HOME RANGE AND SPATIAL ORGANIZATION OF MANED WOLVES IN THE BRAZILIAN GRASSLANDS

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The maned wolf (*Chrysocyon brachyurus*) is the largest canid in South America, weighing up to 30 kg, and exhibits an omnivorous diet based on fruits and small vertebrates. Maned wolves are considered to live in monogamous pairs defending a common territory, with mates living a largely solitary life, but these conclusions come from few studies with small samples. We captured maned wolves in Emas National Park, central Brazil, and monitored their use of space using radiotelemetry. Home-range size and overlap of 45 adults, and interactions between members of 5 pairs, were investigated. Home-range sizes of resident adults averaged 80.18 km^2 using the fixed kernel with 95% of the locations, and averaged 13.78 km^2 with 50% of the locations. Overlap of 95% ranges between male–male, female–female, or mixed dyads was similar, approximately 0.20, whereas 50% ranges of maned wolves showed less overlap overall but more tolerance for overlap with the opposite sex. Members of a pair were located alone more often than together, and even when located simultaneously maintained a mean distance of >0.5 km apart, independent of time of day. Results are in agreement with a spatial organization based on monogamous mating pairs with little intrapair sociality, but the latter needs to be investigated in more detail.

Key words: Cerrado, *Chrysocyon brachyurus*, home range, maned wolf, spatial organization

Most mammalian carnivores are solitary and exhibit a social system of intrasexual territoriality, with larger ranges of males encompassing those of several females (Sandell 1989). Most canid species exhibit a system of group territoriality, with group composition ranging from exclusive mating pairs, mainly found among the smaller species, to complex pack structures exhibited by large canids such as gray wolves (*Canis lupus*) or African wild dogs (*Lycaon pictus*—Geffen et al. 1996; Moehlman 1989).

The maned wolf (*Chrysocyon brachyurus*, Illiger, 1811), occurring throughout the grasslands of Argentina, Bolivia, Brazil, Paraguay, Peru, and possibly northern Uruguay (Beccaceci 1992; Dietz 1984; Mones and Olazarri 1990; Richard et al. 1999), is an exeption to this rule relating size and social system. Weighing between 20 and 30 kg and measuring 70–90 cm in height (Silveira 1999), maned wolves are included among the large canids (Moehlman 1989), and are the largest canid in South America. However, free-ranging maned wolves are considered to exhibit a social system characterized by monogamous breeding pairs inhabiting exclusive pair territories (Dietz 1984; Rodrigues 2002), with the members of a pair leading largely solitary lives (Dietz 1984).

The diet of maned wolves is the only extensively studied aspect of their ecology. Maned wolves are opportunistic omnivores, feeding on small vertebrates such as birds, reptiles, and rodents, as well as fruits, especially *Solanum lycocarpum* (e.g., Jácomo et al. 2004; Juarez and Marinho-Filho 2002; Motta-Junior et al. 1996), playing an important role as seed
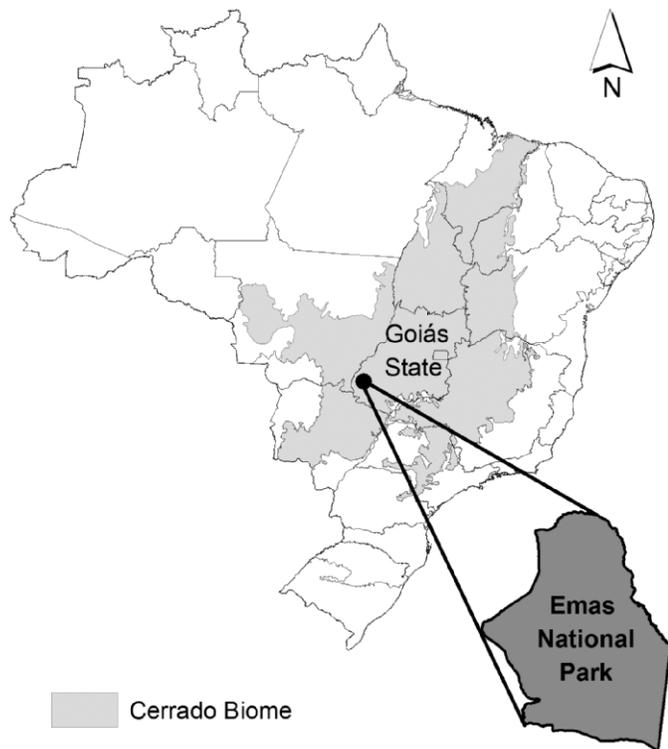
Fig. 1.—Location of Emas National Park within the Cerrado biome of Brazil.

