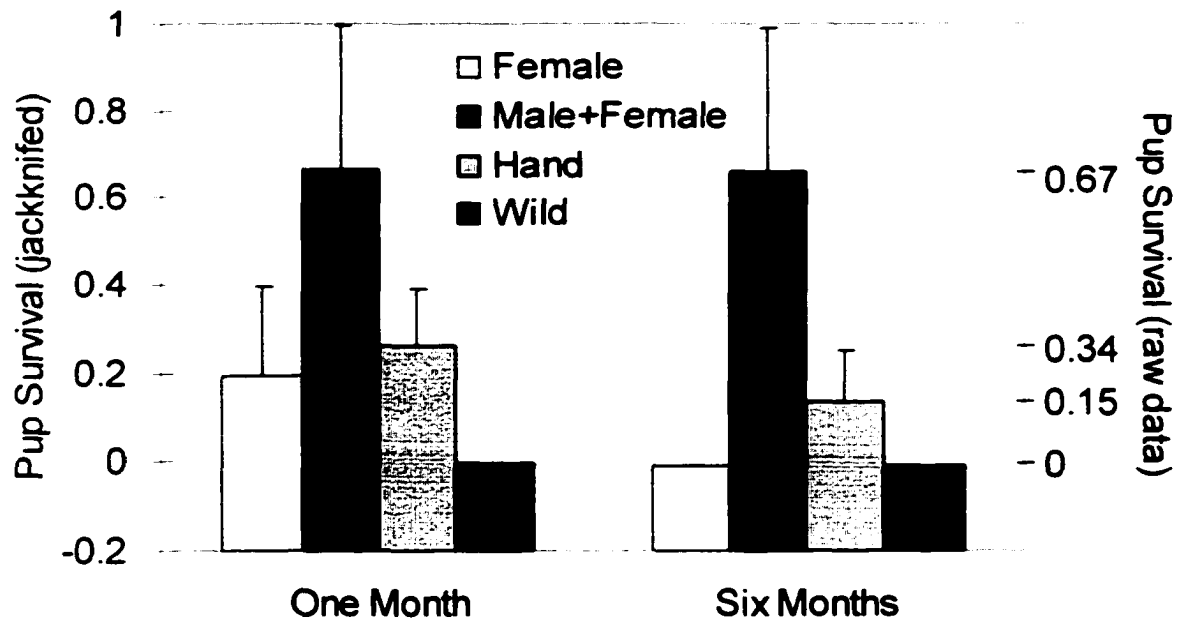


Figure 2.3. Mean (+ SE) proportion of pups surviving (jackknifed values) from 30 maned wolf pairs in relation to how the mother had been reared. Hand-reared females were raised in a zoo nursery. Statistical analyses were performed on jackknifed data.

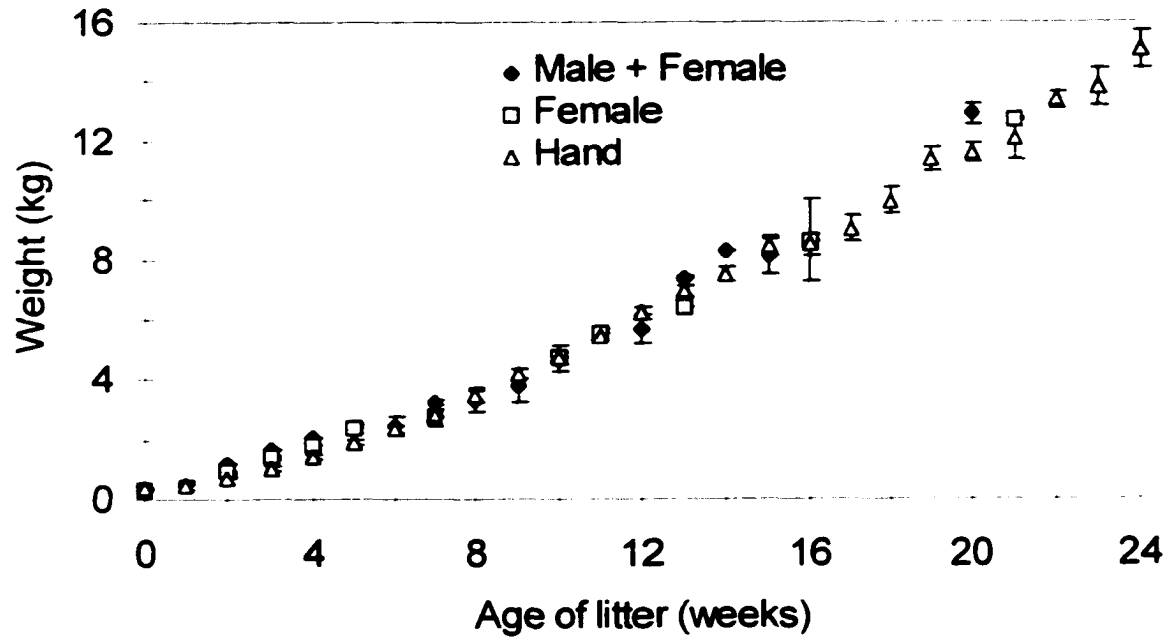


Figure 2.4. Mean (\pm SE) weights of 29 litters born between 1984 and 1998 in relation to how the litter was reared. "Hand" reared pups were reared in a zoo nursery.

CHAPTER III

MATERNAL AND PATERNAL CARE IN CAPTIVE MANED WOLVES (*CHRYSOCYON BRACHYURUS*): THE EFFECT OF MALE PRESENCE ON FEMALE BEHAVIOR

INTRODUCTION

Applications of game theory (Maynard Smith 1982) to the study of parental investment have changed the kinds of questions that are asked about species with biparental care. A fundamental assumption of the game theory approach is that the level of parental investment shown by one parent will depend upon the level of investment shown by the other parent (Maynard Smith 1977; Wuensch 1985; Markman et al. 1996; Kempenaers and Sheldon 1997). Traditionally, this assumption and its consequences have been tested in three ways: (1) comparing the behavior of female and male parents, (2) correlating the behavior of the female and male within a pair, and (3) investigating behavioral changes in females resulting from male removal.

Parental behaviors of males and females have been compared in a wide variety of taxa. Monogamous shorebirds often show little difference in the kind or rates of parental

behaviors, probably because incubation and feeding can be performed equally by female and male parents (Blanken and Nol 1998). Internal gestation and lactation in mammals emancipate the male from early direct care of offspring and often lead to little or no paternal care in most mammals (Kleiman and Malcolm 1981). Nonetheless, in the rare cases in which paternal care is observed in mammals, both males and females are capable of all aspects of parental care except for nursing (but see Francis et al. 1994), so we predict that males and females will give similar types of care at similar levels. This prediction has been tested on monogamous rodents, which show either no sexual differences in parental behaviors (*Microtus ochrogaster*: Gruder-Adams and Getz 1985; *Dicrostonyx richardsoni*: Shilton and Brooks 1989) or slight differences in care (*Peromyscus californicus*: Gubernick and Alberts 1987; *Microtus ochrogaster*: Solomon 1993). In general then, where biparental care is given, it is equally shared.

A more explicit, yet less frequently employed approach to studying parental investment measures the correlation between the behavior of the male and female of a pair. If there is a fixed amount of care given to offspring and equality of care is achieved by individuals adjusting their investment depending on the other parent's care, we expect a negative correlation between the rates of specific care behaviors by individual males and females. For example, Freeman-Gallant (1998) found a negative correlation between the rate of chick feeding by male and female Savannah sparrows.

The third approach in parental investment studies involves observing females' behavior when males are absent, especially right after males have been removed. Male removal experiments have been used frequently in birds (reviewed in Bart and Tornes 1989) and less frequently in mammals, probably due to the scarcity of mammalian species

with biparental care (Kleiman and Malcolm 1981). Many of these studies have shown substantial changes in the female's behavior when the male is absent (e.g. Elwood and Broom 1978; LeSchack et al. 1998). Male removal studies have the added advantage of being able to clarify the male's contribution to offspring survival and/or growth. By changing behavior after male removal, the female may be able to compensate for the male's absence or low level of care, resulting in little or no difference in the survival or growth rate of offspring raised by the female versus those raised by both parents (e.g., Freeman-Gallant 1998). In other cases, females may be unable to compensate for the male's absence, leading to decreased offspring survival and growth (e.g., Markman et al. 1996; Chapter II). So male removal studies serve the dual purpose of illustrating females' altered investment due to male removal as well as verifying whether males' care is essential to offspring growth and survival.

Unfortunately, most studies of mammalian parental investment have focused on only one of the groups with extensive paternal care, the rodents. Very little is known about parental investment in other mammalian groups. One of these neglected groups is the family Canidae, a group in which every well-studied species exhibits direct male care of offspring (Malcolm 1985). Most research on canid parental behavior has focused on only a few species such as the African wild dog, *Lycaon pictus*, (McNutt 1996), the coyote, *Canis latrans* (Bekoff and Wells 1986), and the gray wolf, *Canis lupus* (Mech 1970; Harrington et al. 1983). Whereas paternal care is considered universal within this family, many canids remain relatively unstudied, so their parental behavior patterns are unconfirmed (Malcolm 1985).

One of these relatively unknown canids is the maned wolf (*Chrysocyon brachyurus*), the largest canid in South America. In captivity, males exhibit extensive paternal care (Bartmann and Nordhoff 1984; Rasmussen and Tilson 1984; Bestelmeyer 1999), and this care appears to benefit the pups. In a study of 77 captive maned wolf litters (Chapter II), I illustrate that pups raised by both parents have a higher survival rate to six months than pups raised by the female alone. The mechanism underlying this difference remains elusive. Rates of weight gain of mother-reared and mother- and father-reared pups do not differ (Chapter II), probably because food is offered *ad libitum* to captive maned wolves (Allen 1995). Therefore, pup survival differences may be caused either by a change in the female's behavior when the male is present and/or a benefit directly imparted to the pups by the male. While previous studies show the extensive role captive males play in pup rearing through grooming, guarding, playing with, and regurgitating to pups (Bartmann and Nordhoff 1984; Rasmussen and Tilson 1984; Uka 1986), none of these studies provide a comprehensive, quantitative comparison of male and female parental behavior that would allow an evaluation of the importance of male care.

Between 1994 and 1998, I studied 7 of the 8 pairs of captive maned wolves that successfully reared litters in North American zoos. This study combined the three traditional ways parental investment is generally studied: comparing male and female behavior, measuring the correlation between male and female behavior within a pair, and examining female behavior when the male is present and absent. My two primary objectives are: (1) to provide the first comprehensive, quantitative description of maned wolf parental behavior, thereby allowing a comparison of the types and rates of parental behaviors exhibited by males and females in this monogamous species, and (2) to

compare the behavior of females and males as a function of male presence/absence. With these data, I sought to explain pup survival differences noted in Chapter II and search for evidence of partial female compensation for a lack of male care.

METHODS

Subjects

The maned wolf averages 23.3 kg (Dietz 1984) and stands 75-90 cm at the shoulder (Sheldon 1992). Maned wolves live in monogamous pairs with a diet consisting primarily of fruit, small mammals, and birds (Dietz 1984; Jácomo 1995; Motta-Junior et al. 1996; Chapter VI), although they are capable of successfully hunting larger ungulates (Bestelmeyer and Westbrook 1997). Rapid loss of the maned wolf's primary habitat, the *cerrado* (Ratter et al. 1997), prompted the Argentine (DNFS 1983), Brazilian (Dietz 1984), and United States' (USFWS 1989) governments to list the species as endangered; furthermore, the IUCN has listed it as vulnerable (IUCN 1990). A North American captive breeding program, the Maned Wolf Species Survival Plan (MWSSP), was started in 1985. The MWSSP currently contains 91 maned wolves housed in 27 institutions in the United States (Rodden, pers. comm.).

I observed 7 pairs of maned wolves that gave birth to 10 litters between 1994 and 1998 (Table 3.1). This represents all but one of the pairs that successfully reared pups in the United States during these years. Two litters were reared by the female only, five were reared by both parents, and three litters were born in the absence of the males, but males

were reintroduced when their litters were between 7 and 12 weeks old. Litter sizes ranged from 2-5 pups with a mean of 3.40 ± 0.84 s.e.

Pup survival in the litters in this study followed the pattern found in Chapter II on a much larger sample, with higher survival for litters reared by both parents than for those reared by only the female. All five litters raised by both parents and two of three litters with reintroduced males had 100% pup survival to 6 months. The two litters reared by the female alone had 33% and 66% pup survival. The final litter with the reintroduced male had 50% of the pups survive, after two pups died of an illness. These data indicate that the frequency of litters with 100% survival is not independent of how the litters are reared ($X^2 = 6.83$; $df=2$; $0.025 < P < 0.05$).

Data Collection

I conducted 257.5 hr of continuous, focal animal observation (Altmann 1974) on the adults, either directly or through the use of videotapes sent to me by trained volunteers and keepers at each zoo. Observations began when the pups were 5 weeks old and continued until they were 24 weeks old when possible. All observations lasted 30 or 60 min and were done between 0630 h and 2000 h. During each observation, I recorded the proportion of time the focal animal spent in ten mutually exclusive, exhaustive behavioral states (Table 3.2) and the number of occurrences of 29 behavioral events (Table 3.3). The behavioral descriptions used in this study were based on extensive preliminary observations as well as ethograms by Rodden et al. (1996) and Bestelmeyer and Kinsey (1995). I also recorded the proportion of time each adult spent near a pup or its mate, defined as being within three adult body lengths.

Data Analysis

Because an adult's behavior is not independent from year to year, I calculated a mean proportion or rate of each behavior for those individuals that were observed for two years. Initially, all observations were separated according to the age of the pups: 2 mo, 3 mo, 4 mo, and 5 mo. To normalize the data, I transformed all proportions using the arcsine square root transformation (Zar 1996) and checked transformed values for normality.

I used equal variance t-tests with a Bonferroni adjustment to investigate differences between the behaviors of males and females housed with pups. A repeated measures ANOVA was used to test for changes in parental behaviors as the pups matured. Because there was no change in the proportion of any behavioral state or rate of any behavioral event as the pups matured ($P > 0.10$), all observations were pooled for the remaining analyses. Correlations between female and male behaviors within a pair were evaluated using Spearman rank order correlations. The effect of male presence or absence from pups on female and male behavior was evaluated with Wilcoxon signed-rank tests for the pairs that reproduced under both rearing conditions and with Wilcoxon rank sum tests for the independent pairs, after I randomly eliminated one rearing condition for each of the pairs that was observed both when the male was present and absent in order to satisfy the assumption of independence.

All tests were considered significant at $P < 0.10$, and most tests were two-tailed; the exception was one-tailed tests for correlations between male and female behaviors since I predicted a negative correlation *a priori*.

RESULTS

Time Budgets and Rates of Behaviors

Mean transformed proportions of time in each behavioral state and mean rates of behavioral events for all females and males with pups are shown in Table 3.4. Pacing was a relatively rare behavior and was exhibited by only 3 of the 7 females and 2 of the 6 males. Even though food was always available for adults with pups as recommended by the MWSSP (Allen 1995), eating and drinking were also fairly rare, making up less than 5% of the females' and males' time budgets during all months. There was no significant change in the percentage of time spent in any state or the rate of any behavioral event for females or males as the pups matured ($P>0.10$). Litter size did not affect the amount of time with pups, the rate of affiliative behaviors, or the rate of aggressive behaviors directed to pups (Table 3.5).

Male versus Female Parental Care Patterns

Females and males were similar in the parental behaviors they exhibited, their time budgets, and the rates of all behavioral events. Every parental behavior exhibited by females was also seen in males, except for nursing. Therefore, nursing was excluded from all further analyses. Females and males did not differ in the proportion of time they spent inactive, pacing, eating and drinking, or near their mate during any month or when all months were pooled (Table 3.4). Males spent a higher proportion of time with their pups than females did during every month (Fig. 3.1; sign test; $N=4$; $k=0$; $P=0.06$), and these

monthly differences were significant when pups were 2 mo old ($t_6=-2.66$; $P=0.04$) and when pups were 4 mo old ($t_8=-2.71$; $P=0.03$). When data from all pup ages were pooled, there was no longer a significant difference between the total amount of time spent with pups by females and males (Table 3.4; $t_{10}=-0.84$; $P=0.42$). Compared with their mates, five of the six males spent more of their active time (any behavioral state except lying down, sitting, or out of view while inactive) with pups, but this difference was not significant ($T_+=18$; $N=6$; $P=0.16$). There was also no difference in the amount of time males and females spent with their pups while they were inactive ($T_-=13$; $N=6$; $P=0.69$).

Females and males did not differ in their rates of solitary behaviors, marking behaviors, aggressive behaviors directed to pups, affiliative behaviors directed to mates, or aggressive behaviors directed to mates (Table 3.4). Males directed more affiliative behaviors to their 2 mo old pups than females did ($t_{3,4}=-2.8$; $P=0.06$). This higher rate of affiliative behaviors directed to pups by males than by females was not maintained when data from all months were pooled (Table 3.4; $t_{10}=-1.7$; $P=0.12$).

Correlation of Male and Female Behavior within a Pair

If there is some fixed amount of care given to pups, the amount of care given by the male and female of a pair should be negatively correlated. This correlation did not exist for the total amount of time spent with pups ($r_5=-0.14$; $N=6$; $P>0.50$), the amount of time spent with pups while active ($r_5=0.49$; $N=6$; $0.20<P<0.50$), or the amount of time spent with pups while inactive ($r_5=-0.60$; $N=6$; $0.20<P<0.50$). There was also no correlation between the rate of aggressive behaviors directed to pups ($r_5=-0.50$; $N=6$; $0.20<P<0.50$) by the members of a pair. I found a positive correlation between the rates of males' and females'

affiliative behaviors to pups (Fig. 3.2; $r_s=0.94$; $N=6$; $P=0.02$). The total rate of affiliative behavior by a pair was not related to the size of the litter (Fig. 3.2; $r_s=0.64$; $N=6$; $P=0.17$).

Effects of Male Presence

For the four females who reared pups both with the male present and with the male absent, the male's presence did not affect the proportion of time females were with pups ($T_+=5$; $N=4$; $P>0.90$), the rate of affiliative behaviors directed to pups ($T_+=6$; $N=4$; $P=0.88$), or the rate of marking behaviors ($T_+=6$; $N=4$; $P=0.88$). All four females exhibited a higher rate of solitary behaviors (Table 3.6; $T_+=10$; $N=4$; $P=0.13$) when males were present. Although not significant, there was a trend when males were present towards females spending more time inactive (Table 3.6; $T_+=8$; $N=4$; $P=0.38$), more time eating and drinking (Table 3.6; $T_+=9$; $N=4$; $P=0.25$), and exhibiting fewer aggressive behaviors to pups (Table 3.6; $T_+=8$; $N=4$; $P=0.38$). Only two of the four females ever paced, so it was not possible to evaluate the effect of the male's presence on pacing. Across all females, the only behavior that differed depending on the male's presence was the rate of aggressive behaviors directed to pups, which was lower when males were present (Table 3.7; $W_x=18$; $N=3,4$; $P=0.06$).

All three of the males who were both present and absent during pup rearing showed less inactivity and more eating and drinking when they were housed with their pups, but these comparisons have low power and thus did not reach statistical significance (Table 3.8; $T_+=6$; $N=3$; $P=0.25$). Being with the pups did not change the males' rates of marking or solitary behaviors (Table 3.8). Only one of these males paced, so no evaluation of this

behavior could be done. Across all males, males with pups and males housed alone did not differ in any behavior (Table 3.7).

The effect of female-only or biparental care on pups can be examined by comparing the behavior of females rearing pups alone with the pooled behaviors of males and females rearing their pups together. Of the four pairs that reared litters under both conditions (male present and male absent), three pairs showed more total affiliative behaviors and fewer total aggressive behaviors directed to pups when rearing pups together. There was no consistent change in the total proportion of time pups spent with at least one adult since the proportion was higher in two pairs and lower in two pairs when the male was present.

DISCUSSION

The family Canidae is an unusual mammalian group because of the prevalence of species exhibiting paternal care. Only 5% of mammalian species exhibit direct male parental care (Clutton-Brock 1991), yet every well-studied canid species exhibits direct male care (Malcolm 1985). This study confirms extensive paternal care in maned wolves and provides the first comprehensive, quantitative description of this parental behavior. Previous work with captive maned wolves suggested that male maned wolves play an important role in pup care. For example, Rasmussen and Tilson (1984) showed that males regurgitate to their five- to nine-month-old pups nearly twice as frequently as females. Additionally, many anecdotal reports have illustrated that males play active roles in pup

care by grooming and guarding pups (Bartmann and Nordhoff 1984; Uka 1986), regurgitating to the female (Bestelmeyer, unpublished data), and even eating the placenta as soon as pups are born (Bartmann and Nordhoff 1984).

The striking similarities between the parental behaviors of male and female maned wolves are expected for this monogamous species. Except for a male mammal's inability to lactate (but see Francis et al. 1994), males and females are capable of giving similar types of parental care to their offspring. Therefore, once paternal care is favored, we expect little difference between the parental behaviors of males and females. Within most monogamous species, males and females are similar in their parental behaviors, and the maned wolf appears to be no exception. Until recently, captive male maned wolves were generally removed from the female prior to parturition for fear that either the male would harm pups or the male's presence would stress the female, causing her to harm the pups (Bartmann 1983). It now appears that males play a significant role in pup care, differing little from the typical parental behavior exhibited by females.

The few differences I detected between females' and males' behaviors to pups during certain months can be explained using knowledge of the pups' development. Males spent more time with 2-month-old pups and gave more affiliative behaviors to them than females, reflecting an increasing role for the male once pups begin to emerge from the den at approximately 4-5 weeks (Brady and Ditton 1979). At this time, pups begin to explore their environment and consume solid food, increasing the importance of the male's contribution to guarding, grooming, and regurgitating food to pups. Females begin to wean pups when they are 2-4 months old (Brady and Ditton 1979). During this time, pups are increasingly rebuffed from their attempts to approach females, which explains

why males spend more time with their 4-month-old pups than do females. While being weaned, pups also solicit adults for regurgitated food and may be more successful in their solicitations of males, as illustrated by Rasmussen and Tilson (1984).

A game theory approach to parental investment predicts that individuals will change their parental behavior depending on the presence and behavior of their mates (Maynard Smith 1977). My study provided no support for this prediction for any parental behavior except aggressive behaviors directed to pups by females.

A positive correlation between the rate of affiliative behaviors directed to pups by males and females was inconsistent with game theory predictions. This result suggests that there is no fixed amount of care directed to pups, but rather that some pairs provide more care for their offspring than do others. Increased care does not necessarily lead to increased survival of pups since the three pairs exhibiting the least frequent affiliative behaviors to their pups had 100% pup survival to six months.

The results of this study suggest a mechanism for increased pup survival when sires are present (Chapter II). Aggression by females to pups was reduced when males were present. Female aggression has resulted in pup mortality within the captive population; for example, in 1994 a mother-reared 7.5-week-old pup died from a head wound caused by an attack from the female. Male presence, which decreases the rate of aggression to pups, may therefore result in higher pup survival to six months. For the four pairs reproducing under both rearing conditions, I also detected a trend toward increased inactivity and increased eating and drinking by females when males were present. Both factors may increase the health of the female and result in higher quality milk for the pups.

An alternative hypothesis to explain higher pup survival in the presence of males is that males directly impart some benefit to pups. My data provide only limited support for this hypothesis, since three of four pairs that reared litters under both conditions gave more affiliative and fewer aggressive behaviors to pups when the male was present. On the other hand, there was no change in the total amount of time spent with an adult when the male was present. Determining how important these effects may be for the entire captive population will require further study.

It must be noted that this study was conducted entirely on captive maned wolves, and extreme caution should be used when attempting to generalize from captive animals to their wild counterparts because there are often considerable differences between the two (Kaufmann and Kaufmann 1963; Rowell 1967; Bennett and Fewell 1987; Baker 1994; Bestelmeyer 1998). Nonetheless, numerous details of the maned wolf's natural history suggest that extensive paternal care may be present in free-ranging maned wolves. First, captive pup survival increases due to male presence (Chapter II), providing a substantial benefit from male care. This effect is probably heightened in the wild where food is not provided *ad libitum*. Compared with other canids, maned wolves have a low litter size relative to maternal weight (Geffen et al. 1996), which is explained by several authors (Geffen et al. 1996; Moehlman and Hofer 1997) as a result of low resource availability in the maned wolf's primary habitat. Low resource availability may, in turn, result in the male's care being extremely important for pup survival. The costs of paternal care are probably low in free-ranging maned wolves because females are widely dispersed on 27 km² home ranges (Dietz 1984), making it unlikely that males would encounter additional mating opportunities if they were not caring for offspring. Therefore, the high benefits

and low costs of paternal care in maned wolves hint at a role for the male in rearing wild pups, but confirmation will require studies of free-ranging maned wolves.

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Table 3.1. Maned wolf pairs observed in this study. Studbook numbers are from Matern (1999).

Zoo / Wildlife Center	Location	Studbook numbers (male/female)	Number of litters	Number of observation hours
Baton Rouge Zoo	Baton Rouge, LA	1147/1236	1	24
Fossil Rim Wildlife Center	Glen Rose, TX	1184/1191	2	44.5
Fossil Rim Wildlife Center	Glen Rose, TX	1385/1285	1	37.5
Houston Zoo	Houston, TX	971/1029	2	71
Little Rock Zoo	Little Rock, AR	523/610	1	12.5
White Oak Conservation Center	Yulee, FL	1384/1321	2	44
Wild Canid Survival & Research Center	Eureka, MO	1830/1661	1	24

Table 3.2. Definitions of maned wolf behavioral states.

Inactive

Lying down: mid-section of body in contact with the ground

Sitting: only the back part of body in contact with the ground; usually when animal is scratching

Not visible-inactive: not in view; consider inactive once animal has been out of view in same location for 60 sec

Active

Standing: stationary upright position

Walking: locomoting without in-air phase

Trotting: locomoting with in-air phase

Pacing: walking back and forth over the same area; pace begins on the third consecutive pass over the same ground and ends when the animal walks to a new area

Eating: consuming solid food

Drinking: consuming water or another liquid

Not visible-active: not in view

Table 3.3. Definitions of maned wolf behavioral events. Rates of several behaviors (indicated with asterisks) were adjusted for the amount of time the animal was outside of the den box since they could occur (and would not be recorded) when the animal was in the den box, out of view.

Solitary Behaviors

- *Self-groom: lick own body
- *Sniff: investigate ground or object with nose
- *Dig: scratch ground with one or both front paws to make a depression
- *Cache: bury food in hole or cover food with substrate

Elimination / Marking Behaviors

- Leg lift: urination with hindleg lifted off the ground
- Squat: urination with back legs bent; sometimes one hindleg lifted slightly off the ground
- Urinate over: urinate in the same spot another wolf urinated or defecated within 5 minutes
- Taste urine: lick urine of another wolf; usually accompanied by flehmen
- Flehmen: rapid teeth chatter; lips often pulled back
- Straddle: stand over and rub genital region on bush, grass, or another object
- Face rub: rub face or neck on a surface
- Defecate: self-explanatory

Affiliative Behaviors

- *Regurgitate: disgorge partly digested food to mate or pups
- *Nurse: suckle; female may be lying down or standing
- *Groom: lick part of body of pup or mate
- *Sniff: investigate mate or pup with nose
- *Sniff/lick anogenital region: sniff or lick another wolf's anogenital region
- Tail out: tail lifted or held horizontally while approaching or standing near mate or pup
- Tail up: tail raised above the level of the back while approaching mate or pup
- Play invitation: stamp or bow on forelegs, facing other animal or use foreleg to paw at shoulder of other animal
- Play chase: chase mate or pup, usually with ears forward and not piloerect
- Open mouth: head and ears up, alert, mouth open with tongue out directed to another wolf
- Wrestle: wolves stand on hindlegs, front legs on other's shoulders, usually with open mouth

Agonistic Behaviors

- *Muzzle bite: bite the muzzle of mate or pup, often in response to regurgitation solicitation
 - *Growl: low frequency vocalization directed at mate or pup
 - Charge / lunge: advance towards another wolf, piloerect, stiff forelegs, ears back
 - Agonistic chase: chase mate or pup, usually with ears back and piloerect
 - Piloerect pace: walk with stiff forelegs, head down, piloerect, ears usually back
 - *Bite: snap jaws shut on another animal
-

Table 3.4. Mean proportion (\pm SE) of time in each behavioral state and mean rate [number of behaviors / hr] (\pm SE) of each behavioral event by 6 pairs of maned wolves raising pups together. Proportional data are reported in raw proportions as well as arcsine square root transformed units. Transformed data were used in statistical tests of behavioral states, whereas raw data were used for statistical tests of behavioral events. There were 10 degrees of freedom for each test. A Bonferroni adjustment made the *P*-value required for significance equal 0.009 (0.10/11).

	Means of Raw Data		Transformed Data		t	P
	Females	Males	Females	Males		
<u>Behavioral States</u>						
(proportion)						
Inactive	0.56 \pm 0.73	0.53 \pm 0.06	0.85 \pm 0.07	0.81 \pm 0.06	0.41	0.69
Pace	0.005 \pm 0.02	0.02 \pm 0.01	0.04 \pm 0.02	0.03 \pm 0.02	0.56	0.59
Eat/Drink	0.05 \pm 0.02	0.02 \pm 0.01	0.18 \pm 0.05	0.14 \pm 0.03	0.84	0.42
With Pups	0.14 \pm 0.08	0.24 \pm 0.09	0.33 \pm 0.10	0.47 \pm 0.12	-0.84	0.42
With Mate	0.07 \pm 0.03	0.06 \pm 0.02	0.24 \pm 0.06	0.23 \pm 0.05	0.18	0.86
<u>Behavioral Events</u>						
(number/hr)						
Solitary	6.3 \pm 1.4	8.5 \pm 2.1	-	-	-0.88	0.40
Marking	2.4 \pm 0.9	3.5 \pm 1.4	-	-	-0.67	0.52
Affiliative to pups	1.4 \pm 0.6	4.1 \pm 1.5	-	-	-1.69	0.12
Aggressive to pups	0.4 \pm 0.2	0.7 \pm 0.2	-	-	-0.97	0.35
Affiliative to mate	0.9 \pm 0.6	0.6 \pm 0.3	-	-	0.51	0.62
Aggressive to mate	0.7 \pm 0.3	0.8 \pm 0.4	-	-	-0.38	0.72

Table 3.5. Effect of litter size on parental behaviors of captive maned wolf males and females rearing their pups together. For all tests, there were 1 (numerator) and 6 (denominator) degrees of freedom.

Behavior	Males		Females	
	F	P	F	P
Time with pups	3.1	0.13	0.18	0.69
Affiliative behaviors to pups	0.16	0.70	0.003	0.95
Aggressive behaviors to pups	1.95	0.21	3.04	0.13

Table 3.6. Behaviors of 4 females that raised pups both alone and with the male present. Inactive and eating/drinking are presented as percentages of the total time budget. Aggressive and solitary behaviors are presented as the number of events per hour.

Female	Inactive (Percent of Time)		Eating/Drinking (Percent of Time)		Aggressive Behaviors (rate)		Solitary Behaviors (rate)	
	Alone	With Male	Alone	With Male	Alone	With Male	Alone	With Male
	Akela	4	50	1	3	0.24	0	27.09
Katie	51	31	3	9	8.91	1.15	9.20	6.92
Lita	5	62	0.4	0.1	0	0.36	38.56	4.53
Violeta	67	84	2.7	3	0.94	0	10.63	1.47

Table 3.7. Comparison of behaviors of adults raising pups with and without the male present. For all comparisons, four individuals were observed while the male was present and three individuals were observed without the male present during pup rearing. Males could not be with pups or direct affiliative or aggressive behaviors to pups when they were not housed with them, so these comparisons could not be made for males.

Behavior	Females		Males	
	W_x	P	W_x	P
Inactive	13	0.86	15	0.40
Eating and Drinking	12	>0.90	9	>0.90
Pacing	12	>0.90	14.5	0.63> P >0.40
Marking	11	>0.90	12	>0.90
Solitary	15	0.40	12	>0.90
Time with Pups	15	0.40	-	-
Affiliative Behaviors to Pups	15	0.40	-	-
Aggressive Behaviors to Pups	18	0.06	-	-

Table 3.8. Percentage of time inactive and eating/drinking for 3 males that were observed when housed without their pups (alone) and when housed with their pups.

Male	Inactive		Eating/Drinking	
	Alone	With Pups	Alone	With Pups
Caesar	56	54	1	4
Saco	88	46	0.18	0.23
Waylon	84	55	1	4

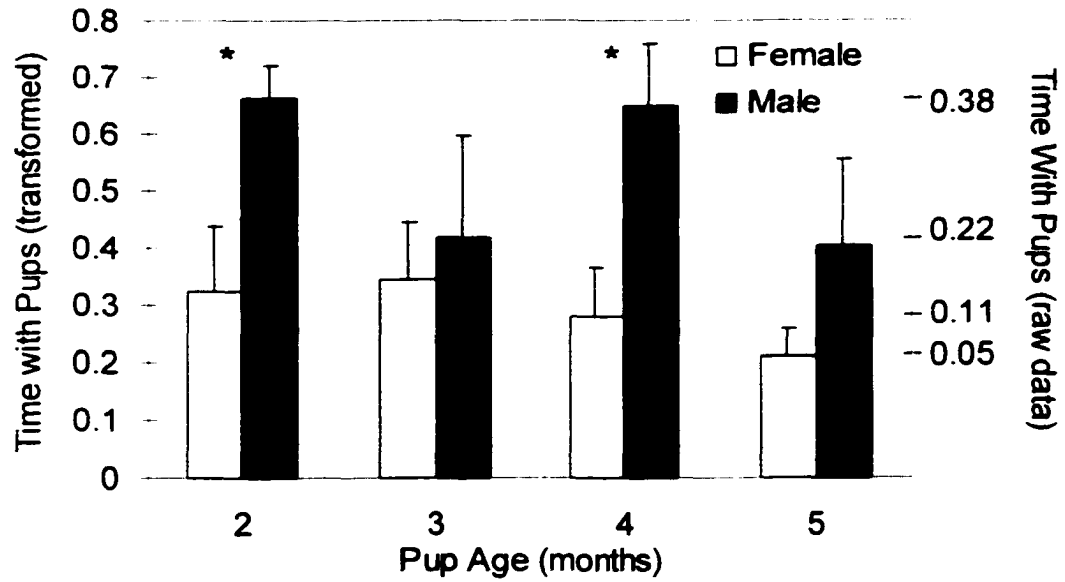


Figure 3.1. Proportion of time spent within three adult body lengths of 2-5 month-old pups by female and male maned wolves. Transformed values [arcsine (proportion^{0.5})] were used in statistical analyses. Asterisks indicate $P < 0.05$.

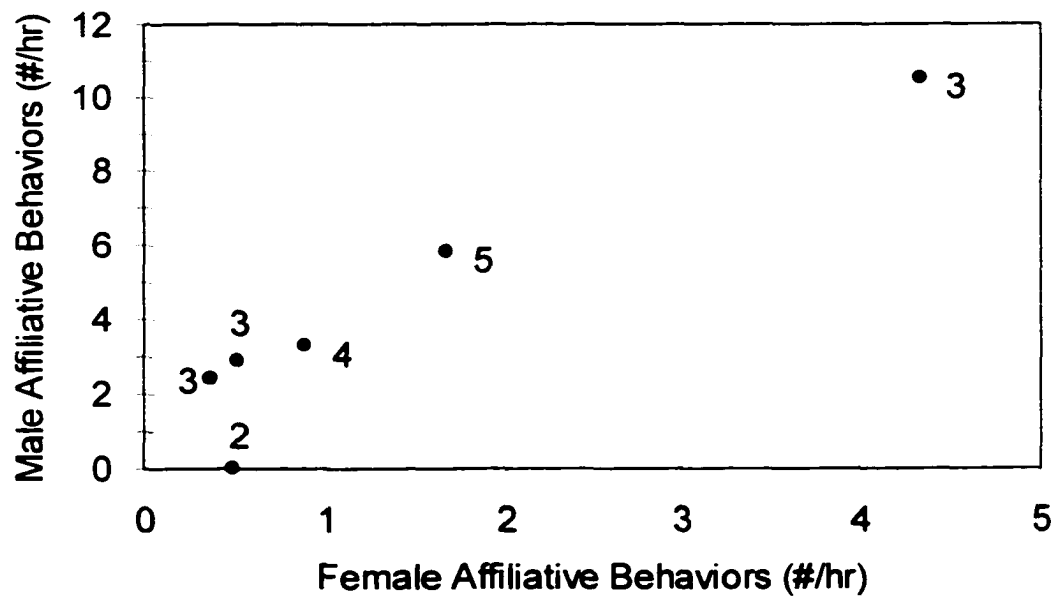


Figure. 3.2. Association between the rates of affiliative behaviors (number / hr) directed to pups by the female and male of a maned wolf pair. Numbers next to each point represent the number of pups in each litter. There is a positive correlation between male and female rates of affiliative behaviors ($r_s=0.94$; $N=6$; $P=0.02$), but there is no association between the litter size and total rate of affiliative behaviors ($r_s=0.64$; $N=6$; $P=0.17$).

CHAPTER IV

BEHAVIORAL CHANGES ASSOCIATED WITH INTRODUCTIONS OF MALE MANED WOLVES (*CHRYSOCYON BRACHYURUS*) TO FEMALES WITH PUPS

(*Zoo Biology*, 1999, 18:189-197)

INTRODUCTION

Although paternal care is not common in mammals (Kleiman and Malcolm 1981; Woodroffe and Vincent 1994), it is considered widespread in the family Canidae because no canid has been shown to lack male parental care (Malcolm 1985). However, most research on canid parental behavior has focused on only a few species such as the African wild dog, *Lycaon pictus*, (van Lawick-Goodall and van Lawick-Goodall 1970; McNutt 1996), the coyote, *Canis latrans* (Bekoff and Wells 1986), and the gray wolf, *Canis lupus* (Mech 1970; Harrington et al. 1983). Many canids are relatively unstudied, so their parental behavior patterns are unknown (Malcolm 1985).

One of these relatively unstudied canids is the maned wolf, *Chrysocyon brachyurus*, an endangered species native to central South America (Dietz 1984). Male maned wolves have been observed caring for pups in captivity, but the extent of paternal care in the wild is not known. Until recently, managers generally removed males 1-3 weeks before the

birth of pups in North American zoos (Brady and Ditton 1979; Rodden 1986) and sometimes in European zoos (Faust and Scherpner 1967; Encke 1971; Pithart et al. 1986) and South American zoos (Veado 1997). Bartmann (1983) believes that the habit of removing the male resulted from incorrect reports between the 1920's and 1960's that wild maned wolves were solitary, and therefore the male did not participate in rearing pups. Based on this information, it was feared that if the male remained with the pups, either the male would harm the pups or the female would harm the pups because of nervousness caused by the male's presence. However, on several occasions when males have remained with females and pups, they have been observed grooming pups (Bartmann and Nordhoff 1984; Uka 1986), guarding pups (Uka 1986), regurgitating to pups (Rasmussen and Tilson 1984), regurgitating to the female (Bestelmeyer, unpubl. data), and even eating the placenta (Bartmann and Nordhoff 1984). Between 1995 and 1998, males were continuously housed with females and pups at the Little Rock Zoo, White Oak Conservation Center, and Wild Canid Survival and Research Center. In these cases, the males routinely groomed, guarded, played with, and regurgitated to their pups, especially once the pups began to come out of the den at approximately 4-5 weeks (Bestelmeyer, unpubl. data).

Based on these successes, the Maned Wolf Species Survival Plan (SSP) currently recommends that zoos either leave the male with the female and pups from the time of birth or introduce the male shortly after birth (Rodden, pers. comm.). Although no male maned wolf has ever been observed directly harming pups housed with him (Rodden, pers. comm.), some managers are apprehensive about continuously leaving male maned wolves with pups due to the long-held belief that males would harm newborns. Adding to

this apprehension is one published report of a male being continuously aggressive to his pups through a chain-link fence (Biben 1983). When doubts exist about continually leaving the male with the female and pups, managers may prefer to remove the male before parturition and then introduce him when the pups are older and less vulnerable.

Unfortunately, managers choosing to introduce males have been unable to find any published protocols. While introductions of male maned wolves to females and pups have been attempted before with mixed success (Biben 1983; Pithart et al. 1986), no report describes the methods used. There is also no information on the differences between successful and unsuccessful introductions to guide managers. In this paper, I describe the procedures used to successfully introduce three male maned wolves to their 7-12 week-old pups, and I document differences in the adults' behavior before and after the introduction. I define a "successful" introduction as one in which the male can continuously be housed with his mate and pups. Behavioral data presented here show that the male's presence may also have numerous beneficial effects, including an improvement in the dam's health.

METHODS

Subjects and Housing

I studied three pairs of maned wolves that had pups in 1994 or 1995 (Table 4.1). The housing and diet of Pair 1 were described by Steinhaus (1995). Pairs 2 and 3 were housed in large, outdoor, off-exhibit enclosures at the Fossil Rim Wildlife Center in Glen Rose,

Texas. Each pair's daily diet consisted of 6 cups of ProPlan adult dog food, 2 whole quail, and 0.5 cups of a variety of fruits including apples, grapes, bananas, and other seasonal fruit.

Introduction Procedure

The introduction procedure consisted of three stages. Each stage began at slightly different times for each litter (Table 4.2) due to our desire to test the success of this procedure for litters of varying ages. In Stage 1, males were allowed visual, olfactory, and limited tactile contact with their pups through a 0.6 m by 1.0 m chain-link panel (howdy door; Pair 1) or a common chain-link fence (Pairs 2 and 3). Male 1 had access to the howdy door for 1-4 hr/day for 11 consecutive days. For Pairs 2 and 3, the males' and females' enclosures were adjoining, so these males had continuous contact with their pups through a common chain-link fence when the pups emerged from their den boxes at approximately 4-5 weeks of age. During Stage 2, we put both adults into the male's enclosure for 1-3 hr at a time without the pups present. During Stage 3, we put the male in the enclosure with the female and pups. For the first 4 days, Male 1 was with the pups for 1.5-3 hr/day, always with at least one observer present. After Day 4, he was housed continually with the female and pups. Male 2 was with the pups for approximately 2.5 hr for the first 2 days and continually thereafter. Male 3 was continually housed with the pups from the time he was first introduced.

Behavioral Observations

I performed continuous, focal animal observations (Altmann 1974) during all stages of the introductions. To determine if there were behavioral changes associated with the introductions, I used 150 hr of observations to compare the wolves' behavior for 7 days before Stage 2 (hereafter referred to as "before the introduction") with their behavior during 7 observation days between Day 2 and Day 13 of Stage 3 (hereafter referred to as "after the introduction"). All observations were conducted within the 3 hr after sunrise or the 3 hr before sunset. During the observations, I recorded the amount of time the individual spent inactive (lying down) and active (standing, walking, trotting, pacing, eating, or drinking). I also recorded the amount of time the adult spent near the pups, defined as being within two body lengths of a pup. Finally, I recorded all behaviors directed to the pups by the adults. The definitions of all behaviors are given by Bestelmeyer and Kinsey (1995). Affiliative behaviors included grooming, regurgitating, nursing, sniffing, play inviting, putting the tail out, carrying, and attempting to carry pups. Aggressive behaviors included growling, biting, and muzzle biting. I conducted all 43 hr of observations on Pair 1, 41 of 50 hr for Pair 2, and 52 of 57 hr for Pair 3. Three observers I trained at the Fossil Rim Wildlife Center conducted the remaining 14 hr of observation.

Data Analysis

To normalize the data, all proportions were transformed by taking the arcsine of the square root of each proportion. Because observations were conducted in the mornings and in the afternoons, I tested for a time-of-day effect with a factorial analysis of variance

(ANOVA). There was no effect of the time of sampling on the proportion of time spent active ($F_{1,20}=0.03$; $P=0.87$) or the proportion of time spent with pups ($F_{1,20}=0.33$; $P=0.57$). Therefore, morning and afternoon observations were pooled.

I performed a factorial ANOVA to test for differences in the proportion of time spent active by males and females before and after the introduction. Independent variables included pair, gender, and period (before or after the introduction). If the model was significant ($P<0.05$), I used paired t-tests to test for changes in activity levels in females and males. The amount of time adults spent with pups and the average rates of affiliative and aggressive behaviors shown by each adult to the pups were compared using paired t-tests. In all cases, I compared females before and after the introduction, males before and after the introduction, and the female and male of a pair after the introduction. One-tailed tests were used when comparing female activity, male activity, and female time with pups before and after the introduction due to an *a priori* expectation that female activity would decline, male activity would increase, and female time with pups would decrease after the introduction; these expectations were based on the behavior of pairs continuously housed together during pup rearing (Chapter III). All other tests were two-tailed.

RESULTS

Introduction Procedure

Stage 1: No aggressive interactions were observed between the males and females or the males and pups during this stage. The male and female of Pair 1 frequently sniffed

each other through the howdy door and occasionally used a whine vocalization. Few interactions between the males and females of Pairs 2 and 3 were observed. However, it is likely that these pairs interacted when no observer was present because they had continuous access to their common chain-link fence. All three males sniffed their pups during Stage 1. Males 1 and 2 often accompanied the sniffing with pulse whines (Bestelmeyer and Kinsey 1995), vocalizations often heard prior to an adult regurgitating food to pups (Bestelmeyer, unpubl. data). All three females were calm when the males and pups interacted.

Stage 2: Numerous affiliative behaviors and no aggressive interactions between the males and females of a pair were observed during this stage. The females generally walked around the enclosures, scent-marked, interacted with the males, and then rested.

On one occasion, Pair 2 and Female 3 engaged in an aggressive encounter under the wood fence between their adjoining enclosures. This encounter resulted in a broken leg on Female 3 and a lacerated forefoot on Male 2. We temporarily postponed the introduction procedures due to this event but continued when the injured individuals' behavior returned to normal. It is important to note that this aggression was not caused by the introduction procedure, and all aggression was between pairs rather than within a pair.

Stage 3: Immediately after the introduction, the pups were submissive to the males, crouching and whining in front of them. Within 5 min of Male 1 being introduced to the pups, Female 1 walked away and lay down. Male 3 was lying down with a pup crawling over his back within 1.5 hr of being introduced. Two mildly aggressive interactions were noted between males and their pups in the first few days after the introduction; Male 1

growled when 4 pups simultaneously walked under him, and Male 3 growled when a pup tried to nurse from him.

Behavioral Changes

After the males were introduced, the females' activity decreased, while the males' activity increased (Fig. 4.1), producing a significant interaction between gender and introduction period ($F_{1,6}=18.61$; $P<0.01$). Females were more active before the introduction than after the introduction ($t_2=4.44$; $P=0.02$), while males were less active before the introduction than after the introduction ($t_2=-2.26$; $P=0.08$).

Females spent less time near their pups after the introduction than before (Fig. 4.2; $t_2=3.12$; $P=0.04$). However, because males spent time with pups after the introduction, the amount of time pups spent with at least one adult did not decrease (Fig. 4.2; $t_2=0.70$; $P=0.56$). Males and females did not differ in the amount of time they spent with their pups (Fig. 4.2; $t_2=0.65$; $P=0.58$). The amount of time an adult (either male or female) spent near at least one pup increased as the number of pups in the litter increased, but this correlation was not statistically significant ($r=0.95$; $P=0.20$).

There were no differences in the rates of affiliative or aggressive behaviors performed by females to the pups before and after the introductions (affiliative: Fig. 4.3; $t_2=1.90$; $P=0.20$; aggressive: Fig. 4.4; $t_2=1.41$; $P=0.30$). After the introduction, males and females did not differ in their rates of affiliative behaviors directed to the pups (Fig. 4.3; $t_2=-0.60$; $P=0.61$) or their rates of aggressive behaviors directed to the pups (Fig. 4.4; $t_{24}=0.06$; $P=0.96$). The rate of behaviors directed to pups by both adults was not correlated with litter size ($r=-0.85$; $P=0.35$).

DISCUSSION

Despite the recent success of leaving the male with the female throughout the birth and rearing of litters at the Little Rock Zoo, White Oak Conservation Center, and Wild Canid Survival and Research Center, managers at some zoos are still wary of this practice. The introduction procedure discussed here provides a more cautious option that minimizes early risk to pups but still allows the male to participate in pup care. The facilities and personnel necessary to complete this procedure are relatively modest. Males must be housed in enclosures with a howdy door or chain-link fence joining them to the females' and pups' enclosure. This requirement is generally already fulfilled in zoos with maned wolves. Personnel are required to observe the initial phase of each introduction stage, but it should become apparent within the first few hours if there are aggressive interactions between individuals.