dispersers (Lombardi and Motta-Junior 1993; Santos et al. 2003). Thus, relative to the large body size of the maned wolf, food availability is low, food items are likely evenly distributed, and exclusive mating pair territories are in accordance with the resource dispersion hypothesis (Carr and Macdonald 1986; Geffen et al. 1996). For predators feeding on small prey, presence of a conspecific likely reduces foraging efficiency (Sandell 1989), corroborating the observation that maned wolf pairs do not forage together. Recently, Melo et al. (2007) found indications of a higher level of sociality during daytime resting hours in a pair of maned wolves, questioning the categorization of the maned wolf as a largely solitary animal.

To date, all studies of the home-range size, space use, and social organization of maned wolves relied on extremely small sample sizes (e.g., Carvalho and Vasconcellos 1995; Dietz 1984; Melo et al. 2007). In our study, we use data from long-term radiotracking of 50 maned wolves from central Brazil to investigate these parameters. Based on the assumed structure of monogamous breeding pairs, we predicted a 1:1 adult sex ratio (Moehlman 1986), little sexual dimorphism, little to no difference in home-range size between sexes (Geffen and Macdonald 1992), and little to no overlap between nonpair individuals. Additionally, we provide information on intrapair spatial association and interaction.

MATERIALS AND METHODS

Study area.—Emas National Park (Fig. 1) is situated in central Brazil in the extreme southwest of the state of Goiás

(18°19′S, 52°45′W) and is 1 of Brazil's most representative Cerrado reserves. The Cerrado is considered a hotspot biome (Myers et al. 2000) and Emas National Park was listed as a Human Heritage Reserve by the United Nations Educational, Scientific and Cultural Organization. Its 132,000 ha protects large tracts of grassland plains (97%), small patches of shrub fields or Cerrado sensu stricto (1%), marshes, and riparian forest (2%). During the wet season (October–March), rainfall is around 1,500 mm. There is virtually no rain the rest of the year, when daytime temperatures reach 40°C and may drop as low as −1.5°C at night (IBDF/FBCN 1981). Emas National Park is situated in 1 of the most productive agricultural areas of central Brazil, where soybean and corn plantations dominate and fragment the regional landscape. The park is literally an island of natural vegetation within agricultural land.

Capturing maned wolves.—We captured maned wolves using custom-made metal cage traps ($0.8 \times 0.8 \times 2.0$ m) baited with a live pigeon, and with padded leghold traps. We set a total of 50 live traps along trails in Emas National Park and the surrounding farmland at every 1.5–2.0 km and checked them daily for a minimum of 90 days at each trap site before moving them to a different location. In addition, we distributed 28 leghold traps along natural animal trails to increase the trapping effort, and checked them twice a day. The necessary permits for trapping and subsequent procedures were issued by the Brazilian government environmental agency (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, license 241/1995–241/2007), and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

We used a combination of tiletamine and zolazepam (Zoletil, Virbac S. A., Carros-Cedex, France—Furtado et al. 2006) to immobilize captured maned wolves, and after sedation the individuals were weighed, measured, and fitted with a very-high-frequency (VHF) radiocollar (Advanced Telemetry Systems, Inc., Isanti, Minnesota). A sequence of physical and oral examinations was done and blood, feces, urine, and ectoparasites were sampled for each individual captured. We classified the individuals as adults or subadults based on body mass, dentition, and morphological measurements.

Radiotracking.—From September 1995 to July 2007, we tracked radiocollared maned wolves by vehicle, splitting effort between daytime (0600–1800 h) and nighttime (1801–0559 h) hours. We used a minimium of 2 directional bearings from different locations to determine each location of an individual (Millspaugh and Marzluff 2001; White and Garrot 1990) in LOCATE II (Nams 2000). Subsequent bearings on each individual were taken immediately; the maximum time that passed between 2 bearings was about 20 min.

Data analysis.—We performed Student's *t*-tests to evaluate differences between mean values of weight and body measurements of males and females to investigate sexual dimorphism. We used a binomial test to investigate departure of males and females captured from a 1:1 ratio.

For the home-range and overlap analyses, we only considered locations taken at least 12 h apart to minimize serial spatial correlation (Swihart and Slade 1985). We

analyzed adults and subadults separately and only performed home-range analyses for maned wolves with ≥ 10 locations.