There appears to be some flexibility in when the introductions can be done. We successfully introduced males to pups ranging from 7-12 weeks of age. It is possible that the introductions could be done even earlier; Pithart et al. (1986) recommended introductions begin no earlier than 3-6 weeks after parturition. This procedure worked for adult wolves that were themselves raised by their dam or in a nursery, and for litter sizes ranging from 2 to 4 (Table 4.1). All adult wolves in this study were relatively young animals (Table 4.1), but maned wolves are capable of reproducing until they are approximately 10 years old (Weinhardt and Rodden 1995). Careful observations should

be done when first attempting to use this procedure with older individuals because older maned wolves can have difficulty adjusting to new surroundings (Weinhardt and Rodden 1995).

The behavioral changes in adults suggest a few of the benefits of allowing the male to participate in rearing the pups. First, females rest more when the male is in the enclosure. This result appears to be due to the males' presence rather than simply a change occurring as the pups mature since all three females decreased their activity, despite the fact that their pups varied from 7-12 weeks of age. Decreased activity will likely result in better health of the female, especially when she is nursing. During nursing, female maned wolves' coat condition and general health often decrease (Bestelmeyer, pers. obs.). Introducing the male and allowing him to assume some of the care of pups may help alleviate this problem. Second, males are significantly more active when they are housed with their pups. This increased activity may decrease the incidence of stereotyped behaviors like pacing (Bestelmeyer 1998), thereby enhancing the male's health and the zoo visitor's experience. Finally, pup survival to 6 mo is increased if males are housed with females and pups from the time they are born (Chapter II). This increase in survival may also occur if males are introduced to their pups and allowed to participate in pup care.

The large amount of parental care shown by male maned wolves in this study is similar to that reported by other authors. Rasmussen and Tilson (1984) found that males regurgitated to their 5-9 month old pups twice as frequently as did females. Bartmann (1983) reports on male parental care in many European zoos. It remains unclear if this extensive paternal behavior seen in captive males indicates similar behavior in free-

ranging males. Kleiman and Malcolm (1981, p. 352) suggest that paternal care seen in captivity should be treated with caution. "unless the persistence of male parental care in a variety of individuals under a variety of conditions indicates that such behavior could be occurring in nature..." Conclusions about the presence of paternal care in wild maned wolves will likely require further behavioral studies of the species in its native habitat. However, captive males can play an important role in pup care (Chapter III). The introduction procedure described here is an effective way of giving the male the opportunity to exhibit this care and may ultimately result in enhanced pup survival.

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Table 4.1. Maned wolves used in this study.

		Studbook		Age at Birth	Hand- or		Litter Sex
	Location	Number	Sex	of Litter	Dam-	Litter Date	Ratio
				(years)	Reared	of Birth	(male:female)
Pair 1	Houston	971	Male	5	Dam	1-13-94	2.2
	Houston	1029	Female	5	Dam		
Pair 2	Fossil Rim	1184	Male	4	Hand	1-24-95	2.0
	Fossil Rim	1191	Female	4	Hand		
Pair 3	Fossil Rim	1385	Male	3	Hand	2-24-95	1.2
	Fossil Rim	1285	Female	4	Dam		

Table 4.2. Age of pups (in weeks) at the beginning of each stage of the introduction

Introduction Stage	Age of Pups (weeks)		
	Pair 1	Pair 2	Pair 3
1. Male given visual, olfactory, and modest tactile contact with pups	9	4-5	4-5
2. Male and female introduced in male's yard (without pups present)	11	9	6
3. Male introduced to pups (female present)	12	11	7

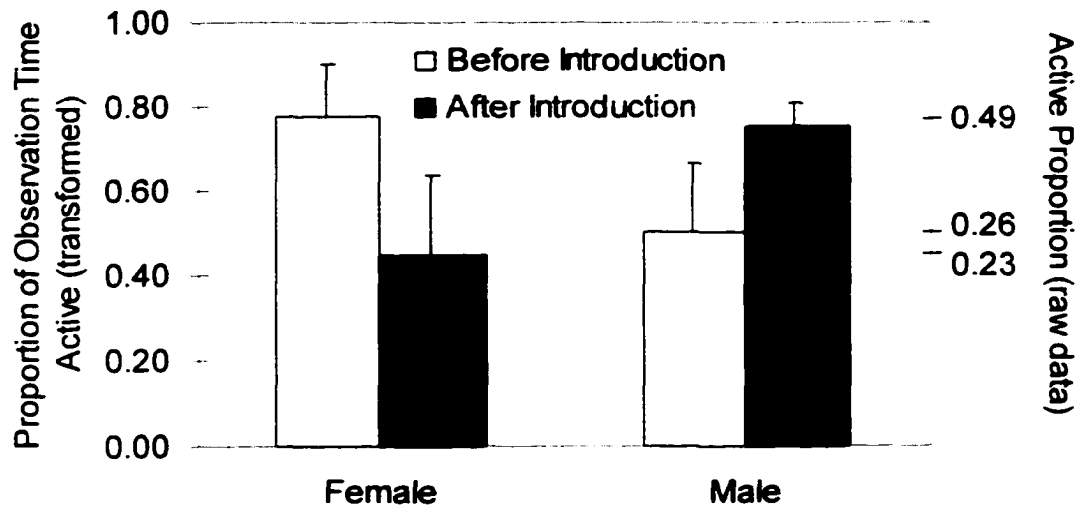


Fig. 4.1. Mean (+ SE) proportion of observation time spent active by three adult female and male maned wolves before and after the males were introduced to the females and pups. Transformed values [$\arcsin(\text{proportion}^{0.5})$] were used for statistical analyses.

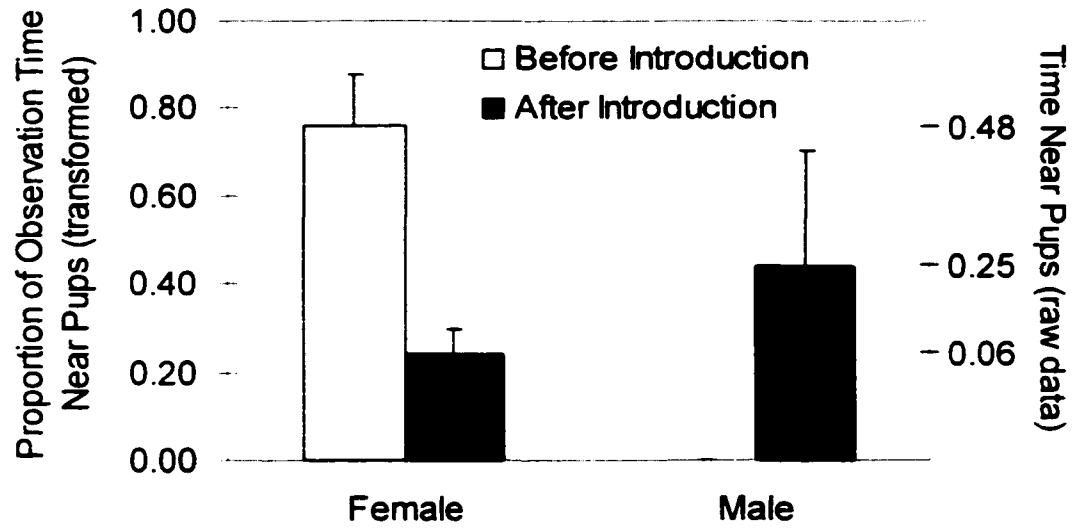


Fig. 4.2. Mean (+ SE) transformed proportion of observation time spent within two body lengths of pups by three adult female and male maned wolves before and after the males were introduced to the females and pups. Transformed values [arcsine (proportion^{0.5})] were used for statistical analyses.

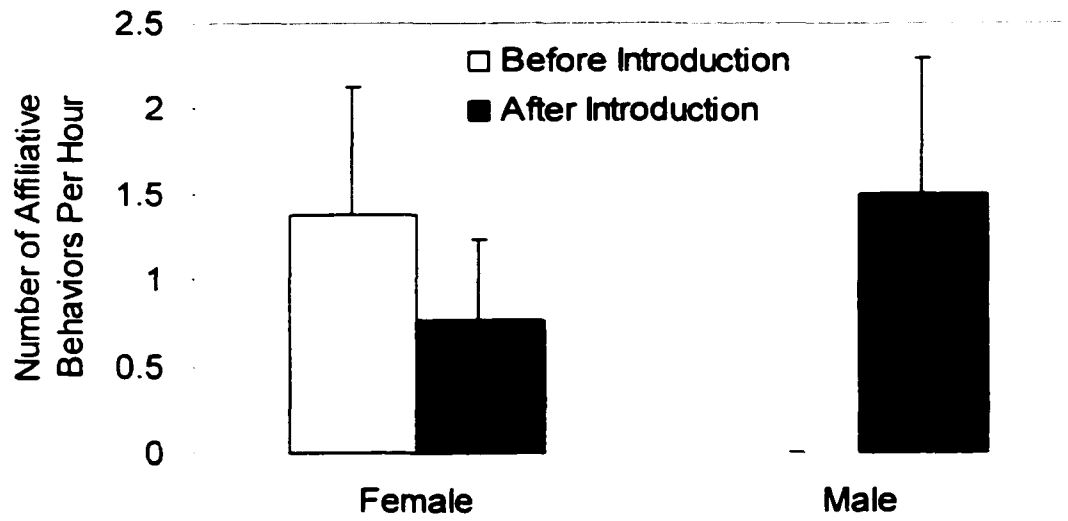


Fig. 4.3. Mean (+ SE) number of affiliative behaviors directed to pups by three adult female and male maned wolves before and after the males were introduced to the females and pups.

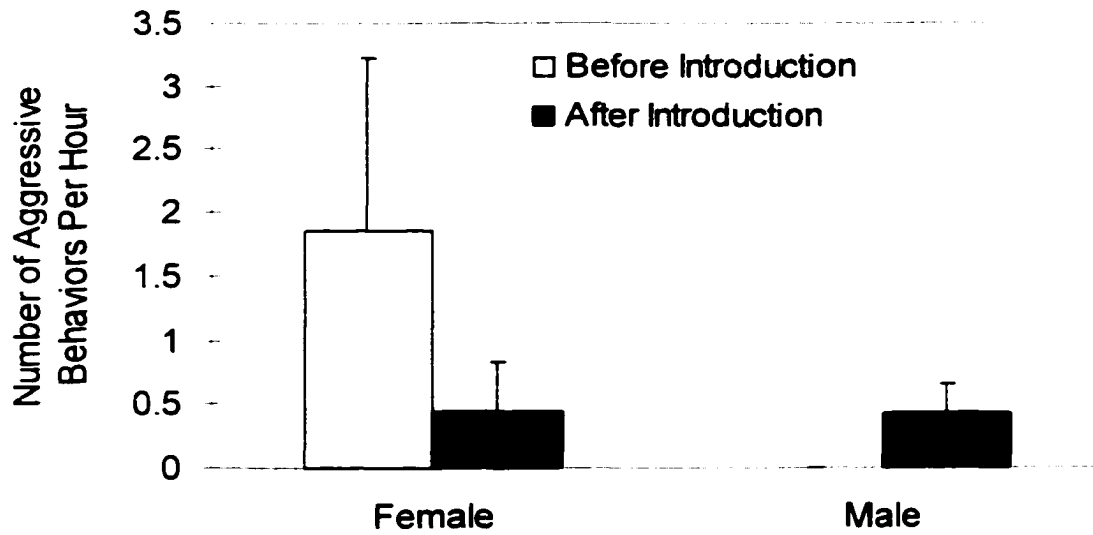


Fig. 4.4. Mean (+ SE) number of aggressive behaviors directed to pups by three adult female and male maned wolves before and after the males were introduced to the females and pups.

CHAPTER V

TIMING AND BEHAVIORAL PATTERNS OF ESTRUS IN MANED WOLVES

(CHRYSOCYON BRACHYURUS)

INTRODUCTION

Most mammals are seasonal breeders (Estep and Dewsbury 1996) that can use a variety of proximate cues to initiate breeding. Ims (1990a) identifies three classes of cues: environmental, social, and internal. Environmental cues are studied most frequently, and reproductive timing has been linked in various mammals to photoperiod (harbor seals: Temte and Temte 1993; Himalayan tahrs: Paré et al. 1996), temperature (Dall's sheep: Rachlow and Bowyer 1991; pallid bats: Lewis 1993), rainfall (African bats: Cumming and Bernard 1997), snowfall (Alaskan caribou: Adams and Dale 1998), food abundance (mink: Ben-David 1997), and plant chemicals (voles: Berger et al. 1981). Social cues, primarily pheromones, affect the timing of breeding in at least a few mammals (humans: McClintock 1984; Stern and McClintock 1998). Finally, internal cues belong to a broad class that can include everything from an individual's physiological state to endogenous rhythms. This class of cues is difficult to study and therefore has been studied

infrequently, so it is unclear how often internal cues are used to initiate breeding (Ims 1990a).

Each class of proximate cues has a different effect on reproductive timing and reproductive synchrony in solitary species. Social cues, like pheromones, are probably not very important to the initiation of breeding in solitary, widely dispersed mammals because they rarely come into contact with other individuals' pheromones. Considerable individual variation in internal factors means that if these factors were responsible for estrous timing, asynchronous reproductive periods may result. Since all females in one region simultaneously experience similar environmental factors, environmental cues could lead to general estrous synchrony, even for solitary species.

The degree of estrous synchrony, and therefore the class of cues triggering estrus, affect mating systems and parental care systems. Estrous synchrony often leads to monogamy since males have few opportunities to find additional receptive females after they have courted and mated with one female (Emlen and Oring 1977; Maynard Smith 1977; but see Kempenaers 1997). When males have little chance for additional mating, paternal care should be favored as well. Knowlton (1979) suggests that synchronous reproduction may evolve as a strategy to encourage male investment in offspring care. On the other hand, if solitary females enter estrus asynchronously, males may encounter multiple receptive mates (Westneat 1987), thus promoting polygyny and lack of paternal care. Ims (1988) developed a model confirming the effects of estrous synchrony on mating systems by showing that the temporal distribution of receptive females may have a larger effect on variation in male mating success than female spatial distribution or the sex ratio. Therefore, we can predict that internal cues that result in asynchronous estrous

periods could lead to polygyny whereas environmental cues that result in general estrous synchrony could lead to monogamy.

Knowing the proximate cues that initiate a breeding period not only allows us to predict mating systems but also allows us to predict when an animal will enter estrus. This ability is important in captive breeding programs for endangered species. If reproduction is desired, animals must be housed together during their generally short receptive periods. Conversely, zoo space is limited (Soulé et al. 1986), so unrestricted reproduction cannot be allowed. Therefore, predicting the estrous period enables managers to place animals that are not recommended for breeding on contraception or separate them during the receptive period (Asa et al. 1996).

Captive breeding programs also provide an ideal setting to study the influence of individual factors that are generally correlated in the wild. For example, food availability and food quality vary with temperature and season, making it difficult to determine which one of these cues triggers breeding. In zoos, animals are generally fed constant amounts of standard quality food throughout the year, so the effects of temperature *per se* can be studied. Furthermore, animals are frequently moved between zoos as part of a breeding program. These moves provide data for testing the effects of latitude and temperature on estrous timing.

This study examines cues triggering estrus in the maned wolf, *Chrysocyon brachyurus*, an endangered species that has been the focus of intense captive breeding efforts in the United States since 1985 (Dietz 1984; Fletchall et al. 1995). In the wild, maned wolves live in solitary pairs with relatively large home ranges (Dietz 1984) and appear to be behaviorally monogamous, although no genetic studies have been done to

confirm that inference. Therefore, determining which cues trigger breeding will contribute to predictions about the mating system.

Like most canids (Asa and Valdespino 1998), maned wolves enter estrus only once each year. In North America, the approximately five day estrous period (Rodden et al. 1996) occurs between late September and early January (Weinhardt and Rodden 1995), but the exact timing is determined only with detailed analyses of hormone profiles or by observing a pair in a copulatory tie. This easily recognized behavior is common to all canids and occurs when the base of the penis becomes so distended during copulation that withdrawal from the female's reproductive tract is temporarily prevented (Beach and LeBoeuf 1967). Unfortunately, maned wolves may not copulate if disturbed or observed closely (Brady and Ditton 1979), so obvious breeding behavior may not be seen. It is therefore important to determine which cues trigger breeding so that estrous dates can be predicted without observing mating behaviors. If internal factors control estrous timing, it will also be helpful to identify behaviors other than copulatory ties that change during estrus. Rodden et al. (1996) show that several behavioral events in maned wolves vary according to estrous stage. I will extend one part of their study by providing the first examination of maned wolf time budgets across the breeding season.

I examined 77 captive maned wolf estrous dates and observed three maned wolf pairs throughout the breeding season in order to accomplish three objectives: (1) investigate the degree of estrous synchrony in captive maned wolves, (2) determine if environmental cues or internal factors are most important in triggering estrus, and (3) determine if there are easily measured behavioral changes in adults that indicate estrus.

METHODS

Estrous Timing

Using the Maned Wolf International Studbook (Matern 1999), I listed all births in North American zoos between the 1984/85 and 1997/98 breeding seasons. During this time, 81 litters were born to 32 dams at 20 zoos and wildlife centers in the United States (Table 5.1) as part of the North American maned wolf captive breeding program, the Maned Wolf Species Survival Plan (MWSSP). I did not analyze two litters that were listed as “possible” in the studbook and one litter with an unconfirmed date of birth. Estrous dates were calculated by subtracting 65 days (the gestation length in maned wolves; Brady and Ditton 1979) from the day of birth.

I also collected data on two variables that may indicate internal control of estrous date (dam identity and dam age) and four potential environmental cues (latitude as an index of photoperiod and temperatures during the month of estrus, one month before estrus, and two months before estrus) defined as follows:

Dam identity: Twenty-two of the thirty-two dams reproduced more than once, so the dam’s identity was entered as a classification variable.

Dam age: The dam’s age at the time of each birth was rounded to the nearest year. This variable was nested within dam identity for all analyses, since 22 dams gave birth more than once.

Latitude: I obtained the latitude of each zoo from Bair (1992), Wood (1998), and the US Census Bureau.

Temperatures during estrus, one month before estrus, and two months before

estrus: Mean monthly temperatures ($[\text{average maximum} + \text{average minimum}] / 2$) for each city, each year were obtained from the National Climatic Data Center. Temperatures were taken from a weather station near each zoo; in most cases these stations were in the same city as the zoo (Table 5.1).

Breeding Behavior

I conducted 340.5 h of continuous, focal animal observations (Altmann 1974) on two pairs of maned wolves housed at the Oklahoma City Zoo during the 1993/94 breeding season and one pair housed at the Denver Zoo during the 1994/95 breeding season (Table 5.2). Observations took place during the pre-estrous, estrous, and post-estrous periods, defined according to Rodden et al. (1996). The estrous period contained the 14 days surrounding an observed copulatory tie. In one pair where no tie was seen (Pair 1), the estrous date was calculated by subtracting 65 days from the litter's date of birth. The pre-estrous period included observations from the start of the breeding season (1 October) until the estrous period, and the post-estrous period included observations from the end of the estrous period until pups were born (Pairs 1 and 2) or until the end of December (Pair 3).

During each observation, I documented the time budget of each animal by recording the proportion of time spent in six behavioral states (Altmann 1974): inactive (lying down, sitting, or not visible while inactive), standing, walking, pacing, eating/drinking, and not visible while active. These behaviors were defined according to the ethogram of Bestelmeyer and Kinsey (1995). I also recorded the proportion of total observation time

that the focal animal was near its mate, defined as being within three body lengths.

Finally, I recorded the rates (number / hour) of 27 behavioral events (Altmann 1974) that were categorized as breeding, affiliative, aggressive, marking, or solitary behaviors (Table 5.3).

Data Analysis

Before analysis, all estrous dates were converted into Julian days. Seasonality in estrous dates was tested using the Rayleigh test for circular data (Batschelet 1981). I used Akaike's Information Criterion values with a correction for small sample size (AIC_c ; SAS 1989; PROC MIXED; Burnham and Anderson 1998) to determine the best of ten *a priori* candidate models explaining estrous dates. These models included: (1) latitude, (2) dam identity, (3) dam age, (4) temperature during estrus, (5) temperature one month before estrus, (6) temperature two months before estrus, (7) latitude and dam identity, (8) latitude and dam age, (9) dam identity and dam age, and (10) latitude, dam identity, and dam age. Models 1-6 were selected as candidates to test if there was a single cue triggering estrus. Models 7-10 were combinations of variables found to be important in other studies of mammalian breeding timing (Bunnell 1982; Adams and Dale 1998). Because temperature is seasonal, residuals from the regression between each temperature variable and estrous dates were used for analyses of the effects of temperature on estrous dates as well as for AIC selection of the best approximating model. The effects of each variable from the best approximating model were tested for effects on estrous dates using hierarchical ANOVA (age nested within dam identity).

To normalize the behavioral data, I transformed the proportions of time spent in each behavioral state with the arcsine square root transformation and checked transformed values for normality. Changes in the adults' time budgets and rates of behavioral events were analyzed using multivariate analysis of variance (MANOVA). If the MANOVA resulted in a significant difference, individual behaviors were analyzed with ANOVA. I also used an ANOVA to examine differences in the proportion of time adults spent near their mates across the three reproductive periods. Tests were considered significant at $P < 0.10$, and all error bars indicate one standard error.

RESULTS

Estrous Dates

Between the 1984/85 and 1997/98 breeding seasons, female maned wolves entered estrus between 4 August and 29 January. Estrous dates did not conform to a uniform distribution throughout the year, but clustered around a mean of 5 November (Fig. 5.1; Rayleigh test; $r = 0.84$; $N = 78$; $P < 0.001$). Over 93% of the variance in estrous dates was explained by the global model that included all independent variables: dam identity, dam age nested within dam identity, latitude, temperature 2 mo before estrus, temperature 1 mo before estrus, and temperature during estrus ($R^2 = 0.936$), thus justifying the use of AIC to select the best model (Burnham and Anderson 1998). However, the best candidate model included only two of these variables: dam identity and dam age, and no other model was strongly supported ($\Delta_i < 2.0$; Table 5.4). Dam identity was the best single

variable explaining estrous dates, performing better than all other single variable models and appearing in all four of the top models (Table 5.4). Within the best approximating model, dam identity had a significant effect on estrous dates (Fig. 5.2; $F_{31,45}=5.15$; $P<0.0001$), indicating that individual dams tended to enter estrus at about the same time each year. Dam age did not have a significant effect on estrous dates within the best model ($F_{45,1}=0.49$; $P>0.25$). However, for just the dams that gave birth more than once, dam age and estrous dates were negatively related ($F_{9,38}=2.19$; $P=0.05$). There was also a negative relationship between dam age and estrous date for the 10 females who gave birth only once (Fig. 5.3; $F_{4,5}=3.83$; $P=0.09$). When a dam's previous estrous dates are unavailable, either because they are unknown or because the dam has never cycled, a model including latitude and the dam's age can still be used. For the females who gave birth only once, dam age and latitude explained 67% of the variation in estrous dates ($F_{2,7}=7.05$; $P=0.02$; $R^2=0.67$). Within this model, the effect of age was significant ($F_{1,7}=13.74$; $P=0.01$), as was the effect of latitude ($F_{1,7}=4.17$; $P=0.08$). Age and latitude were related to estrous dates of one-time dams according to the equation $y = 4.40x_1 - 11.39x_2 + 207.77$, where y is the estrous date in Julian days, x_1 is the latitude in degrees North, and x_2 is the dam's age in years.

Breeding Behavior

I observed Pairs 2 and 3 mating. Pair 2 was never seen in a copulatory tie, but during one observation session the male mounted the female 1.0 time per hour for an average of 6.5 ± 3.5 s.e. sec. The male and female of Pair 3 were not housed together at night, so when they were placed together during the female's estrous period, they exhibited unusually

high rates of breeding behavior. During the hours they were housed together, the male mounted the female an average of 41 times per hour. These mounts averaged 27.5 ± 4.9 s.e. sec. Pair 3 engaged in a copulatory tie which lasted 165 sec.

Females' behaviors did not change across the pre-estrous, estrous, and post-estrous periods (time budget: MANOVA: $F_{10,2}=4.23$; $P=0.21$; time near mate: Fig. 5.4; $F_{2,5}=1.75$; $P=0.27$; $R^2=0.41$; rates of behavioral events: MANOVA: $F_{8,4}=0.93$; $P=0.57$). Males' time budgets were different depending on the breeding period (Fig. 5.5; MANOVA: $F_{10,2}=18.14$; $P=0.05$); however, when individual states were examined, none showed significant changes (inactive: $F_{2,5}=0.20$; $P=0.83$; $R^2=0.07$; standing: $F_{2,5}=0.39$; $P=0.70$; $R^2=0.13$; walking: $F_{2,5}=0.23$; $P=0.81$; $R^2=0.08$; pacing: $F_{2,5}=0.33$; $P=0.73$; $R^2=0.12$; eating/drinking: $F_{2,5}=1.65$; $P=0.29$; $R^2=0.39$). Males and females showed a nonsignificant trend toward more time near their mates during the estrous period (Fig. 5.4; $F_{2,5}=1.96$; $P=0.23$; $R^2=0.44$). Males' rates of behavioral events did not differ across reproductive periods ($F_{8,4}=0.48$; $P=0.83$).

DISCUSSION

Maned wolf estrous dates appeared to be influenced most strongly by internal factors, with dam identity being the best single variable for predicting estrous dates, and dam identity and dam age being the best overall model (Table 5.4). Female age also affects reproductive timing in Alaskan caribou, with younger females giving birth later than older females (Adams and Dale 1998), similar to the effects we saw in maned wolves.

Latitude did not appear in the best model, despite the fact that latitudinal effects would help explain why maned wolf estrus is shifted by nearly six months in the southern hemisphere, where mating occurs between April and June (Silveira 1968). There was a positive relationship between latitude and estrous date in maned wolf dams that reproduced only once, indicating that latitude may play a small role in estrous timing. Studies of the effects of latitude on ungulate reproductive timing demonstrate species-specific results. In mountain sheep, the lambing period starts later at higher latitudes (Bunnell 1982), but there is no effect of latitude on breeding time in captive red deer (Fletcher 1974) or captive Himalayan tahr (Paré et al. 1996).

These results have important implications for the maned wolf's social structure, which is poorly understood. Dietz (1984) found that maned wolves are behaviorally monogamous, but no paternity study of free-ranging maned wolf pups has ever been done to confirm genetic monogamy. Because females' estrous periods apparently are controlled more strongly by internal factors than environmental factors, extreme estrous synchrony in maned wolves is unlikely. Therefore, male maned wolves at least have the potential to mate with multiple females each year. Whether or not males fulfill this potential may depend on other factors, including how widely dispersed females are (Ims 1988).

Most explanations of breeding synchrony in social animals focus on the reduced likelihood of predation on offspring born synchronously. Reduced predation may result from (1) adults cooperatively defending their young, (2) predators becoming confused while hunting in a large group of young (predator confusion), or (3) predators being unable to consume all young (predator swamping; Rutberg 1987; but see Ims 1990b).

However, within solitary or pair-living species that reproduce in isolation, none of these benefits can accrue. Another explanation for breeding synchrony is that it forces males to be monogamous by allowing them little time to mate with more than one female (Knowlton 1979). This mechanism may be particularly effective in species with widely dispersed females (Ims 1988), including the maned wolf (Dietz 1984).

Alternatively, selection may not act on reproductive synchrony, but rather on the timing of reproduction in individuals. For example, animals may time their reproduction using an environmental cue that will ultimately lead to offspring being born at a time in which they have the highest chances of surviving. This may lead to breeding synchrony, but it does not mean that synchrony itself has been selected. Bowyer et al. (1998) demonstrate that moose time their reproduction by using long-term climatic changes, resulting in highly synchronized births, even though synchrony does not affect predation rates. This could be true for the maned wolf due to the slight influence of latitude on estrous timing.

Studying captive animals, in zoos as well as in laboratories, has considerable advantages (Robinson 1990), but caution should be exercised whenever attempting to generalize to free-ranging individuals. My results indicate that free-ranging maned wolves may have the potential to mate with more than one female, but this question requires long-term field studies.

These results can facilitate captive management of the maned wolf. Although most maned wolves in the northern hemisphere enter estrus between October and December, numerous females enter estrus outside this period (Fig. 5.1). These outliers have resulted in unexpected births from pairs not recommended for breeding. Managers could only

obtain a hint at when a female would enter estrus by doing extensive, long-term behavioral observations. The data presented here show that females tend to enter estrus at the same time each year, thereby facilitating a manager's prediction. Even for dams with no previous breeding history, estrous dates may be approximated using the equation presented above.

Although more precise estimations of estrous dates could be made if non-mating behaviors signaled estrus, I detected few behavioral changes, except for a nonsignificant trend toward more time with the mate during estrus. Rodden et al. (1996), using 30 second scans (Altmann 1974), also found an increase in the amount of time spent near the mate during the estrous period. Since these studies have similar findings despite using different methods, this trend may be a robust indication of estrous timing. The amount of time spent near the mate is also an important signal of estrus in other canids (Mech and Knick 1978; Andelt 1985). The significant overall change in the time budget of males is probably of limited value for zoo managers since no individual behavior differed across the breeding season.

Rodden et al. (1998) found an increase in affiliative behaviors during estrus, but I observed no similar increase. The discrepancy between the two studies may be caused by a few differences in the way affiliative behaviors were defined. I included "sniff mate" in the affiliative category whereas Rodden et al. (1996) did not record this behavior. Additionally, the three pairs I studied never exhibited the "tail up" or "wrestle" behaviors recorded by Rodden et al. (1996). Although these methodological differences may explain the disparate results, maned wolves likely show considerable individual variation in affiliative behaviors, making generalization difficult. Affiliative behaviors therefore

may be unreliable estrus predictors in some pairs. If this is true, the value of predicting estrous dates based on non-behavioral measures is magnified.

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TABLE 5.1. Location of all captive maned wolf births in North America between the 1984/85 and 1997/98 breeding seasons.

Zoo / Wildlife Center	Latitude	Weather Station	Number of dams ^a	Number of litters ^b
Baton Rouge Zoo	30.53	Baton Rouge WSO AP	2	9
Center Hill	28.6	Brooksville, FL	1	1
Denver Zoo	39.75	Denver WSFO AP	1	1
Dickerson Park Zoo	37.23	Springfield, MO Reg. AP	1	4
Fossil Rim Wildlife Center	32.24	Glen Rose, TX 2W	2	6
Houston Zoo	29.97	Houston WSCMO AP	1	3
John Ball Zoo	42.88	Grand Rapids, MI WSFO	1	3
Kansas City Zoo	39.32	Kansas City WSMO AP	2	2
Lincoln Park Zoo	41.98	Chicago O'Hare WSO AP	1	2
Little Rock Zoo	34.73	Little Rock CWOS AP	1	3
Los Angeles Zoo	34.05	Los Angeles WSO ARPT	2	2
Louisville Zoo	38.18	Louisville WSFO AP	1	5
NZP Conservation/Research Center	38.92	Washington WSO Dulles	5	9
Oklahoma City Zoo	35.4	Oklahoma City Airport	5	12
Riverbanks Zoo	33.95	Columbia, SC WSFO AP	1	3
San Antonio Zoo	29.53	San Antonio Int. AP	1	5
White Oak Conservation Center	30.65	Fernandina Beach, FL	3	6
Wild Canid Survival/Research Center	38.5	St. Louis WSCMO Airport	1	1
Wildlife World Zoo	33.5	Litchfield Park, AZ	1	3
Woodland Park Zoo	47.45	Seattle Tacoma Airport	1	1

^a Two dams reproduced at two different zoos.

^b Two litters listed as "possible births" in the studbook and one litter whose birth date was unconfirmed at the time of analysis are included in this table, but were not used in analyses.

TABLE 5.2. Maned wolves observed during the breeding season

	Location	Studbook Number ^a	Sex	Age	Date of Birth of Litter	Number of Observation Hours
Pair 1	Oklahoma City	680	Male	6	14 January 1994	71
	Oklahoma City	857	Female	6	14 January 1994	72
Pair 2	Oklahoma City	571	Male	8	23 January 1994	82
	Oklahoma City	1148	Female	4	23 January 1994	82
Pair 3	Denver	1185	Male	4	no litter born	16.5
	Denver	1261	Female	4	no litter born	17

^a Studbook numbers are from Matern (1999).

TABLE 5.3. Ethogram for maned wolf breeding behavior observations. This ethogram is an abbreviated form of the ethogram of Bestelmeyer and Kinsey (1995).

Breeding Behaviors

Attempt Mount: male attempts to mount female, but never exhibit pelvic thrusts

Mount: male mounts female and exhibits pelvic thrusts

Tie: male and female become "stuck;" occurs after the mount and lasts > 60 seconds

Affiliative Behaviors

Groom Mate: lick body of mate

Sniff Mate: investigate another wolf anywhere except the anogenital region

Sniff Anogenital Region: sniff or lick another wolf's anogenital region

Tail Out: tail lifted or held horizontally along line of back

Play Invite: bow on forelegs facing other wolf or use foreleg to paw shoulder of other wolf

Present Anogenital Region: female stands or walks with anogenital region oriented to male's face with base of tail deflected up or to the side

Aggressive Behaviors

Charge: advance quickly toward other wolf, piloerect, with stiff forelegs and ears back

Growl: growl at another wolf

Chase: trot or run after another wolf, usually with ears back

Piloerect Pace: walk with stiff forelegs, head down, hair standing up, ears usually back, often moving parallel to other animal

Submissive Crouch: body in crouch or semi-crouch and oriented sideways to other animal, head rolled sideways while looking at other animal and often whining

Marking Behaviors

Leg Lift: urination with hindleg lifted off the ground

Squat: urination with back legs bent, sometimes one hindleg lifted slightly off the ground

Straddle: stand over and rub genitals on bush, grass, or other object

Face Rub: rub side of face or neck on a surface

Defecate: self-explanatory

Urinate Over: urinate in the same spot another wolf urinated or defecated within 5 min

Taste Urine: lick urine of another wolf, often accompanied by flehmen

Flehmen: teeth chatter; lips sometimes pulled back

Solitary Behaviors

Dig: scratch ground with one or both front paws to make a depression

Self-groom: lick own body

Sniff: investigate object with nose

Bark: short, loud, hoarse vocalization

Cache: bury food in hole or cover food with substrate

Table 5.4. Results of the use of Akaike's Information Criterion to select the best candidate model explaining estrous date. K represents the number of parameters estimated in the model, and AIC_c represents the information criterion from PROC MIXED (SAS 1996) adjusted for small sample size (Burnham and Anderson 1998). Models are ranked according to the difference between the lowest AIC_c and every other model (Δ_i). Models with Δ_i values less than 2.0 have strong support.

Model	K	AIC_c	Δ_i
Dam identity and dam age	4	368.75	0
Dam identity, dam age, latitude	5	412.23	43.48
Dam identity and latitude	4	426.05	57.30
Dam identity	3	439.12	70.37
Dam age and latitude	4	652.55	238.8
Dam age	3	661.82	293.07
Temperature 1 mo before estrus (residuals)	3	678.32	309.57
Temperature during estrus (residuals)	3	693.6	324.85
Temperature 2 mo before estrus (residuals)	3	708.92	340.17
Latitude	3	761.42	392.67

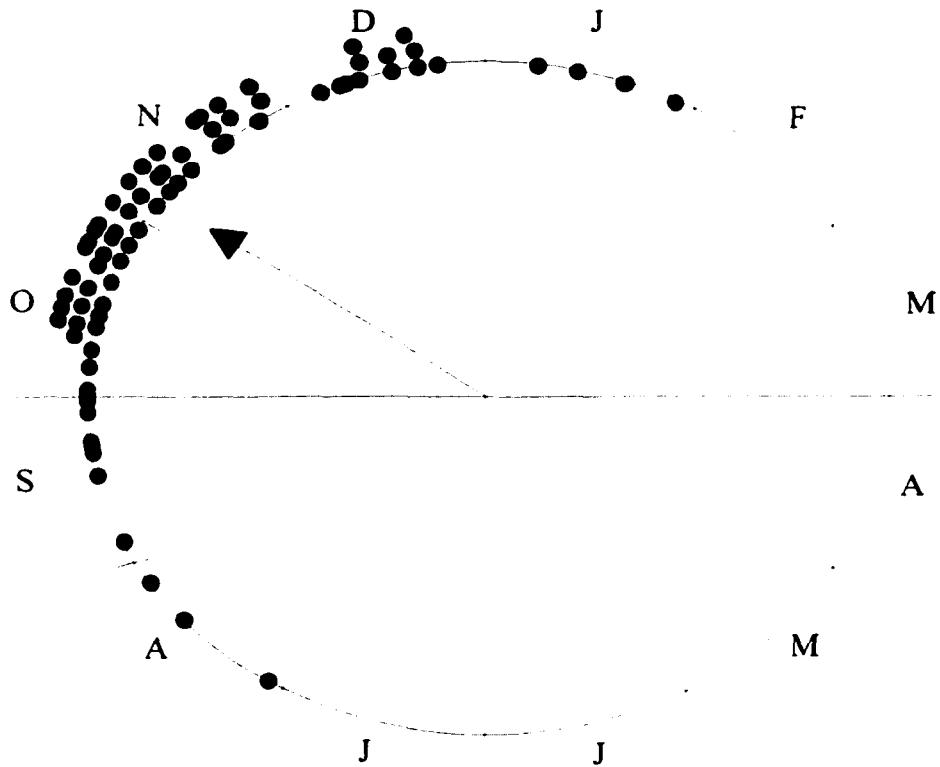


Figure 5.1. Annual distribution of estrous dates in captive maned wolves that gave birth between 1984/85 and 1997/98 in North America. The arrow represents the mean vector. The direction of the mean vector shows the mean estrous date, and the length represents the degree of non-randomness in the distribution of points (Batschelet 1981).

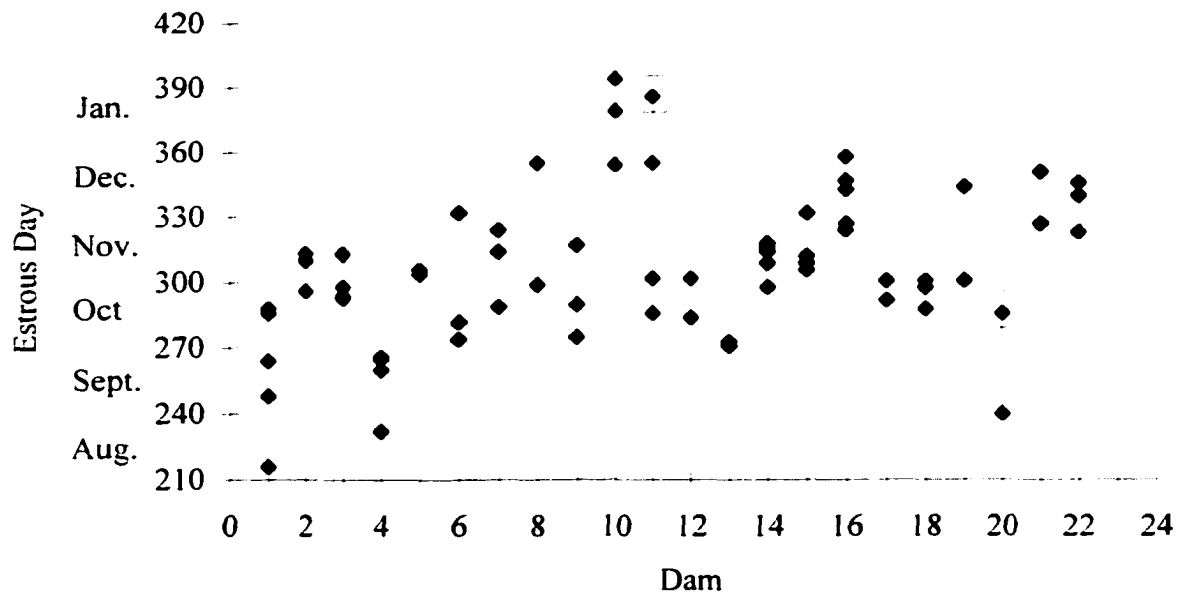


Figure 5.2. Estrous dates in multiple years by 22 captive maned wolf females that gave birth more than once. Female numbers correlate with the latitude (low to high) of the zoos where the dams were housed. Data points with boxes around them are estrous dates for two females that were moved to a zoo at a higher latitude.

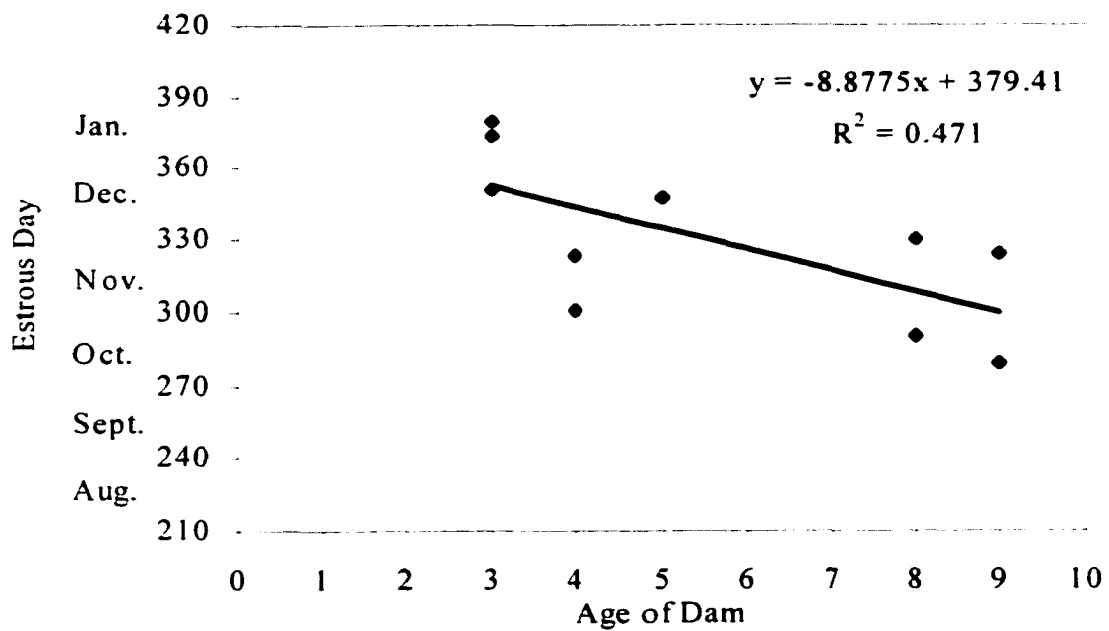


Figure 5.3. Relationship between estrous dates and the dam's age in for captive maned wolf females that gave birth only once. Dam age has a significant effect on estrous day ($F_{9,38}=2.19$; $P=0.05$; $R^2=0.471$).

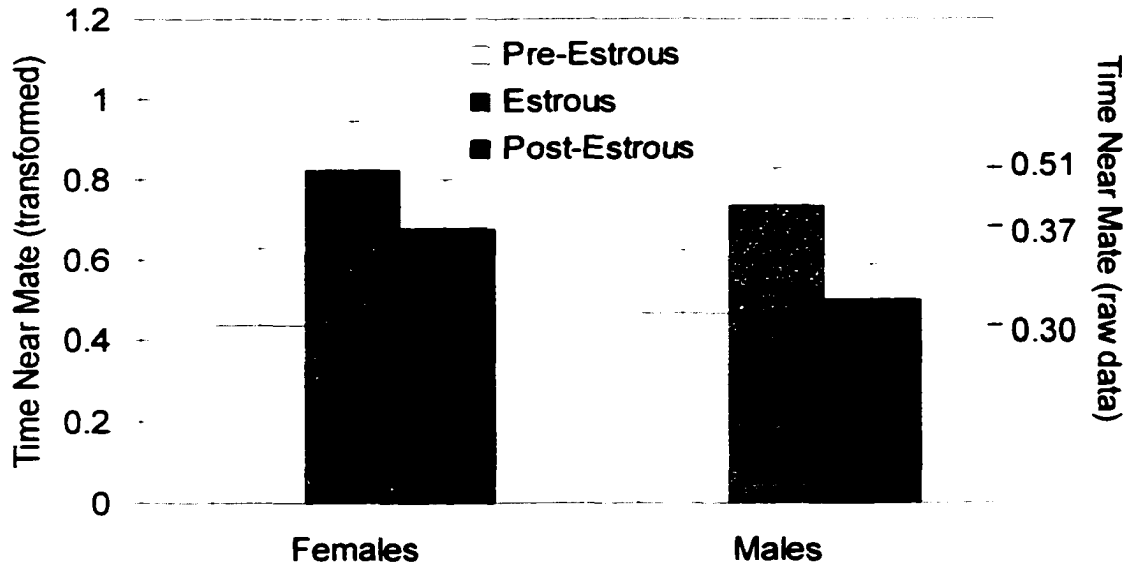


Figure 5.4. Proportion of time (+ standard error) adult maned wolves spent within three body lengths of their mates during the pre-estrous, estrous, and post-estrous reproductive phases. Transformed values [$\arcsin(\text{proportion})^{0.5}$] were used in statistical analyses.

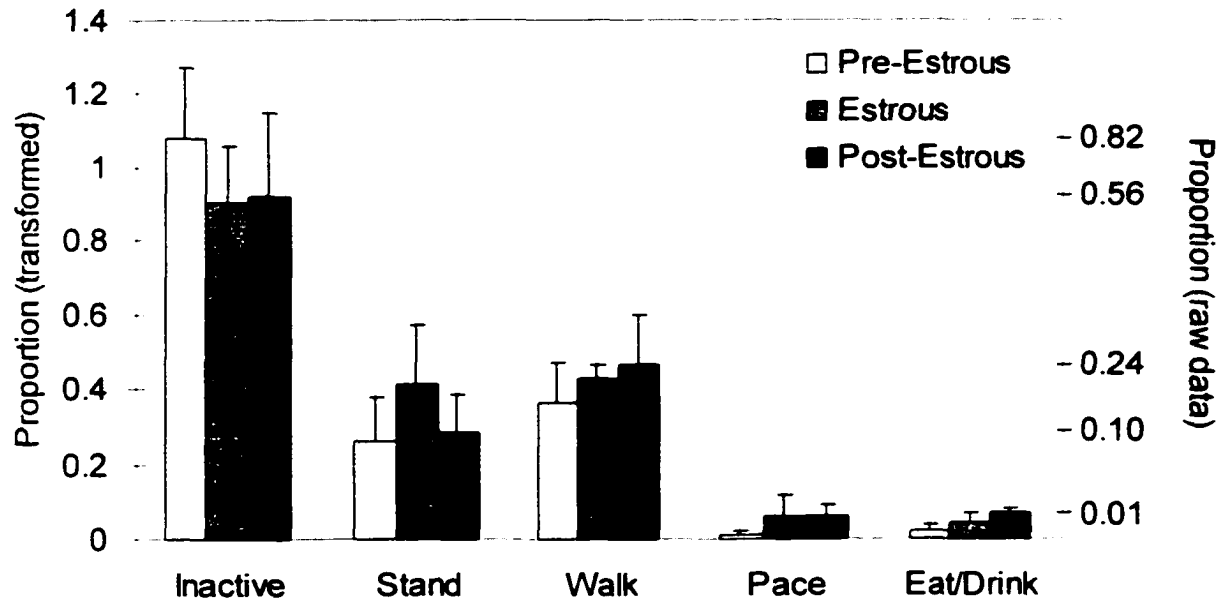


Figure 5.5. Proportion (+ standard error) of time adult male maned wolves spent in five behavioral states during the pre-estrous, estrous, and post-estrous reproductive phases. Transformed values [$\arcsine(\text{proportion})^{0.5}$] were used in statistical analyses.

CHAPTER VI

MANED WOLF (*CHRYSOCYON BRACHYURUS*) BEHAVIOR AND ECOLOGY IN EMAS NATIONAL PARK, BRAZIL

INTRODUCTION

The family Canidae is a diverse group of approximately 35 species that range in size from the 1.5 kg fennec fox of Africa to the more than 30 kg gray wolf of North America and Eurasia. Within the family are species living in a wide range of social groupings, from mated pairs (e.g., San Joaquin kit fox, *Vulpes macrotis mutica*; White and Ralls 1993) to large packs averaging 13.7 individuals (African wild dogs: *Lycaon pictus*; Maddock and Mills 1994). Mean litter sizes range from 2.0 pups (Blanford's fox, *Vulpes cana*) to 10.1 pups (African wild dog; Geffen et al. 1996), and nonparental individuals aid in offspring care in many species (e.g., golden jackal: *Canis aureus*; Moehlman 1979). Some canids are almost entirely carnivorous (e.g., dhole, *Cuon alpinus*; Fox 1984), many are omnivorous (e.g., red fox, *Vulpes vulpes*; Larivière and Pasitschniak-Arts 1996), and others are primarily insectivorous (e.g., hoary fox, *Lycalopex vetulus*; Dalponte 1997).

Much of this impressive diversity in social systems and diet is correlated with body size. Large canids (>13 kg) tend to live in large groups (Bekoff et al. 1981; Creel and Macdonald 1995; Moehlman and Hofer 1997) with monogamous to polyandrous mating systems (Moehlman 1989), large litter sizes (Geffen et al. 1996; Moehlman and Hofer 1997), and nonparental individuals helping with offspring care (Moehlman 1989; Moehlman and Hofer 1997). Large canids also tend to be cooperative hunters (Gittleman 1985; Moehlman 1989), allowing them to hunt large vertebrate prey (Gittleman 1985; Redford and Eisenberg 1992).

Although these general patterns explain the characteristics of the majority of large canids, one species, the maned wolf (*Chrysocyon brachyurus*), is an obvious exception to almost all patterns. Standing 75-90 cm tall at the shoulder (Sheldon 1992) and averaging 23.3 kg (Dietz 1984), the maned wolf is the largest canid in South America and the fourth largest canid worldwide. Based on its size, we expect the maned wolf to live in large groups, have large litters, and have nonparental individuals helping with offspring care. Yet almost all reviews of canid social organization list the maned wolf as an interesting exception to every rule (Bekoff et al. 1984; Moehlman 1986; Moehlman 1989; Creel and Macdonald 1995; Geffen et al. 1996; Moehlman and Hofer 1997). As is the case for many canids (Sheldon 1992), little is known about the maned wolf outside of captivity since only a few field studies have been done (Dietz 1984; Bartmann and Bartmann 1986; Carvalho and Vasconcellos 1995; Silveira et al. 1997). The most thorough field study to date was conducted by Dietz from 1978 to 1980 in Serra da Canastra National Park, Brazil (Dietz 1984). He revealed that maned wolves live in monogamous pairs rather than large groups, and he saw no evidence of alloparenting or cooperative hunting.

Furthermore, Dietz's analysis of 740 maned wolf feces indicates that maned wolves are omnivorous, consuming a variety of fruits as well as small animals. Similar results have been obtained from more recent studies of maned wolf diet (Motta-Junior 1991; Jácomo 1995; Motta-Junior et al. 1996). Although fourth largest in body size, the maned wolf has the second smallest canid litter size (2.62 pups; Chapter II), larger only than the very small Blanford's fox (Geffen et al. 1996).

There are at least two hypotheses for the maned wolf's anomalous natural history. First, several authors suggest that the maned wolf lives in a habitat where food is limited, thereby imposing an energetic constraint on group size, litter size, and hunting strategies (Bekoff et al. 1984; Moehlman 1989; Geffen et al. 1996; Moehlman and Hofer 1997). Alternatively, maned wolves' social organization and diet may vary in response to local resources; examples of intraspecific variation in other canid species are widespread (Bowen 1981; Bekoff et al. 1984; Moehlman 1989). Since Dietz's study is the source of virtually all information about free-ranging maned wolves, characteristics currently attributed to the entire species may only apply to the population in his study site, Serra da Canastra National Park, Brazil. Distinguishing between these two hypotheses for the maned wolf's unusual natural history requires additional field studies.

Additional information on maned wolf natural history also aids in formulating conservation strategies for this endangered species (Thornback and Jenkins 1982). The maned wolf is one of at least 100 mammal species (Redford and Fonseca 1986) living in the cerrado, a xeromorphic vegetation zone in central Brazil that contains a mixture of woodland, scrub, savanna, and grasslands (Eiten 1978). The cerrado vegetation zone has high plant diversity, with at least 774 species of trees and shrubs (Heringer et al. 1977)

and approximately 4000 plant species in the ground layer (Ratter et al. 1997). Over the last 25 years, cerrado has been converted rapidly into agricultural fields of primarily soy, corn, and rice. By 1994, 35% of the total area of cerrado had been converted to such uses (Ratter et al. 1997). Only 1.5% of the cerrado is currently protected within Brazil, making the animals that live in this habitat vulnerable to population declines. Due to these factors, the maned wolf is classified as endangered by the Argentine (DNFS 1983), Brazilian (Dietz 1984), and United States' (USFWS 1989) governments. It is also considered vulnerable by the IUCN (IUCN 1990) and is on Appendix II of CITES (CITES 1984).

Answering questions about the maned wolf's unusual natural history and designing conservation plans for the species require detailed information on behavior. Much of this information can only be obtained by habituating maned wolves and directly observing their behavior. Dietz (1984) was unable to conduct many direct observations of maned wolves due to the study site's extreme topographic relief and the maned wolves' shy temperament. In fact, he only saw five maned wolves without the aid of radiotelemetry during two years (Dietz 1984). Therefore, the direct behavioral observations needed to answer both basic and conservation questions are lacking.

The purpose of my study was to provide the first quantitative description of maned wolf behavior. I collected 57.5 hours of observational data on habituated individuals in Emas National Park, Brazil. Although the number of observation hours is admittedly small, these are the first comprehensive, quantitative observations of free-ranging maned wolves. Through these observations, I sought to provide information on the maned wolf's time budget and rates of solitary, hunting, marking, social, and parental behaviors.

Furthermore, I wanted to search for intraspecific variation in behavior by comparing the diet and habitat use of the maned wolf population in Emas National Park with the population studied by Dietz in Brazil's Serra da Canastra National Park (Fig. 6.1). These observations will provide a preliminary step in understanding the maned wolf's unusual natural history and aid in the development of a sound conservation plan for this endangered species.

STUDY AREA

Emas National Park (Fig. 6.1; 18°16' S and 52°53' W) is a 131,868 hectare park located in the extreme southwest corner of Goiás state, Brazil near the borders with Mato Grosso do Sul and Mato Grosso. Established in 1961, it is the largest protected area of continuous cerrado vegetation in the country (Redford 1985). Elevation within the park ranges from 800-1000 m. At least five, fairly distinct vegetation types exist in the park: (1) open grassland, sometimes with a few low shrubs, (2) scrubland with higher densities of shrubs and some trees, (3) cerradão, characterized by higher densities of tall trees and a fairly open canopy, (4) veredas (grassy marshes), and (5) gallery forests, tropical forest patches found strictly along waterways. Approximately 60% of Emas National Park is the grassland habitat type (Redford 1985), where *Tristachya cciostachya* is the primary grass.

Approximately 1600 mm of precipitation falls in the park each year (Pivello 1992), separated into distinct wet and dry seasons. The wet season occurs from October to April, when an average of 201.4 mm of rain falls per month and the mean temperature is 21.7°

C (Table 6.1; Pivello 1992). During the dry season, from May to September, only 42.4 mm of rain falls per month and the mean temperature is 19.8° C (Table 6.1; Pivello 1992). Rainfall during 1997 was similar to the previous 12 years, with the exception of an unusually wet June (Table 6.1). Winds within the park generally come from the north and northeast.

Emas National Park is inhabited by numerous carnivores in addition to the maned wolf, including the crab-eating fox (*Cerdocyon thous*), hoary fox (*Lycalopex vetulus*), jaguar (*Panthera onca*), puma (*Felis concolor*), pampas cat (*Felis colocolo*), crab-eating raccoon (*Procyon cancrivorus*), hog-nosed skunk (*Conepatus semistriatus*), and grison (*Galictis cuja*). Other large mammals in the park include the giant armadillo (*Priodontes maximus*), giant anteater (*Myrmecophaga tridactyla*), tamandua (*Tamandua tetradactyla*), Brazilian tapir (*Tapirus terrestris*), white lipped peccary (*Tayassu pecari*), pampas deer (*Ozotoceros bezoarticus*), and marsh deer (*Blastocerus dichotomus*). Emas National Park is also home to over 300 species of birds (M. Barroso Ramos Neto, unpubl. data), most notably the rhea (*Rhea americana*) for which the park is named.

Emas National Park receives relatively few visitors each year, primarily due to its distance from major population centers. Nonetheless, human impact on the park's fauna may be serious since the park is now completely surrounded by agricultural fields. Thus, extreme shifts in vegetation, as well as a fence, demarcate the park boundaries.

METHODS

Behavioral Observations

Emas National Park is renowned for the relative ease with which animals are observed, since many individuals seem fairly unwary of humans (Erize 1977). Nonetheless, interpretation of behavioral observations of maned wolves required that the wolves be completely used to human presence to avoid observer effects. Therefore, before observations began, I habituated each maned wolf to being followed by a vehicle. Habituation took varying lengths of time depending on the individual maned wolf; some individuals were calm and relatively unwary of being observed whereas other individuals had to be followed repeatedly at increasingly closer distances before they were accustomed to being observed. Unhabituated individuals were able to trot away from observers easily and therefore make observations impossible. A maned wolf was considered habituated when it did not look at the observers more than once every 5 minutes and did not trot for more than 25% of the observation period. After habituation, behavior did not seem to be affected by the observers' presence; individuals routinely slept, ate, and scent marked while being observed. Furthermore, one female even went to her den site and regurgitated food to her pup while being followed. All observations reported here were collected after the habituation process was complete.

Eight of nine observed individuals were not radiocollared, so they were located by searching over 150 km of dirt roads within the park. This may slightly bias the results towards higher activity. However, this bias is at least partially mitigated because (1) four observation sessions were done on wolves that were resting near the roads when first located and (2) the average observation session was over two hours long (see below),

giving the maned wolves ample opportunity to rest, even if they were active when first seen. After habituated animals were located, they were followed both on and off roads throughout the park.

Between May and November 1997, I observed 3 females, 5 males, and 1 individual of unknown sex. Individuals were recognized based on distinguishing characteristics such as scars, facial markings, and cuts on ear margins. Sexes were determined based on observing the genitalia of a resting individual (n=1) or observing the individuals urinating (n=7); male urine originated from between the hind legs whereas female urine originated from just under the tail. Since males and females both use the leg-lift urination posture, that behavior alone was useless for distinguishing the sexes (Kleiman 1966).

I conducted 57.5 hr of continuous, focal animal observations (Altmann 1974) during 26 observation periods averaging 132.7 min (range 2.13 min to 10.8 hr). Observations occurred during every hour of the day and night. I used an ethogram that contained 12 behavioral states (ongoing behaviors with appreciable durations; Table 6.2; Altmann, 1974). I also recorded the rates of 57 behavioral events (relatively instantaneous behaviors; Table 6.3) that were divided into 5 categories: (1) solitary, (2) hunting, (3) marking, (4) affiliative, and (5) parental. When a maned wolf ate, the food item was classified by taxonomic category in accordance with studies of maned wolf scat samples (Dietz 1984; Jácomo 1995; Motta-Junior et al. 1996).

Vegetation Measurements

At the exact location of 42 maned wolf sightings, I measured the vegetation in a 20 m diameter circle centered on the location where the wolf was first seen. I collected

information on the distance from the nearest road, the width of that road, the number of shrubs greater than 0.5 m high, the average vegetation height, the proportion of each ground cover type (bare ground, grass, shrubs, and herbaceous cover), and the number and average height of termite mounds. Ground cover was estimated by measuring cover along four, 10 m transects originating at the spot of the sighting. The first transect was oriented in a randomly selected direction, and subsequent transects were oriented 90, 180, and 270 degrees from the first. Average vegetation height was determined by averaging heights at the sighting point as well as at 5 m and 10 m from the point along each of the four transects. Vegetation measurements were not made for two of the sightings; one location was in an area that was intentionally burned as a firebreak shortly after the sighting, and another was at the den site (which I studied separately; see below). I conducted the same vegetation measurements on 45 additional points along the roads we routinely searched for maned wolves. I selected these points by first dividing roads into 3.5 km sections. At the midpoint of each section, we randomly chose one side of the road and a random distance from the road (between 0 m and 98 m) and then performed the vegetation measurements at each location. All points were within 98 m of the road because this was the average distance a wolf could be spotted from the road under the worst circumstances (with a spotlight at night).

Data Analysis

Mean proportions and rates of behaviors were calculated for each individual observed during more than one observation session. Using these means, I compared male and female time budgets with multivariate analysis of variance (MANOVA), after arcsine

square root transforming the proportional data to satisfy the assumption of normality. If the MANOVA resulted in a significant difference, individual states were compared with ANOVA. Drinking and running were not included in the analysis since each state comprised less than 0.5% of the overall time budgets. “Out of view-active” was also not included in the MANOVA since this was not technically part of the wolves’ time budgets. Rates of males’ and females’ solitary, hunting, and marking behaviors were analyzed with equal or unequal variance t-tests after testing for the equality of variances. Due to the multiple tests conducted, I used a Bonferroni adjustment (Sokol and Rohlf 1995). Rates of use and success rates for the four hunting strategies were compared with ANOVA. The numbers of marking behaviors on different substrates and on different sides of substrates were compared with chi-square tests. Finally, habitat characteristics where maned wolves were sighted and in random locations were compared with t-tests, after again using a Bonferroni adjustment due to the multiple tests performed.

RESULTS

Activity Cycle and Time Budgets

Maned wolves in Emas National Park were primarily nocturnal. Activity began to increase between 1800 h and 2100 h, and the wolves were primarily active during at least 45% of all observation periods throughout the night (Fig. 6.2). Activity remained low during the day, from 0600 h until 1500 h (Fig. 6.2).

Maned wolves spent $46.9 \pm 9.0\%$ of their time walking, $33.6 \pm 11.7\%$ lying down, $9.1 \pm 2.1\%$ standing, $4.8 \pm 3.0\%$ out of view, $4.4 \pm 2.2\%$ eating, $1.0 \pm 0.5\%$ trotting, $0.1 \pm 0.04\%$ sitting, $0.04 \pm 0.03\%$ drinking, and $0.03 \pm 0.02\%$ running. Males' and females' time budgets differed (Fig. 6.3; Wilks' Lambda=340.1; $df=6,1$; $P=0.04$), but the percentage of time they spent active did not differ ($t_6=-0.29$; $P=0.78$). Only one individual behavioral state differed between males and females, with males standing more than females ($F_{1,6}=4.71$; $P=0.07$). There were no significant differences in any other states (lying down: $F_{1,6}=0.08$; $P=0.78$; sit: $F_{1,6}=3.62$; $P=0.11$; walk: $F_{1,6}=0.00$; $P=0.97$; trot: $F_{1,6}=0.01$; $P=0.94$; eat: $F_{1,6}=1.30$; $P=0.30$).

Solitary Behaviors

Most observations were of solitary maned wolves; only 3.44 hr (6.0%) of the 57.5 observation hours occurred while a wolf was near a conspecific, and only 3 (7.3%) of 41 maned wolf sightings overall were of two individuals together. Maned wolves performed ten solitary behaviors, and nine of these behaviors were performed at rates of less than one per hour (Table 6.3). Males and females did not differ in their rates of all solitary behaviors combined ($t_6=-1.08$; $P=0.32$) or the rate of any individual behavior (Table 6.4).

I heard maned wolves use a roar bark vocalization (described by Brady 1981) on 11 occasions. Vocalization bouts occurred during all major time periods (3 between 0000h and 0600h, 2 between 0600h and 1200 h, 1 between 1200 h and 1800 h, and 5 between 1800h and 0000h) and were heard in June ($n=1$), July ($n=4$), August ($n=1$), September ($n=3$), and October ($n=2$). Each vocalization bout contained 11.4 ± 1.3 barks (range 4-20) at 4.31 ± 0.52 sec intervals (range 2-9.6 sec). Only two bouts were definitely antiphonal,

with two wolves vocalizing back and forth to each other, although it is possible that only the closest wolf was heard in the other nine instances. Two vocalization bouts were especially interesting. In the first instance, a female that had killed a pampas deer barked 14 times while standing over the kill (Bestelmeyer and Westbrook 1998). In the second instance, a female was lying down resting when a bark was heard in the distance. The female stood up, barked four times, and then walked in the direction of the barks. No other wolf was seen after either vocalization bout.

Diet and Hunting Behaviors

Foraging and eating were frequent activities for the maned wolves, with 71% of all observation hours containing at least one foraging bout, hunting attempt, or eating bout. The majority of maned wolves' active time was spent either foraging or eating, so the time of day spent looking for or consuming food mirrored the activity cycle. Eighty-two percent of the observation periods between 1500 h and 0559 h contained at least one foraging or eating bout, compared with 30% of the observation periods between 0600 h and 1459 h.

I observed maned wolves consuming 7 categories of animal food (Table 6.5) and 6 categories of vegetable food (*Solanum lycocarpum* fruit, *Anadenanthera colubrina* fruit, three unidentified fruit types, and grass). The composition of animal prey types in this study differs from analyses of maned wolf scat by Dietz (1984), Jácomo (1995), and Motta-Junior et al. (1996) ($X^2=709$; $df=18$; $P<0.0001$). I observed fewer small mammals and birds being consumed and had a much larger proportion of unidentified prey (Table 6.5). These differences could be caused by the different methods used to study diet

(observations vs. scat analyses). However, the diet in the three scat studies also differed ($X^2=159$; $df=12$; $P<0.0001$), suggesting some variation in maned wolf diet across sites. Differences are not due to seasonal changes in diet because all three scat studies were conducted during the wet and dry seasons (Dietz 1984; Jácomo 1995; Motta-Junior et al. 1996).

Maned wolves foraged opportunistically, feeding on abundant food sources. For example, individuals often walked from one shrub to another when the shrub species was in fruit. Also, beetles were consumed in high numbers during a massive beetle emergence in October. Grass probably passed through the digestive tract rapidly; one female defecated primarily grass 7.87 min after she started eating. She had not eaten in the previous 5 hr of observation. Altmann (1972) and Carvalho and Vasconcellos (1995) also report rapid grass passage times of 7 –20 min in maned wolves.

All fruits except *Solanum lycocarpum* were relatively small, so it was impossible to determine how many individual fruits a wolf was eating in one mouthful. Therefore, the only way to compare vegetable and animal portions of the diet from direct observations is to compare the amount of time spent eating each class of food, although this comparison does not take into account different handling times. In Emas National Park, maned wolves spent 22.22% of their eating time consuming vegetable material and 77.78% eating animal material. Fecal studies have found occurrences of vegetable and animal items in ratios of 51% to 49% (Dietz 1984), 52% to 48% (Jácomo 1995), and 46.7% to 53.3% (Motta-Junior et al. 1996).

The most surprising animal prey was the pampas deer, a species previously thought to be too swift for a solitary maned wolf to hunt. I observed one successful and three

unsuccessful pampas deer hunts; descriptions of these events are provided by Bestelmeyer and Westbrook (1998). Although I never saw maned wolves eating eggs. I found a broken rhea egg with maned wolf tracks within 15 cm.

Maned wolves used 11 behaviors during foraging and hunting (Table 6.3). One of these behaviors, "paw bush," has never been described before, but it occurred when a wolf used his foreleg to strike in a downward motion on a bush to dislodge fruit. The dislodged fruits were then picked off the ground and consumed. Males and females did not differ in their rates of combined foraging and hunting behaviors ($t_6=-1.09$; $P=0.32$) or the rates of any individual behavior (Table 6.4).

Several hunting behaviors were components of four primary strategies used by maned wolves. The first strategy generally started with a stalk and ended with a pounce, foreleg pounce, or foreleg stamp (defined in Table 6.3). The tail out or tail up behavior occasionally accompanied the stalk. This strategy was used most frequently to capture small mammals and reptiles in the grass. The second strategy was a dig, with the wolves digging rapidly with their front legs to capture either armadillos or occasionally small mammals. The third strategy was a midair leap to capture insects or birds mid-flight. Finally, the two wolves that hunted pampas deer used a chase behavior, which consisted of a full-speed run at the fleeing deer. The rate at which the four hunting strategies were used did not differ significantly, probably due to small sample sizes (Fig. 6.4; $F_{3,32}=1.72$; $P=0.18$). Only 21.4% of all hunting attempts by all wolves were successful, and there was no difference in the success rate of the individual strategies (Fig. 6.5; $F_{3,12}=0.01$; $P=0.98$).

Marking Behaviors

Maned wolves exhibited seven marking/elimination behaviors (Table 6.3). The leg lift behavior was the only marking behavior exhibited more than once per hour (Table 6.3). There was no difference in males' and females' rates of total marking behaviors ($t_6=0.7$; $P=0.51$) or their rates of any individual marking behavior (Table 6.4).

Scent marks were deposited on termite mounds, ant mounds, shrubs, trees, grass, roads, and an armadillo carcass (Table 6.6). The distribution of leg lift urination sites was not random ($X^2=3459$; $df=1$; $P<0.001$), with more marks left on termite mounds and fewer left on shrubs relative to their abundances in the 85 vegetation measurement sites (1 termite mound : 56.7 shrubs). Leg lift urination marks were left on all sides of objects, but more marks were left on the north, northeast, and northwest sides combined ($n=68$) than the south, southeast, and southwest sides combined ($n=44$; $X^2=5.14$; $df=1$; $P<0.025$). All maned wolves who used the leg lift behavior lifted both left and right legs to urinate, and there did not appear to be a preferred leg used overall ($X^2=0.086$; $df=1$; $P>0.10$).

One male's marking behavior was very different from all other individuals. This male required the largest number of attempts to habituate, and he was observed for a total of 2.25 hr after habituation. During these 2.25 hr, he was always active, but he did not perform any marking behaviors. This contrasts with all other male maned wolves, who performed between 4.0 and 11.9 marking behaviors per hour, even though some of the observation time on these males was when they were inactive. This male was located in an area occupied by another male and female maned wolf.

The one female with an active den site (see below) did not use any scent marking behaviors during the 4.60 hr that she was within 500 m of her den site. Overall, this female used marking behaviors an average of 5.7 times per hour.

Den Site Characteristics and Parental Behaviors

I located one active den site, in the grassland habitat approximately 1.5 km from the nearest road. The den was in a 16 cm depression under a 133 cm tall shrub that had 94 cm of space between the bottom of the canopy and the ground. Three other shrubs, ranging from 142.5 to 282 cm in height, were within 2 m of the den. Within a 30 m diameter circle around this spot, there were 115 shrubs (11 of them were *Solanum lycocarpum* shrubs) and two trees. The ground cover was 16.1% bare ground, 71% grass, 11.6% shrubs, and 1.3% herbaceous plants. Visibility was high in this area due to a relatively low average vegetation height of 28.3 cm. There were numerous trails, bed sites (identified by compressed grass), and tunnels under tall grass throughout the area around the den. One pup resting site was a 69 cm tall termite mound with a hole at the base on one side. The hole had a maximum height, depth, and width of 35 cm, 37 cm, and 25.5 cm, respectively.

All my information on parental behavior in the field comes from this one habituated female. I first saw the obviously pregnant female on 30 June 1997 and estimated, based on the distension of her sides, that she would give birth in approximately 2 days. Unfortunately, extensive searches in the area where she was seen on 30 June did not reveal her den site. It was not until 23 August that I saw the female again, and she eventually went to her den, where an approximately seven-week-old pup was waiting.

Comparisons of the female's distended sides on 30 June with the size of captive females before birth suggest that the female in Emas National Park gave birth to at least 2 pups. There was no evidence of multiple den sites, so it remains unclear what happened to the remaining pup(s) between birth and seven weeks.

Between 23 August and 12 October, I conducted 29.8 hr of observations on the female. She spent only 15.7% of this time within 500 m of the pup. During the day, she would frequently go over 2 km from the den to the vereda near the stream and sleep while the pup remained at the den. At night, she made at least several hunting forays away from the pup for periods up to at least 8.24 hr. When the female was near the pup, she performed four different parental behaviors. Upon returning to the den after being away for at least 8 hr, the female regurgitated pampas deer meat to the pup once and allowed the pup to nurse once for 12 seconds. During all her time with the pup, the female sniffed the pup 0.85 times per hour. She also performed 0.85 gape behaviors to the pup per hour.

On 2 September 1997, the approximately 8-week-old pup returned to the den with the female, presumably after a night spent hunting. My last sighting of the female and pup occurred when the pup was approximately 14 weeks old (9 October 1997). At that time, it was over 1 km from the den site with the dam, confirming that dispersal must occur after this age. During a 2.56 hr observation of the female 3 days later (12 October 1997), the pup was not observed.

I observed an adult male maned wolf that may have been the sire of the pup on two occasions for a total of 9.11 hr. This male was observed within 1.2 km of the den site, but he did not go to the den site or interact with the pup while being observed.

Social Behavior

Two adult maned wolves were seen together once. When I located this adult male and female on 14 August 1997, they were lying down approximately 5 m from each other at 1806 h. They rested near each other for 0.90 hr. When they stood up, they interacted with each other for 0.38 hr before separating from each other by walking in different directions. During the interaction, the male sniffed the female twice and groomed her once. The female groomed the male four times. The male performed a play invite behavior (Table 6.3) to the female, and he licked and face rubbed a termite mound right after the female urinated on it.

Habitat Use

Maned wolves tended to use areas that had a higher percentage of bare ground and a lower percentage of shrub cover than randomly selected areas (Table 6.7). They were also seen first near wider roads in the park. There were no other significant differences between the locations where maned wolves were sighted and randomly selected areas (Table 6.7).

DISCUSSION

Using direct behavioral observations to study a species' natural history has numerous benefits over indirect studies using scat analysis and radio telemetry. The first benefit of

direct observations is that they allow for the collection of information that cannot be gathered through indirect methods. For example, although previous scat studies of maned wolves have shown what maned wolves eat (Deitz 1984; Jácomo 1995; Motta-Junior et al. 1996), my study provided the first description of maned wolf hunting strategies, hunting success rate, and time of day when hunting occurs. In addition, scat studies may give a biased representation of an animal's diet (Mersmann et al. 1992) and should therefore be compared with direct observations of hunting animals. Furthermore, my direct observations confirmed that maned wolves kill pampas deer rather than simply scavenging deer carcasses killed by other predators. This information is crucial to disproving many assumptions previously used to explain why maned wolves do not live in large groups (see below). A second advantage of direct observations is that they allowed me to make precise determinations of maned wolf habitat use. Radio telemetry can estimate an animal's location, but this estimation may be associated with large error, especially in complex habitats (White and Garrott 1986). Finally, many behaviors cannot be studied based on indirect methods alone. Even with the development of activity monitors and tip switches on radio collars (Gillingham and Bunnell 1985), studying detailed solitary, hunting, marking, and social behavior can only be done directly. For example, the data I collected on maned wolf urine marking is the first of its kind since it is often difficult to tell where an individual marked without observing it directly.

Direct methods also have disadvantages. The primary drawback is the time necessary for direct observations. For example, each hour of observation time required an average of 30 hr of work in the field habituating and then searching for wolves. The high effort to yield ratio was a consequence of my inability to trap and radio collar maned wolves

because they were trap-shy. However, even using radio telemetry to locate animals for observations requires that the animal first be captured and marked, extremely time-intensive activities. Other drawbacks of direct observations are the close proximity required of the observer and the difficulty of recording many rapid behaviors. For example, many small prey items could not be identified because they were consumed too quickly (Table 6.5), and this high number of unidentified prey probably resulted in the significant dietary differences between this study and previous diet studies. Silveira et al. (1997) also had difficulty identifying maned wolf prey in their six observation sessions. An analysis of scat contents would be more suitable for making prey identifications.

Canids' adaptability, both within and among species, allows these species to live in a wide range of habitats under highly variable conditions (Kleiman 1967). However, this adaptability also means that documenting the "typical" behavior of a canid species requires extensive studies in several locations. My work, compared with previous studies, suggests that intraspecific variation in activity, social organization, and diet may not be as widespread in maned wolves as it is in many other canids. Maned wolves in Serra da Canastra National Park (Dietz 1984) and maned wolves in Emas National Park are primarily nocturnal and solitary, with marking behaviors playing an important role in their interactions with other individuals. Furthermore, individuals in both populations consumed large quantities of small animal prey and fruit.

Three behavioral differences between the two maned wolf populations are either based on rare occurrences or can be attributed to significant study site differences. First, Dietz (1984) did not detect pampas deer remains in any maned wolf scats, but I confirmed that solitary maned wolves can successfully hunt pampas deer (Bestelmeyer and Westbrook

1998). Shortly before Dietz initiated his study, an anthrax outbreak spread by cattle decimated the local pampas deer population (Dietz, pers. comm.). Therefore, the lack of pampas deer remains may simply reflect a temporary disappearance of this prey, rather than a major difference in diet between the two populations. A second difference is that Dietz (1984) never detected two maned wolves resting together, but I did. However, the low occurrence of pair sightings in my study indicates that such interactions may be rare. Third, I never observed maned wolves enter the gallery forest habitat type, whereas Dietz noted that resting maned wolves used this habitat. This difference might reflect a difference in the percentage of available gallery forest; in Serra da Canastra National Park, gallery forest comprises 15% of the land (Dietz 1984) whereas gallery forest represents less than 10% of the land in Emas National Park.

Most large canids live in groups (Creel and Macdonald 1995; Moehlman and Hofer 1997), but the behavioral measures presented here support the hypothesis that the maned wolf primarily is solitary or pair-living and forages alone. Before this study, many authors attributed the maned wolf's unusual social organization to a lack of large prey in their habitat (Moehlman and Hofer 1997) or generally low food availability (Bekoff et al. 1984; Geffen et al. 1996). Scarce food resources eliminate the possibility for large groups, cooperative hunting, and large litter sizes because no more than one or two adults can be supported in an area (Macdonald 1983). My study and other evidence do not support this hypothesis. First, large prey, such as the pampas deer, are both available in the cerrado (Dietz 1985; Redford 1987; Jackson 1987) and consumed by maned wolves. Second, the cerrado may support a higher abundance of small mammals than previously believed. Mares and Ernest (1995) found high densities of small mammals in gallery

forests, and Redford and Fonseca (1986) suggest that many large and small cerrado mammals use the gallery forests at least as temporary refuges. Dietz (1983) showed that mammal densities in Serra da Canastra National Park may not be as limited as generally believed, especially during the dry season. Furthermore, maned wolves' hunting success rate of 21.4% (this study) to 28% (Silveira et al. 1997) is remarkably similar to the 22.2% and 25% success rates of solitary wild dogs and golden jackals, respectively (Packer and Rutten 1988). Both of the latter species typically live in groups (Maddock and Mills 1994; Moehlman 1979). If hunting success is an index of prey availability, similar hunting success rates in species with different social organizations shows that cooperative hunting is not sufficient to explain why some species form groups whereas others do not. Other authors have also suggested that the benefits of cooperative hunting alone cannot explain the formation of social groups in carnivores (Packer and Caro 1997; but see Creel 1997). Finally, the maned wolf is an opportunistic omnivore, confirmed by its exploitation of temporarily abundant food sources like some insects and fruit. This ability to match food choice with food availability makes it less likely that maned wolves would be limited by food resources alone. So although additional studies are needed to estimate the biomass and energy content of maned wolf diet items (e.g., Motta-Junior et al. 1996), current information does not support the hypothesis that maned wolf social organization is limited by low prey availability.

The maned wolf's solitary social system and foraging strategies may be reflections of the ancestral condition, with a lack of strong selection pressure for larger groups. Although social groups are the norm for large canids, they are rare in carnivores overall because 85-90% of carnivore species are solitary outside of the breeding season (Creel

and Macdonald 1995). This suggests that solitary animals, or perhaps pairs (Kleiman and Eisenberg 1973), are ancestral in carnivores, including canids. Therefore, larger groups in some species must have been selected due to one or more benefits accrued by living in a group. Potential benefits for carnivores include increased food through cooperative hunting, better defense of carcasses against scavengers, and less risk of interspecific predation (Creel and Macdonald 1995). None of these benefits seem likely for maned wolves. For instance, solitary maned wolves can capture the large ungulate prey in the cerrado, the pampas deer. Therefore the advantages of hunting solitarily for small prey items (Moehlman 1986) in combination with the ability to hunt large prey alone would not favor cooperative hunting. Maned wolves also possess two behavioral characteristics that reduce the likelihood of their prey being stolen by scavengers. First, they have large stomachs, allowing them to eat large portions at a time (Bestelmeyer and Westbrook 1998). Second, maned wolves hide food by caching it, as do many smaller canids (Kleiman 1972; Macdonald 1976), thus reducing the likelihood of scavenging. Furthermore, the density of scavengers is probably much lower in the cerrado than in the grasslands of Africa where many social carnivores live (e.g., Fanshawe and Fitzgibbon 1993). Finally, maned wolf adults have few, if any, natural predators in the cerrado, so forming groups to avoid interspecific predation seems unlikely.

This study revealed numerous behaviors facilitating the maned wolf's solitary or pair-living organization. Long-range vocalizations allow individuals to communicate with their mates and neighboring individuals, as suggested by Kleiman (1967; 1972). Observations of captive maned wolves show that the mate frequently appears after one maned wolf barks (Bestelmeyer, pers. obs.). Another adaptation for territorial living is the

presence of frequent marking with urine and feces. Maned wolf urine and feces are left in prominent locations, most frequently on the upwind side of termite mounds. This directional quality of marking on conspicuous objects fulfills Kleiman's (1966) definition of scent marking and suggests territoriality. The behavior of the young male maned wolf that did not scent mark during over two hours of observation may indicate that this was a non-territorial (floater) male. Rothman and Mech (1979) showed that lone gray wolves also rarely scent mark. Dietz (1984) detected three maned wolves traveling on the periphery of pairs' home ranges and hypothesized that non-territorial individuals' presence may explain why vacancies left by an individual's death or emigration are quickly filled. These individuals without territories also suggest that vacant, suitable habitat is not available.

Information on the maned wolf's mating system and parental care system is limited, but my data support the contention that maned wolves are monogamous and may exhibit paternal care. Monogamy and paternal care are rare in mammals (Kleiman 1977; Kleiman and Malcolm 1981) but are relatively common in carnivores and are probably old characteristics of this group (Kleiman and Eisenberg 1973). Species with monogamous mating systems and paternal care tend to display little sexual dimorphism (Ralls 1977). The inference of monogamy in maned wolves is supported by the lack of behavioral differences between males and females, even in scent marking (Table 6.4). Furthermore, there is little difference in size or coloration of male and female maned wolves (Fletcher 1995). Monogamy is often associated with paternal care in mammals (Clutton-Brock 1991), but paternal care in wild maned wolves has not yet been confirmed. Due to the small number of observation hours of the pup's probable sire,

paternal care cannot be ruled out by this study. The male could have been at the den while I followed the female during her often long periods of time away from the den. Furthermore, Dietz's (1984) study suggests some paternal care since residents there reported seeing two maned wolf litters accompanied by two adults. Extensive field studies of parental behavior will be the only way to confirm whether or not the male participates in offspring care.

Data on the maned wolf's behavior and habitat use may help develop conservation strategies for the species. Current efforts are hampered by a lack of data and limited, dated estimates of the maned wolf's population size (Thornback and Jenkins 1982; Medel and Jaksic 1988). Schaller and Tarak (1976) estimated that 1000-1500 individuals live in Argentina, and Beccaceci (1992) estimated a similar number in Argentina 16 years later, with a maximum of 300 individuals in Corrientes province (Beccaceci 1993). Estimates from Brazil range from 1500-2000 in 650,000 km² (Silveira 1968), and estimates from Paraguay and Uruguay do not exist. More precise and current estimates are necessary to understand the severity of the maned wolf's situation.

Nonetheless, several aspects of the maned wolf's behavior may facilitate conservation efforts. First, maned wolves are primarily nocturnal, thereby limiting their interactions with humans. This may explain why inhabitants of farms and ranches around Emas National Park did not express any negative feelings about the species. Nevertheless, education efforts should continue to ensure that the maned wolf remains appreciated by local populations rather than attaining pest status for occasional raids on chicken coops (Dietz 1984). The largest threat to the maned wolf's continued existence will remain loss of cerrado habitat through conversion to agriculture. Maned wolves' omnivorous diet and

preference for traveling in areas with bare ground and low shrub densities, however, may mean that they can hunt even in agricultural fields. Beccaceci (1992) notes the use of pine plantations by maned wolves hunting cuis (*Cavia aperea*). Still, native cerrado will likely remain an important retreat for maned wolves. The Brazilian government requires that 20% of a piece of private land be preserved in native cerrado (Ratter et al. 1997). Although this policy is not strictly enforced, it is a good first step in preserving the maned wolf as well as other cerrado species.

The most important information now required for drafting conservation plans is an assessment of maned wolf use of agricultural land and the amount of native cerrado needed to preserve a healthy population. Such an evaluation should include the threat of natural and human-caused fires, which are common in the cerrado (Hutchins and Schischakin 1994; Pivello and Norton 1996; Mistry 1998). Being hit by vehicles may also be a significant source of mortality for maned wolves, especially since this study found that maned wolves prefer to travel on wide roads (Table 6.7). I saw two adult maned wolves killed on roads neighboring the park, and road kills have been reported by Beccaceci (1992). This threat will probably increase as more paved roads are built throughout central Brazil.

In summary, this study provides important behavioral information that may be used to conserve the maned wolf. The focus of future research and conservation efforts should be (1) to gather reliable, current population estimates, (2) to continue environmental education programs about the maned wolf and its role in the cerrado, and (3) to learn about the maned wolf's ability to use agricultural land and its need for native cerrado.

The combination of these three efforts will best allow us to preserve this fascinating species.

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Table 6.1. Monthly mean temperature and rainfall in Emas National Park. Rainfall values between 1985 and 1996 are from Pivello (1992). January – September 1997 values are means from 35 rainfall gauges throughout the park (M. Barroso Ramos Neto, unpubl. data).

Month	Temperature (° C)	Rainfall (1985-1996)	Rainfall (1997)
January	22.2	248	276
February	21.5	208	186
March	22.7	229	163
April	21.1	111	135
May	19.9	62	82
June	17.6	35	195
July	19	9	4.9
August	20.8	26	11.4
September	21.7	80	109
October	21.8	164	-
November	21	213	-
December	22	237	-

Table 6.2. Behavioral states exhibited by maned wolves in Emas National Park, Brazil.

Behavioral State	Definition
Lying Down	Mid-section of body in contact with the ground
Sit	Back part of body in contact with the ground; usually occurs while animal is scratching
Stand	Stationary upright position
Walk	Locomotion without in-air phase
Trot	Locomotion with in-air phase where hindlegs do not extend forward past the midline of the body
Run	Locomotion with in-air phase where hindlegs extend forward past the midline of the body
Eat	Consume solid food
Drink	Consume water or another liquid
Out of View	Not in view of observer; always when active

Table 6.3. Descriptions and rates (\pm SE) of behavioral events exhibited by maned wolves in Emas National Park, Brazil. Astericks indicate behaviors exhibited by only 1 or 2 maned wolves; therefore, rates are not given. See text for details on these behaviors.

Behavior	Definition	Rate (#/hr)
SOLITARY		
Self-Groom	Lick own body	0.31 \pm 0.16
Sniff	Investigate object with nose; nose <10 cm from object	5.51 \pm 1.84
Bark	Short, loud, hoarse vocalization	0.12 \pm 0.12
Scratch	Scratch own body with hindleg, often while sitting	0.77 \pm 0.35
Sneeze	Self-explanatory	0.38 \pm 0.37
Yawn	Self-explanatory	0.15 \pm 0.06
Body Shake	Rapid side-to-side movement of body; often occurs after standing up	0.70 \pm 0.35
Head Shake	Rapid side-to-side movement of head	0.18 \pm 0.09
Stretch	Place forelegs in front of body and shift weight slowly from primarily on hindlegs to full standing position	0.30 \pm 0.17
Lick	Touch tongue to object	0.05 \pm 0.05
HUNTING		
Dig	Scratch ground with foreleg(s) to make a depression	1.0 \pm 0.65
Cache	Bury food in hole or cover food with substrate	0.10 \pm 0.08
Stalk	Ears erect and forward, body tense and either standing or moving slowly with attention focused forward	1.25 \pm 0.6
Pounce	Jump forward, lifting all legs off of the ground	1.23 \pm 0.55
Foreleg Pounce	Jump forward, with only forelegs lifted from ground	0.08 \pm 0.05
Leap	Jump nearly straight up with all legs off of the ground	0.08 \pm 0.04
Foreleg Stamp	Rapidly hit one foreleg onto the ground	0.14 \pm 0.08
Tail Out	Tail lifted or held horizontally along line of back	0.53 \pm 0.29
Tail Up	Tail raised above the level of the back	0.11 \pm 0.07
Paw Bush	Raise foreleg and strike bush in downward motion	0.01 \pm 0.01
Chase	Run in pursuit of prey	0.16 \pm 0.15
MARKING		
Leg Lift	Urination with hindleg lifted off ground	5.07 \pm 1.77
Squat	Urination with back legs bent; sometimes one hindleg is lifted slightly off ground	0.67 \pm 0.37
Defecate	Self-explanatory	0.12 \pm 0.05
Straddle	Stand over and rub genital region on bush, grass, or other object	0.18 \pm 0.10
Face Rub	Rub face or neck on a surface	0.15 \pm 0.08
Body Rub	Rub side of body on a surface	0.11 \pm 0.06
Taste Urine	Lick urine of another wolf; often accompanied by flehmen	0.07 \pm 0.07
AFFILIATIVE		
Sniff conspecific	Investigate another wolf with nose	*
Groom conspecific	Lick body of another wolf	*
Play invite	Stamp or bow on forelegs with ears up, facing other animal, or use foreleg to paw at shoulder of another animal	*
PARENTAL		
Regurgitate	Disgorge partly digested food to mate or pups	*
Nurse	Suckle; female may be lying down or standing	*
Sniff pup	Investigate pup with nose	*
Gape	Open mouth, ears back, teeth bared; often occurs during weaning	*

Table 6.4 Comparison of female (N=3) and male (N=5) rates (#/hr) of solitary, hunting, and marking behaviors in Emas National Park.

Behavior	Female Rate	Male Rate	t	df	P
SOLITARY					
Self-Groom	0.04±0.04	0.52±0.26	-1.89	4.13	0.13
Sniff	3.27±3.27	7.94±2.28	-1.21	6	0.27
Bark	0.35±0.35	0±0	1.00	2	0.42
Scratch	1.23±1.09	0.64±0.13	0.54	2.06	0.64
Sneeze	0.02±0.02	0.67±0.67	-0.95	4.02	0.40
Yawn	0.08±0.08	0.23±0.10	-1.17	6	0.29
Body Shake	1.31±1.06	0.47±0.07	0.79	2.02	0.51
Head Shake	0.19±0.19	0.21±0.14	-0.08	6	0.94
Stretch	0.41±0.31	0.29±0.26	0.29	6	0.78
Lick	0±0	0.08±0.08	-1.0	4	0.37
HUNTING					
Dig	0.23±0.23	1.66±1.12	1.21	4.33	0.29
Cache	0.23±0.23	0.04±0.04	0.82	2.12	0.50
Stalk	0.55±0.55	1.93±0.98	-1.0	6	0.36
Pounce	0.67±0.67	1.82±0.87	-0.89	6	0.41
Foreleg Pounce	0.03±0.03	0.12±0.08	-0.79	6	0.46
Leap	0.12±0.12	0.07±0.04	0.66	6	0.53
Foreleg Stamp	0.21±0.21	0.12±0.08	0.44	6	0.67
Tail Out	0.10±0.10	0.89±0.47	-1.25	6	0.26
Tail Up	0.02±0.02	0.18±0.13	-0.83	6	0.44
Paw Bush	0±0	0.02±0.02	-1.0	4	0.38
Chase	0.02±0.02	0.27±0.27	-0.86	4.13	0.43
MARKING					
Leg Lift	6.87±5.17	3.86±1.56	0.70	6	0.51
Squat	1.30±1.06	0.40±0.26	1.06	6	0.33
Defecate	0.10±0.10	0.14±0.07	-0.32	6	0.76
Straddle	0.30±0.30	0.14±0.09	0.65	6	0.54
Face Rub	0.03±0.03	0.24±0.14	-1.13	6	0.30
Body Rub	0.10±0.10	0.14±0.14	-0.29	6	0.78
Taste Urine	0±0	0.14±0.14	-1.0	4	0.37

Table 6.5. Proportion of occurrence of categories of animal food items in the diet of maned wolves in Emas National Park. Proportions are based only on the animal prey. The results of this study based on focal observations is compared with diet studies based on fecal samples by Jácomo (1996) in Emas National Park in 1994, Dietz (1984), and Motta-Junior et al. (1996).

Diet Category	Focal Observations	Fecal Samples		
	This Study	Jácomo	Dietz	Motta Jr. et al.
Small mammals	0.304	0.489	0.526	0.414
Birds	0.065	0.292	0.231	0.259
Insects	0.130	0.037	0.115	0.037
Armadillos	0.065	0.080	0.063	0.173
Amphibians, reptiles	0.022	0.080	0.006	0.049
Deer	0.022	0.002	0	0.012
Unidentified animal	0.391	0	0.007	0

Table 6.6. Locations where scent marks were deposited by habituated maned wolves during observations in Emas National Park. In 85 sites where extensive vegetation measurements were done, termite mounds and shrubs were found in a ratio of 1 : 56.7.

Location	Leg Lift	Squat	Straddle	Defecate	Body Rub	Face Rub
Termite mound	102	1	0	1	0	0
Shrub	65	1	12	0	4	0
Grass	34	13	2	2	0	1
Tree	1	0	0	0	0	0
Road	0	1	0	6	0	0
Ant mound	1	0	0	2	0	0
Carcass	0	0	0	0	0	1

Table 6.7. Comparison of habitat characteristics of areas where maned wolves were sighted in Emas National Park with sites chosen in a systematic random procedure. Due to the multiple tests conducted, a Bonferroni adjustment was used, making the *P* value required for significance equal to 0.0042 (0.05/12). Asterisks indicate significant differences using the Bonferroni adjusted significance level.

Variable	Random	Sighting	df	t	<i>P</i>
Distance from road (m)	50.16±4.04	35.24±10.02	51.5	1.38	0.17
Width of Road (m)	2.82±0.08	3.77±0.27	39.5	-3.37	0.0017 *
Number of Termite Mounds	1.42±0.38	1.08±0.30	80	0.72	0.48
Termite Mound Height (cm)	31.91±5.67	59.01±8.69	39	-2.71	0.01
Number of Shrubs	90.04±11.28	50.25±9.99	83	2.61	0.0106
Number of <i>Solanum</i> Shrubs	0.07±0.05	0.15±0.10	55.7	-0.72	0.47
Number of Trees	0.36±0.27	0.28±0.14	65.4	0.27	0.79
Mean Vegetation Height (cm)	31.33±6.79	28.59±5.99	83	0.30	0.77
Percent Bare Ground	25.93±3.14	42.03±4.19	83	-3.12	0.0025 *
Percent Grass	52.37±3.83	45.28±4.52	83	1.20	0.23
Percent Shrub	18.16±1.74	8.25±1.46	83	4.31	< 0.0001 *
Percent Herbs	3.55±0.56	4.43±1.14	57.1	-0.70	0.49

3.

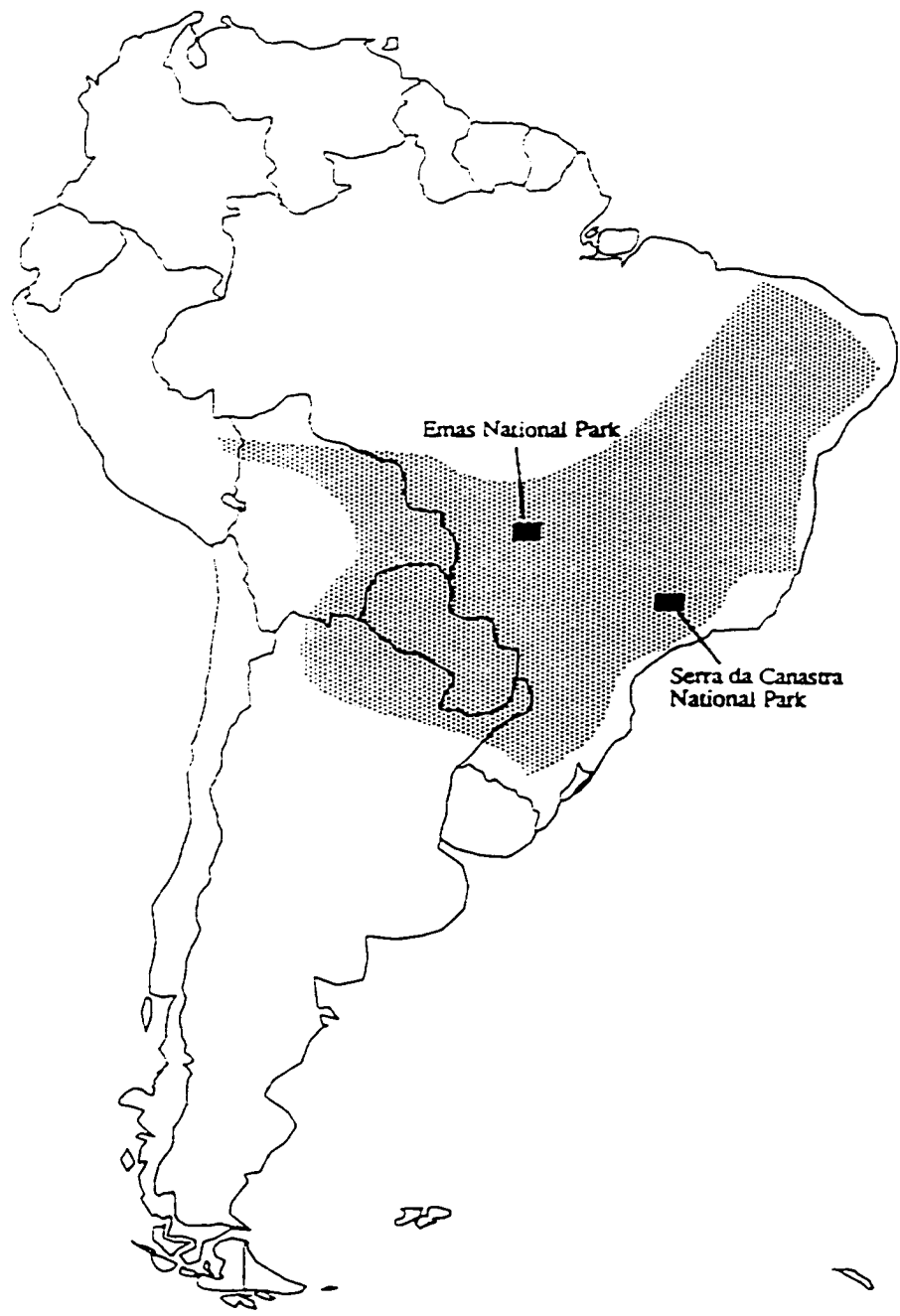


Figure 6.1. Location of Emas National Park, the site of this study, in central Brazil. The shaded area represents the maned wolf's distribution (Dietz 1985). The location of Serra da Canastra National Park, the site of Dietz's study, is also shown.

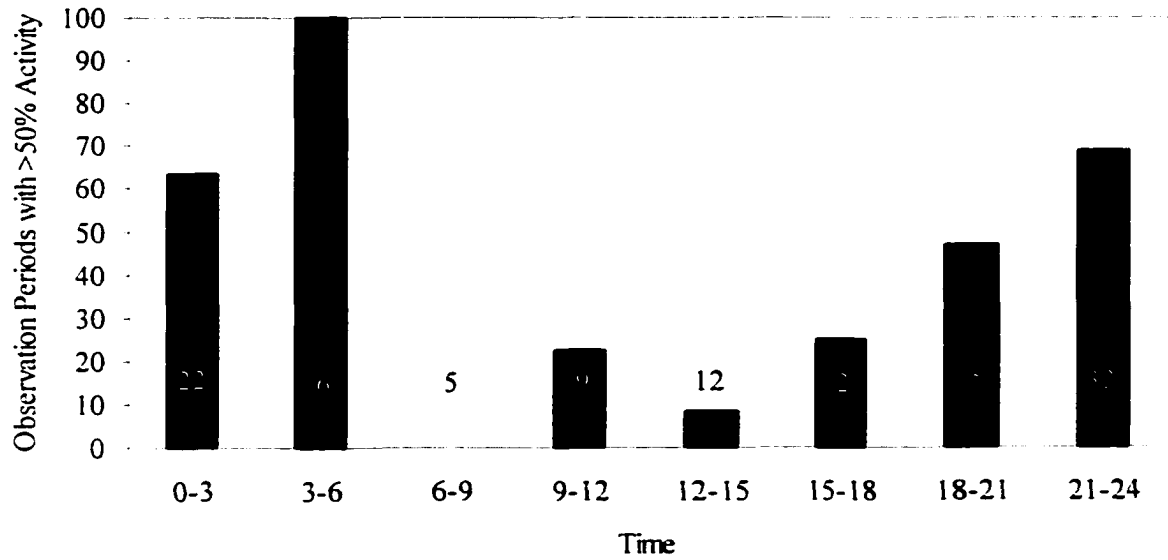


Figure 6.2. Percentage of 30-min observation periods that contained at least 15 min of activity. Numbers of observation sessions within each time period are shown in or above each bar.

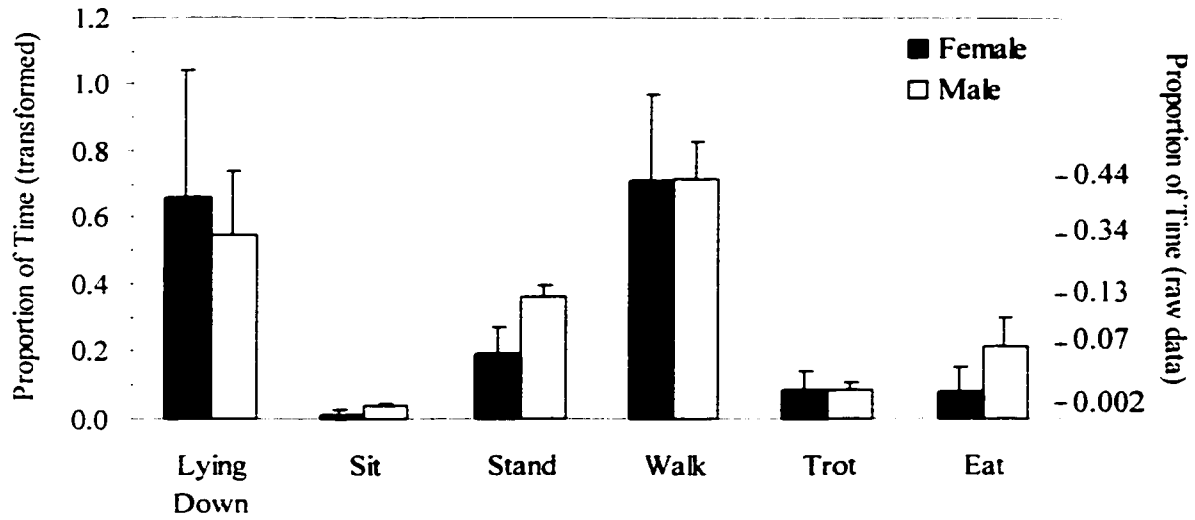


Figure 6.3. Mean (+ SE) transformed proportion of time spent in each behavioral state by 5 male and 3 female maned wolves. There is a significant difference overall in time budgets between males and females (Wilk's Lambda=340.1; $df=6,1$; $P=0.04$) and in the proportion of time standing ($F_{1,6}=4.71$; $P=0.07$).

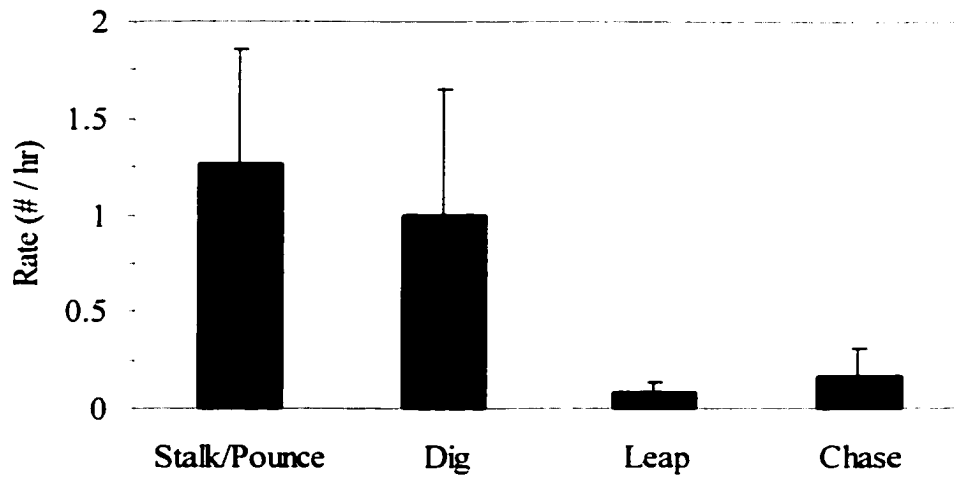


Figure 6.4. The mean (+ SE) rate (number per observation hour) of each animal hunting strategy exhibited by 9 maned wolves. Descriptions of the hunting strategies are given in the text.

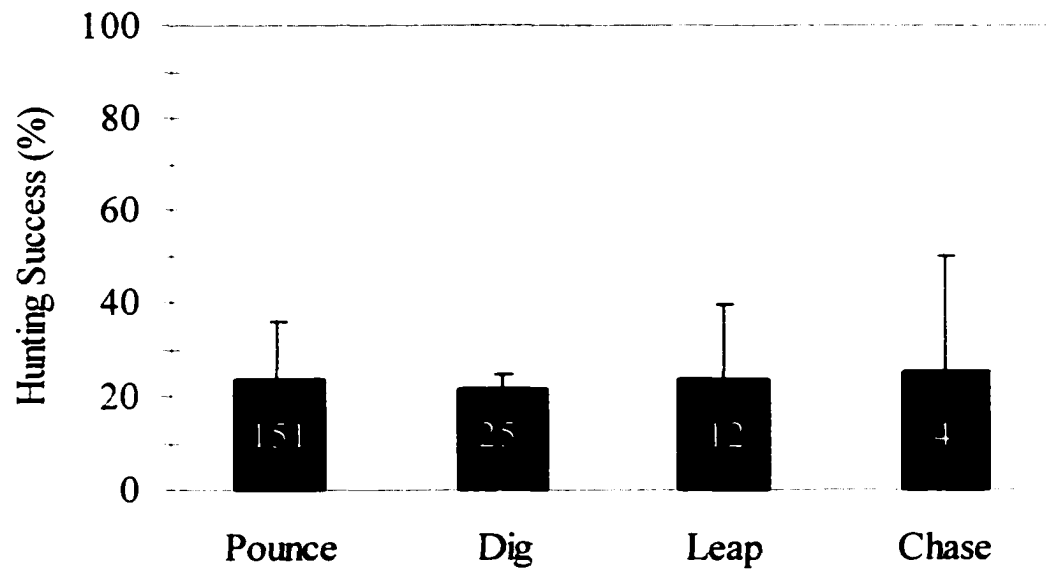


Figure 6.5. The mean (+SE) percent of maned wolf hunting attempts using each hunting strategy that was successful (i.e. ended with the capture of a prey). The number of hunting attempts using each strategy is shown within each bar.

CHAPTER VII

CAPTIVE AND FREE-RANGING MANED WOLVES' BEHAVIOR: A QUANTITATIVE COMPARISON

INTRODUCTION

When many people envision behavioral studies of large carnivores, they picture an observer with large binoculars following and recording the behavior of an animal as it moves through its natural habitat. In reality, however, many behavioral studies of large carnivores are conducted on animals housed in zoos since there are numerous advantages to using captive animals in behavioral research (Robinson 1990). Primary among these is the large number of observations possible due to the near certainty of locating an animal inside its enclosure. Second, relatively large sample sizes can be obtained in zoos that house more than one individual of a species. It is also possible to control the social and physical environment of captive animals more readily than their free-ranging counterparts. Finally, zoo animals on exhibit are generally habituated to humans, so the lengthy habituation process necessary in field studies can be bypassed.

Many behavioral studies done in zoos seek to answer questions specifically about the captive condition. For example, we often want to determine if there are differences in behavior associated with husbandry practices, exhibit design, or an enrichment program (e.g. Forthman et al. 1992; Kreeger et al. 1996; Lyons et al. 1997). For these types of questions, a study of captive animals is appropriate. However, the results of other behavioral studies of captive animals have sometimes been generalized to the entire species, including free-ranging individuals. The temptation to generalize is especially great for the many species for which virtually no behavioral information is available from free-ranging animals. Generalizing from captive animals to free-ranging animals carries the obvious, yet often overlooked, assumption that a captive animal's behavior is similar to the species' typical behavior in the wild. Unfortunately, this assumption has rarely been tested, especially for carnivores. In the few cases when the behaviors of captive and free-ranging mammals have been directly compared, large differences are generally found, for example for primates (Rowell 1967; Drickamer 1973) and ungulates (Bennett and Fewell 1987). Comparisons of the behavior of captive and free-ranging carnivores are especially scarce, probably due to the difficulty of studying free-ranging carnivores (Bekoff et al. 1984; Schaller 1994; Creel and Macdonald 1995). Kaufmann and Kaufmann (1963) conducted one of the only direct comparisons, and they found numerous differences between the behavior of captive and free-ranging coatis. We need more studies that compare the behavior of captive and free-ranging carnivores before generalizations are made.

A comparison of captive and free-ranging carnivores' behavior also allows tests of the hypothesis that animals in zoos become domesticated through generations of

unintentional selective breeding. "Domesticate" is a broad term defined in Webster's New International Dictionary (Gove 1971, p. 671) as

to adapt (an animal or plant) to life in intimate association with ... man or another species usually by modifying growth or traits through provision of food, protection from enemies, and selective breeding during generations of living in association and often to the extent that the domestic form loses the ability to survive in nature.

A major argument against the use of zoos in captive breeding and reintroduction programs is that animals in zoos unavoidably become domesticated, rendering them either incapable of surviving in their native environment (Lyles and May 1987; Snyder et al. 1996) or severely disadvantaged relative to wild individuals (Fleming and Gross 1993). Indeed, Griffith et al. (1989) reviewed 198 bird and mammal reintroduction projects and found that projects releasing captive born animals had a significantly lower success rate (38%) than programs releasing wild-caught individuals (75%). In response to these concerns, numerous reintroduction programs for mammals have focused on pre-release training programs to teach the animals to become "wild" again. For example, golden lion tamarins are taught to move on natural vegetation (Kleiman 1989; Box 1991), black footed ferrets are taught to hunt prairie dogs (Miller et al. 1996), and red wolves are taught to eat ungulates and avoid humans (Smith and Phillips 1987). A few studies now show that trained individuals have higher post-release survival than untrained animals (Beck 1991; Biggins et al. 1999), suggesting that if zoo animals do lose survival skills, these effects can be at least partially overcome through training.

Another approach for determining if zoo animals are domesticated is to compare the behaviors of captive and free-ranging individuals using the same methods, the same ethogram, and ideally the same observer. Although the behavioral changes indicating domestication may differ depending on the species, we can expect any one or more of the

following differences to indicate possible domestication in carnivorous, territorial zoo animals: (1) a shift in the time of activity to a cycle that reflects periods of human activity, (2) less total activity, (3) less hunting behavior since captive animals become accustomed to being provided with food, (4) less investigatory behavior like sniffing, and (5) less territorial behavior, including scent marking.

Between 1993 and 1998, I studied 22 captive maned wolves, *Chrysocyon brachyurus*, in zoos throughout the United States and 9 free-ranging maned wolves in Emas National Park, Brazil. Until recently, most published behavioral observations of maned wolves were conducted on captive animals (e.g. Biben 1982; Rasmussen and Tilson 1984; Bestelmeyer et al. 1996). Dietz's (1984) 2-year study in Brazil continues to be the most comprehensive study of free-ranging maned wolves to date. Due to the extreme topographic relief of the study site and the shy temperament of this maned wolf population, Dietz was unable to conduct direct behavioral observations. Therefore, to determine the solitary, reproductive, and social behavior of the species, he studied captive maned wolves at the National Zoological Park's Conservation and Research Center. The lack of behavioral observations of free-ranging maned wolves made it impossible to compare captive and free-ranging maned wolves' behavior until now.

The purpose of this paper is to compare the behavior of captive and free-ranging maned wolves. Using observations of captive and free-ranging individuals, I will test the assumption that the behaviors of captive animals accurately reflect the behavior of free-ranging maned wolves and test for signs of domestication in captive maned wolves.

METHODS

Subjects and Study Sites

I studied 22 captive maned wolves (11 males and 11 females) housed in 8 U.S. zoos (Table 7.1) and 9 free-ranging maned wolves (5 males, 3 females, and 1 individual of unknown sex) in Emas National Park, Brazil (Fig. 7.1). All 8 U.S. zoos are members of the maned wolf captive breeding program called the Maned Wolf Species Survival Plan (MWSSP), and so all follow the husbandry recommendations outlined by Fletchall et al. (1995). Therefore, although enclosure sizes, diets, and the amount of disturbance from zoo visitors vary across the eight zoos, some confounding factors are eliminated since many husbandry practices are standardized. Emas National Park (Fig. 7.1; 131,868 hectares; 18°16' S and 52°53' W) is in the southwest corner of the state of Goiás, Brazil and is the largest protected area of cerrado vegetation (Eiten 1978) in Brazil (Redford 1985). A full description of Emas National Park is given in Chapter VI.

Behavioral Observations

Captive maned wolves were observed from outside their enclosures, and free-ranging maned wolves were observed from the top of a vehicle that followed 15-30 m behind the wolves. Before observations began, I habituated each of the free-ranging maned wolves to being observed. This process took varying lengths of time depending on the maned wolf. Some individuals were calm and unwary of being observed, so official observations could begin on the second encounter with an individual. Other individuals were followed repeatedly at increasingly closer distances before they were accustomed to being

observed. Unhabituated individuals were easily able to trot away from the observers. An individual was considered habituated when it did not look at the observers more than once every 5 minutes and did not trot for more than 25% of the observation period. All observations reported here were collected after the habituation process was complete.

I conducted continuous, focal animal observations (Altmann 1974) using an ethogram that contained 12 behavioral states (ongoing behaviors with appreciable durations; Table 7.2; Altmann, 1974) that were placed into 8 categories: (1) inactive (lying down, sitting, and out of view while inactive), (2) standing, (3) walking, (4) trotting and running, (5) eating and drinking, (6) pacing, (7) out of view while active, and (8) other. I also recorded the rates of 57 behavioral events (relatively instantaneous behaviors; Table 7.3) that were divided into 6 categories: (1) solitary, (2) hunting, (3) marking, (4) affiliative, (5) aggressive, and (6) parental. Due to the small number of observations of free-ranging maned wolves interacting with conspecifics (see below), the rates of behavioral categories requiring interactions with other individuals (affiliative, aggressive, and parental behaviors) were not compared. I did not collect data on the rates of all 10 solitary behaviors for all captive maned wolves; therefore, I only analyzed the rates of those behaviors for which complete data were available (grooming, sniffing and barking).

To control for seasonal behavioral changes, I conducted all observations during the breeding and early pup-rearing seasons. Breeding generally occurs between October and February in the northern hemisphere and between May and October in the southern hemisphere (Dietz 1984). I observed captive animals in North America from between late September and June, 1993 to 1998 (Table 7.1). One pair at the Wild Canid Survival and Research Center gave birth later than normal (late March), so this pair was observed until

August. I observed free-ranging maned wolves between May and October 1997. The captive wolves were observed for 30 or 60 min periods between the hours of 0600 h and 2100 h for a total of 646 h. The free-ranging wolves were observed for periods ranging from 2.13 min to 10.81 h during every hour of the day and night for a total of 57.5 h. Because captive wolves were not observed throughout the night, any result (e.g., activity level, see below) that could be due to inconsistent observation hours between the two groups was also analyzed after eliminating the night observations of free-ranging wolves (2100 h to 0559 h), leaving 27.7 hr of observation. Although the number of observation hours is much greater for captive maned wolves, I eliminated potential bias by standardizing all behaviors according to the number of observation hours; I compared proportions of observation time spent in each behavioral state and rates of each behavioral event per hour of observation.

Data Analysis

Average proportions of time in each behavioral state and average rates of behavioral events were calculated for each individual. Activity cycles of captive and free-ranging wolves were compared with logistic regression. Because behavioral states were mutually exclusive and exhaustive, proportions of time in all 12 behavioral states add to 1.0 for each individual in each observation period. Therefore, to compare data sets, I dropped the states “other” and “trotting and running” from the analysis. Then the proportion of time in each state was transformed with the arcsine square-root transformation which makes proportional data suitable for parametric statistical tests (Zar 1996). I analyzed the transformed values (for behavioral states) as well as the rates of behavioral events per

hour using the Wilk's lambda test statistic from multivariate analysis of variance (MANOVA) tests. If the model was significant, I examined univariate ANOVA results (i.e., t-test results since there were two classes: captive and free-ranging) to determine which behavior(s) differed. To account for the fact that multiple individual tests were examined within each category (solitary, hunting, and marking events), I used the sequential Bonferroni correction (Holm 1979) for each category, which adjusts the *P*-value required for statistical significance.

RESULTS

Number and Form of Behaviors

Eleven of the twelve behavioral states (Table 7.2) were observed in both captive and free-ranging maned wolves. Pacing was never observed in free-ranging animals, but it was seen in 12 (54.4%) of the captive wolves and comprised an average of $1.24 \pm 0.56\%$ of captive animals' time budgets. Twenty-six of the 29 solitary, hunting, and marking behavioral events were observed in captive and free-ranging maned wolves (Table 7.3), and these behaviors were performed identically in both groups of animals. Only one hunting behavior, "paw bush," was seen in free-ranging but not in captive animals. In this newly described behavior, the wolf would raise its foreleg and strike a bush in a downward motion, dislodging fruits that were then consumed. Two marking behaviors, "urinate over" and "flehmen," were observed only in captive maned wolves. Both of these behaviors require interaction with another wolf's urine shortly after it is deposited, so the small number of observation hours (3.44 hr) of more than one wolf at the same

time in Emas National Park makes it unlikely that these behaviors would have been observed in free-ranging animals. Therefore, no conclusions can be made about these behaviors until further observations of free-ranging maned wolves are conducted.

Activity Cycles

Between 0600 h and 2100 h, captive and free-ranging maned wolves' activity patterns were different (Fig. 7.2; $X^2=9.09$; $df=4$; $P=0.06$). These differences were caused by higher activity of captive maned wolves between 0600 h and 0900 h and higher activity of free-ranging maned wolves between 1800 h and 2100 h (Fig. 7.2). Between 0900 h and 1800 h, the activity patterns were similar since both groups were generally inactive; no more than 25% of all 30 min observation periods contained continuous activity in any of these time periods. Most of the free-ranging wolves' activity occurred at night, increasing between 1800 and 2100 and staying consistently high until dawn (Fig. 7.2). No formal observations of captive wolves were conducted between 2100 and 0600, so it is unclear if captive wolves are similar to their free-ranging counterparts in increasing their activity during these nocturnal hours. Informal observations of captive maned wolves suggest that they too may be relatively active at night (Bestelmeyer, pers. obs.).

Time Budgets

The time budgets of captive and free-ranging maned wolves differed (Fig. 7.3; all hours: Wilk's lambda=0.22; $df=6, 24$; $P=0.0001$; 0600 – 2100 h: Wilk's lambda=0.31; $df=6,24$; $P=0.0001$). Time budget differences were caused by a significant difference in three states: inactive, walking, and pacing. Captive wolves spent a larger proportion of time

inactive than did the free-ranging wolves (all hours: $F_{1,29}=7.48$; $P=0.01$; 0600 h – 2100 h: $F_{1,29}=4.76$; $P=0.04$). Free-ranging maned wolves spent significantly more time walking than did the captive animals (all hours: $F_{1,29}=10.59$; $P=0.003$; 0600 h – 2100 h: $F_{1,29}=5.73$; $P=0.02$). As previously mentioned, captive maned wolves paced whereas free-ranging wolves did not; therefore the groups' proportions of time pacing also differed ($F_{1,29}=4.19$; $P=0.0497$). There was no significant difference in the proportion of time spent standing ($F_{1,29}=1.55$; $P=0.22$), eating and drinking ($F_{1,29}=0.10$; $P=0.75$), or out of view ($F_{1,29}=3.48$; $P=0.07$).

Rates of Behavioral Events

Captive and free-ranging maned wolves did not differ in their rates of solitary behavioral events (Fig. 7.4; Wilk's lambda=0.76; $df=3,22$; $P=0.11$), but rates of hunting behaviors did differ (Fig. 7.5; Wilk's lambda=0.27; $df=9,16$; $P=0.003$). Every hunting behavior was performed at a higher rate by free-ranging maned wolves. Even after controlling for the multiple tests conducted, these differences were significant for stalking ($F_{1,24}=45.73$; $P=0.0001$), pouncing ($F_{1,24}=27.18$; $P=0.0001$), leaping ($F_{1,24}=21.16$; $P=0.0001$), foreleg pouncing ($F_{1,24}=16.62$; $P=0.0004$), foreleg stamping ($F_{1,24}=13.54$; $P=0.001$), and caching ($F_{1,24}=45.73$; $P=0.012$). Finally, there was a difference in the rates of marking behaviors by captive and free-ranging maned wolves (Fig. 7.6; Wilk's lambda=0.47; $df=9,21$; $P=0.03$). Body rubbing was the only behavior that showed a significant difference after controlling for the multiple tests conducted ($F_{1,29}=9.99$; $P=0.0037$). There were no differences in the rates of the more common scent-marking behaviors, including leg

lifting ($F_{1,29}=2.38$; $P=0.13$), squatting ($F_{1,29}=3.06$; $P=0.09$), and straddling ($F_{1,29}=2.32$; $P=0.14$).

DISCUSSION

This study showed many behavioral differences between captive and free-ranging maned wolves, consistent with other studies comparing the behavior of captive and free-ranging animals (Kaufmann and Kaufmann 1963; Rowell 1967; Drickamer 1973; Bennett and Fewell 1987). Activity cycles, time budgets, hunting behaviors, and marking behaviors were all significantly different in the two groups, suggesting that behavioral studies of captive maned wolves should not be generalized to the entire species. Given the difficulties of habituating, locating, and carrying out observations on free-ranging carnivores, it is unfortunate that generalizations cannot be made based solely on captive animals. Other authors have suggested that consistent results from many captive studies may render generalizations to free-ranging individuals appropriate. For example, Kleiman and Malcolm (1981, p. 352) argue that paternal care by captive animals should be viewed cautiously “unless the persistence of male parental care in a variety of individuals under a variety of conditions indicates that such behavior could be occurring in nature.” Determining the presence of a particular behavior (such as paternal care) may be implied from studies of captive animals, but confirming this result will ultimately require studies of free-ranging individuals. Furthermore, since many differences exist between captive and free-ranging maned wolves, quantitative predictions about free-

ranging individuals' behavior should only be based on studies of free-ranging animals, despite the many difficulties posed by field studies (Bekoff et al. 1984; Hart 1997).

There appeared to be at least one important use for behavioral studies of captive maned wolves in preparing for a field study. Captive maned wolf studies were sufficient for developing a nearly complete ethogram since only one behavior (paw bush) was seen in free-ranging but not captive animals. Furthermore, the way each behavior was performed was indistinguishable in captive and free-ranging animals. Ethogram development using captive animals is much easier due to the relative ease of collecting the large numbers of observation hours necessary to detect rare behaviors. For example, collecting one hour of observation of a captive maned wolf took 3-4 hr of work when traveling time and set-up time were included (Bestelmeyer, unpubl. data). In contrast, each hour of observation of free-ranging maned wolves required an average of 30 hr of work habituating the wolves and searching for them (Chapter VI). Even after habituation was complete, finding maned wolves in Emas National Park was difficult, and many days passed without finding a maned wolf.

This study provided conflicting evidence regarding domestication of captive maned wolves since a few predictions were confirmed and a few were not supported. This study provided some support for the prediction that captive animals' activity cycles would mirror those of humans. Captive maned wolves were more active than free-ranging maned wolves between 0600 h and 0900 h, a time of high human activity at most zoos, and were less active between 1800 h and 2100 h, when most zoos are closed and human activity decreases. However, captive maned wolves were mostly inactive between 0900 h and 1800 h, despite the fact that these are the hours that zoos are generally open and high

activity occurs. This study supported the prediction that captive maned wolves would have decreased overall activity compared to free-ranging animals. Furthermore, hunting behaviors were significantly decreased, as predicted.

Two predictions regarding domestication were not supported. First, we predicted a lower rate of investigatory behaviors like sniffing for captive maned wolves, but no difference existed. Second, captive maned wolves did not have lower levels of territorial marking behaviors such as leg lifting, squatting, or straddling as we would predict from domesticated animals. Overall, therefore, evidence for domestication of captive maned wolves was mixed.

Several differences between captive and free-ranging maned wolves' behaviors indicate that captive maned wolves may adapt to their environment, but it is unclear if these behavioral differences would lead to low survival in reintroduced animals. For example, it was not surprising that all nine hunting behaviors were performed at higher rates by free-ranging maned wolves, and that the differences in six of these behaviors were significant. Stalking, pouncing, foreleg pouncing, leaping, and foreleg stamping are used to capture small mammals, birds, and insects, which comprise a large portion of animal prey in the maned wolf's diet (Chapter VI; Dietz 1984; Jácomo, 1995; Motta-Junior et al. 1996). Lower rates of these behaviors in captive animals reflect the fact that they do not depend on these food sources to survive. Even so, they have not lost the ability to perform hunting behaviors and will occasionally capture small mammals, birds, and insects in their enclosures (Bestelmeyer, pers. obs.). Furthermore, captive maned wolves' lower activity may simply reflect their much smaller home ranges (i.e., the sizes of their enclosures) and their lack of a need to hunt for food. Many canid species are

notorious for their ability to adapt to local conditions and change their behavior accordingly (Moehlman 1989). Therefore, rather than being an example of the inevitable loss of natural behaviors through domestication in captivity, maned wolves may be one more example of canid behavioral flexibility.

Captive maned wolves' higher proportion of time inactive and pacing, and free-ranging animals' higher proportion of time walking emphasize the importance of attempting to provide enrichment to captive maned wolves to stimulate their activity (Werle et al. 1995). Although the effects of environmental enrichment on captive maned wolves have not yet been studied, we can expect the beneficial effects of increasing activity and reducing stereotyped behaviors that have been confirmed in many other carnivores (e.g., Foster-Turley and Markowitz 1982; Carlstead et al. 1991; Forthman et al. 1992). Furthermore, more active captive maned wolves will enhance the zoo visitor's appreciation for this endangered species.

Although it is unclear if the results of this study apply to other canids, other carnivores, or any other species, it is evident that differences exist between the behavior of captive and free-ranging maned wolves. Therefore, the assumption that a captive animal's behavior is typical of the species' behavior in the wild needs to be tested before generalizations are made based solely on behavioral studies of captive animals. Testing this assumption is difficult because it requires that the same methods and the same ethogram be used for studies of captive and free-ranging individuals. Despite these difficulties, it is the only way to determine which, if any, behavioral studies of captive animals can be generalized to free-ranging conspecifics.

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Table 7.1. Pairs of captive maned wolves studied. Studbook numbers are from Matern (1999).

Studbook Numbers (male/female)	Location	Observation Dates	Observation Hours
1147/1236	Baton Rouge Zoo	12/94 – 4/95	24
1185/1261	Denver Zoo	10/94 – 12/94	33.5
1660/1829	Denver Zoo	9/96 – 11/96	10
1184/1191	Fossil Rim Wildlife Center	3/95 – 5/95 and 2/97 – 5/97	32 13
1385/1285	Fossil Rim Wildlife Center	3/97 – 5/97	37.5
971/1029	Houston Zoo	3/94 – 6/94 and 5/97 – 6/97	72.5 7.5
523/610	Little Rock Zoo	1/95 – 3/95	13
680/857	Oklahoma City Zoo	11/93 – 1/94	169
571/1148	Oklahoma City Zoo	11/93 – 1/94	166
1384/1321	White Oak Conservation Center	3/94- 4/94 and 1/95 – 2/95	4.5 39.5
1830/1661	Wild Canid Survival and Research Center	5/98 - 8/98	24

Table 7.2. Behavioral states exhibited by maned wolves. All states were observed in both captive and free-ranging individuals, except pacing which was seen only in captive animals.

Behavioral State	Definition
Lying Down	Mid-section of body in contact with the ground
Sit	Back part of body in contact with the ground; usually occurs while animal in scratching
Stand	Stationary upright position
Walk	Locomotion without in-air phase
Trot	Locomotion with in-air phase where hindlegs do not extend forward past the midline of the body
Run	Locomotion with in-air phase where hindlegs do extend forward past the midline of the body
Pace	Walk back and forth over the same, small area; pace begins with the third consecutive pass over the same ground
Eat	Consume solid food
Drink	Consume water or another liquid
Out of View while Active	Not in view of observer, but known to be active
Out of View while Inactive	Not in view of observer, but known to be inactive
Other	Behavioral state not included in any other state

Table 7.3. Solitary, hunting, and social behaviors exhibited by both captive and free-ranging maned wolves, by captive maned wolves only, and by free-ranging maned wolves only. Definitions of most behaviors adapted from Bestelmeyer and Kinsey (1995).

Behavior	Definition	Captive and Free-Ranging	Captive Only	Free-Ranging Only
SOLITARY				
Self-Groom	Lick own body	X		
Sniff	Investigate object with nose	X		
Bark	Short, loud, hoarse vocalization	X		
Scratch	Scratch body with hindleg, often while sitting	X		
Sneeze	Self-explanatory	X		
Yawn	Self-explanatory	X		
Body Shake	Rapid side-to-side movement of body; often occurs after standing up			
Head Shake	Rapid side-to-side movement of head			
Stretch	Place forelegs in front of body and shift weight slowly from primarily on hindlegs to full standing position			
Lick	Touch tongue to object			
HUNTING				
Dig	Scratch ground with foreleg(s) to make a depression	X		
Cache	Bury food in hole or cover with substrate	X		
Stalk	Ears erect and forward, body tense and either standing or moving slowly with attention focused forward	X		
Pounce	Jump forward, lifting all legs off of the ground	X		
Foreleg Pounce	Jump forward, with only forelegs lifted from ground	X		
Leap	Jump nearly straight up with all legs off of the ground	X		
Foreleg Stamp	Rapidly hit one foreleg onto the ground	X		
Tail Out	Tail lifted or held horizontally along line of back	X		
Tail Up	Tail raised above the level of the back	X		
Paw Bush	Raise foreleg and strike bush in downward motion			X
MARKING				
Leg Lift	Urination with hindleg lifted off ground	X		
Squat	Urination with back legs bent; sometimes one hindleg is lifted slightly off ground	X		
Defecate	Self-explanatory	X		
Straddle	Stand over and rub genital region on bush, grass, or other object	X		
Face Rub	Rub face or neck on a surface	X		
Body Rub	Rub side of body on a surface	X		
Taste Urine	Lick urine of another wolf	X		
Urinate Over	Urinate in the same spot another wolf urinated or defecated within 5 minutes		X	
Flehmen	Rapid teeth chatter		X	



Figure 7.1. Range of the maned wolf (Dietz 1985) and the location of Emas National Park, Goiás, Brazil.

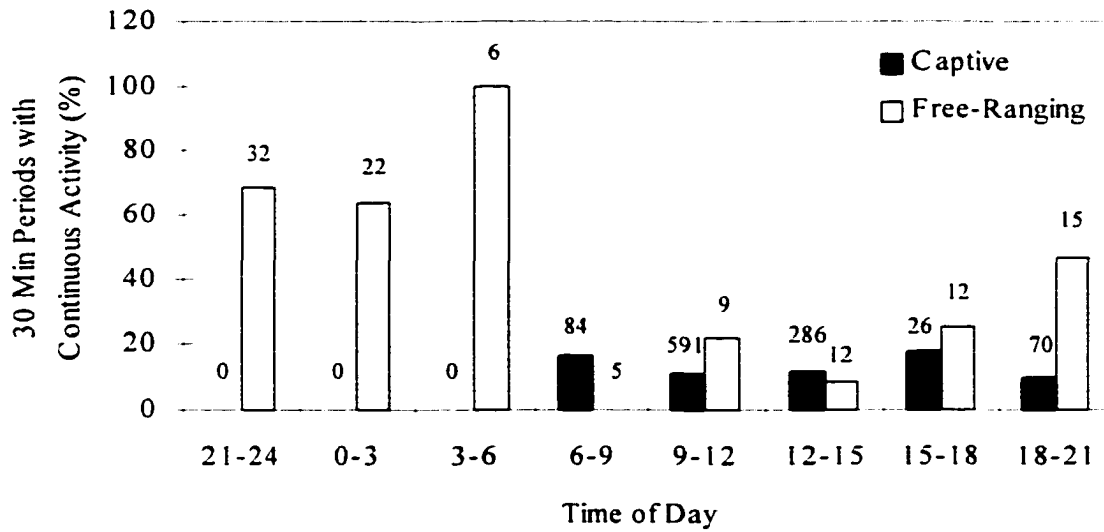


Figure 7.2. Percentage of 30 min observation periods during each time of day when captive and free-ranging wolves are continuously active. Numbers above the bars represent the number of 30 min observations in each time period. No observations of captive maned wolves were conducted between 2100 and 0600, so the activity of captive and free-ranging maned wolves during these hours cannot be compared.

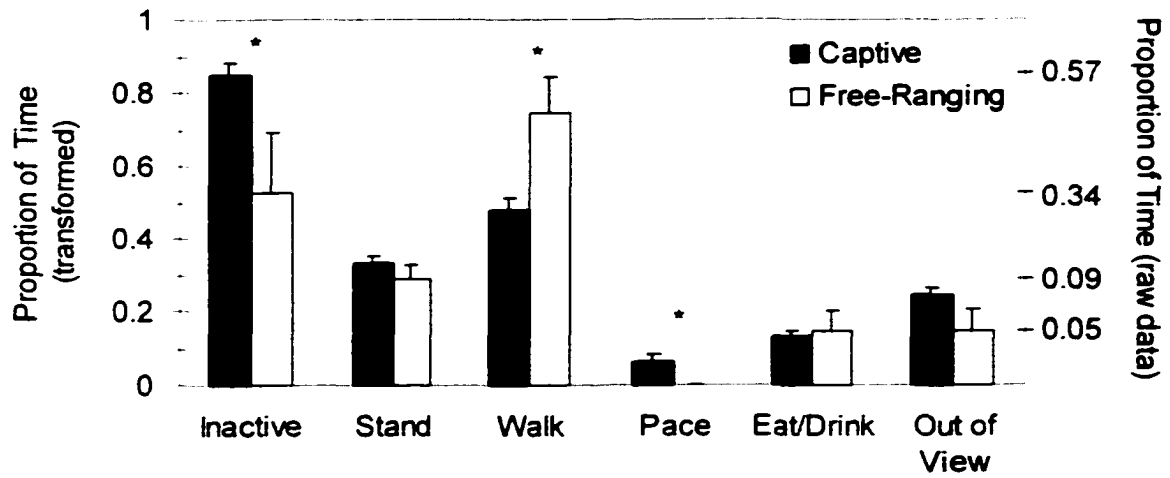


Figure 7.3. Time budgets of captive and free-ranging maned wolves (mean + SE; N=22 captive wolves and N=9 free-ranging maned wolves). Transformed values (arcsine square-root transformed proportions) were used for statistical analyses. Asterisks indicate $P < 0.05$ from ANOVA tests.



Figure 7.4. The number of solitary behavioral events per hour exhibited by captive and free-ranging maned wolves (mean + SE; N=22 captive wolves and N=9 free-ranging maned wolves).

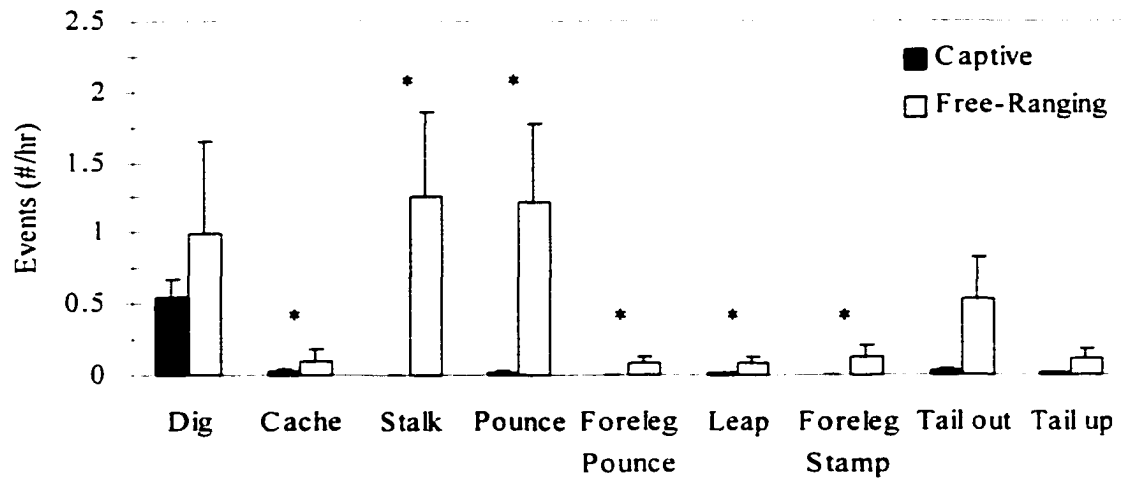


Figure 7.5. The number of hunting behavioral events per hour exhibited by captive and free-ranging maned wolves (mean + SE; N=22 captive wolves and N=9 free-ranging maned wolves). Asterisks indicate significant results from ANOVA with a sequential Bonferroni correction ($P < 0.0125$).

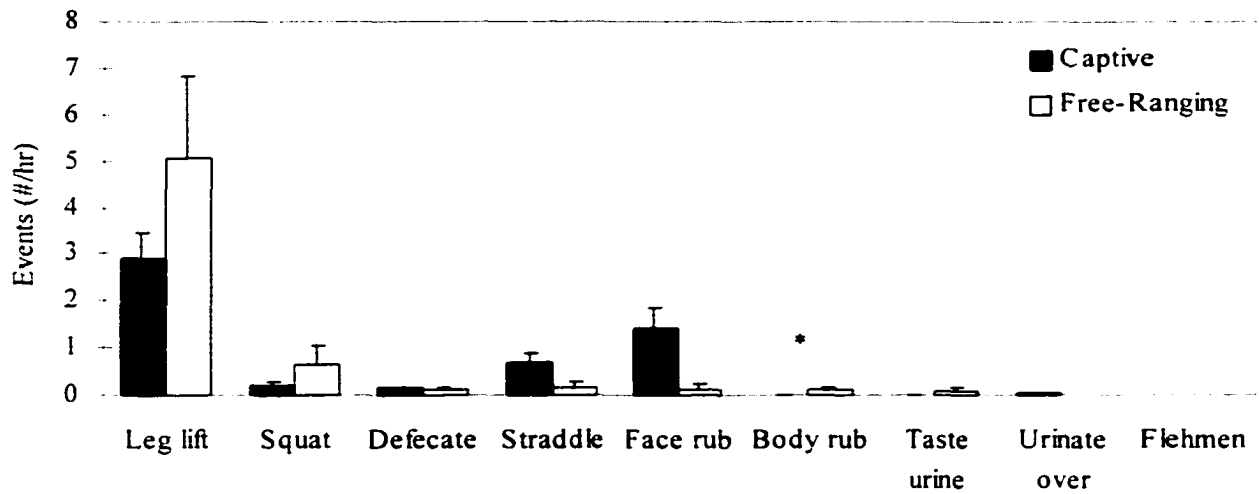


Figure 7.6. The number of marking/elimination behavioral events per hour exhibited by captive and free-ranging maned wolves (mean + SE; N=22 captive wolves and N=9 free-ranging maned wolves). Asterisks indicate significant results from ANOVA with a sequential Bonferroni correction ($P < 0.004$).

CHAPTER VIII

CONCLUSIONS

The rate of recent species extinctions requires that we use every available scientific tool to combat further losses. Animal behavior and behavioral ecology have great potential value to conservation biology (Curio 1996; Ulfstrand 1996; Clemmons and Buchholz 1997; Caro 1998; Sutherland 1998) and therefore should be used more frequently. The previous seven chapters demonstrate that studies useful for the conservation of a species can also provide important information on more basic issues in animal behavior and behavioral ecology.

These studies provide among the first tests of many hypotheses about parental investment in carnivores. For example, I provide evidence supporting the paternal investment hypothesis for maned wolves in Chapter II by showing that pup survival is higher when males provide offspring care. I also demonstrate in Chapter III that males and females are similar in their care patterns, as predicted for monogamous species. A game theory approach to parental investment predicts that males and females will adjust their behaviors depending on the presence and behavior of their mate (Maynard Smith 1977), but my results only weakly supported these predictions in maned wolves. The only

behavioral difference in females with and without males was the rate of aggressive behaviors to pups. Chapter III showed that females may decrease their activity and the amount of time spent with their pups when the male is present. Further research should focus on testing these ideas in other carnivores to determine the generality of patterns I found for maned wolves.

The conservation value of my work on maned wolf parental behavior has already been recognized. My data showed that pup survival is maximized if the male is left with the female. It also showed that the male will play an important role in pup rearing and may have positive effects on the female's health. Based on these data, the maned wolf captive breeding program, the Maned Wolf Species Survival Plan (MWSSP), now recommends that males either be left with the female to help rear pups or that males be reintroduced shortly after birth (Rodden, pers. comm.). For those managers wishing to conduct such a reintroduction, my results (Chapter IV) showed how to carry out the procedure and outlined the benefits to be gained from allowing the male to participate in pup care.

My work also demonstrated that reproductive timing in maned wolves is influenced more by internal factors than by latitude or temperature. These data will contribute to the growing body of knowledge on reproductive timing in mammals (Ims 1990) and provide new information on carnivore estrous periods. This work will prove useful for the MWSSP by helping participants predict when a female will enter estrus and make appropriate preparations.

Finally, my work with free-ranging maned wolves in Emas National Park provided new information on the species' habitat use and behavior. This work suggested that the maned wolf's unusual natural history, compared to other large canids, may not be simply

caused by a lack of large prey, since maned wolves can successfully hunt pampas deer. These observations may force future comparative analyses of canid social organization to search for new theories explaining the variety of group sizes present in the family. From a conservation standpoint, this research provided new information on the maned wolf's habitat use and behavior that will ultimately help in the development of recovery strategies.

The majority of my research was conducted on captive maned wolves, and there are both advantages and disadvantages to working with captive animals. Advantages include the ease of locating and habituating animals, as well as the possibility of collecting relatively large numbers of observation hours (Robinson 1990). Despite the temptation caused by these advantages, the results in Chapter VII provided another example of the problems of generalizing from studies of captive animals to their free-ranging counterparts. Furthermore, there are often relatively few individuals of a species in one zoo, forcing the researcher to conduct research at multiple zoos (Mellen 1994) and introducing many potentially confounding variables. I recognize the severity of these problems, but many studies of large carnivores are difficult to conduct other ways. Thus, whereas the results of such work should be viewed with caution, the data are important for answering basic questions and aiding in conservation strategies.

Effective conservation strategies will likely come from a merging of ideas and information from many sources. Therefore, field studies and behavioral research conducted within zoos should be linked whenever possible (Robinson 1990). My research illustrates the many ways that research on captive and free-ranging animals can benefit each other. For example, I developed the ethogram used in the field study through

hundreds of hours of observations of captive animals. Furthermore, over 70% of the funding for my field project came from zoos within the MWSSP. Although lack of staff and inadequate funds are frequently cited as major barriers to zoos becoming involved in research (Finlay and Maple 1986), contributions in amounts as small as \$400 made this project possible. Much of this money came from zoos not heavily involved in other field conservation and research projects. On the other hand, my research on free-ranging maned wolves can be used to improve the management of captive maned wolves and possibly increase reproductive success within the program (Bestelmeyer 1998).

Conserving the maned wolf and other species will likely require the dedicated, creative work of scientists from many disciplines working in a variety of environments. Knowing more about the maned wolf's behavior and parental care system only provides part of the story, and in isolation cannot conserve the species. Yet animal behavior is an important piece of many conservation puzzles and should certainly be employed more frequently to ensure that species like the maned wolf can be appreciated by many future generations.

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