We estimated home-range size using the minimum convex polygon (MCP—Hayne 1949) so results could be compared to previous studies, because MCP has been the most widely used method for estimating home ranges. We also used the fixed kernel (KER—Worton 1989) estimator, because KER is the recommended estimator for investigations focusing on home-range outlines (Harris et al. 1990; Millspaugh and Marzluff 2001). For both analyses we considered 50% and 95% of the locations, the former to represent the core area of an animal's home range, the latter to represent its full range, excluding outliers (Harris et al. 1990). We processed analyses with the software Ranges6 v1.211 (Kenward et al. 2003).

For each adult individual, we performed an incremental area analysis using the KER 95% estimate, where cumulative areas were plotted against number of locations. Because an asymptote indicates stability of home range (Gese 1990; Kenward et al. 2003), we classified individuals with asymptotic location-area curves as residents, and others as transients (Fig. 2). Transients should have larger home ranges and a larger number of overlapping ranges. We tested our visual choice by comparing home-range estimates between the 2 groups using a *t*-test for independent samples, and number of overlap dyads per individual (see below). We also compared mean number of locations and duration of monitoring per animal, because these parameters can influence home-range estimates.

We used a factorial analysis of variance to test for home-range variation between estimators, seasons, sexes, and age classes, and a Pearson's test for correlation to investigate relationship between number of locations and home-range estimate.

To investigate inter- and intrasexual spatial association among individuals we analyzed home-range overlap following Minta (1992, 1993). For 2 animals, A and B, we calculated mean overlap as the geometric mean of the product of the ratios of overlap size to home-range size. Overlap is expressed in values from 0 to 1, with 1 indicating 100% overlap between ranges of identical size. We calculated mean overlap for all male–male, female–female, and male–female dyads using the 50% and 95% KER, considering only resident animals, and compared means using a Kruskal–Wallis test. We conducted this analysis for year 2003 only, because this was the year with the largest number of individuals monitored and locations obtained.

We identified potential mating pairs of maned wolves as male-female dyads with an overlap of at least 0.75 of the 95% KER range, or at least 0.50 of the 50% KER range core, or both. For these pairs, we calculated a combination of 2 coefficients of association. First, we calculated a coefficient proposed by Cole (1949). Between 2 animals, A and B:

$$C_A = \frac{2AB}{A + B},$$

where A is the total number of times animal A is observed, B is the total number of times animal B is observed, and AB the number of times they are observed together; $C_A > 0.5$ indicates association. Although we would always attempt to locate the

FIG. 2.—Typical examples of location-area curves for adult maned wolves (*Chrysocyon brachyurus*) classified as residents (dashed line) and transients (solid line).

2nd pair member upon detection of the 1st, we defined "together" as located by radiotelemetry within 30 min of each other. Driving at approximately 20 km/h and assuming a mean range of the radiocollar signal of 5 km, we would detect the 2nd pair member by this method if it was up to 10 km away from the 1st animal. Thus, this coefficient provides coarse-scale information on proximity of the members of a pair in the study area.

Second, we calculated an index of interaction, I_I, proposed by Kenward et al. (1993). This index compares the mean distance between observations of 2 animals taken simultaneously (in our case within 30 min of each other) with the mean distance between random pairs of locations. The index takes values between −1, indicating avoidance, 0, indicating random spacing, and 1, indicating close association, and is generally most reliable when the geometric mean of the distances is considered. In our case, it provides information on how closely 2 animals interact when they are generally within the same area and therefore both detectable by radiotelemetry within a short time interval. Ideally, simultaneous locations of pair members should be used for calculation of this index; however, because of a limited number of vehicles and receivers this was not possible. We recognize that by using sequential rather than simultaneous locations for calculation of this index, it is subject to several possible sources of error. For example, the distance between individuals could appear to increase during the time allowed to pass between locating the 2 animals if the animals are active or traveling, causing an overestimation of distance between individuals. However, if the time between successive locations is kept short (in this case, <30 min), we assume that distances between pairs should still be less than random if there is any spatial association.

This index of interaction is implemented in Ranges6 v1.211. To distinguish between association during resting and foraging, we calculated both indices separately for daytime and nighttime locations and used a Mann–Whitney *U*-test to investigate differences. All statistical analyses were performed in SPSS 13.0 for Windows (SPSS, Inc., Chicago, Illinois) and *P*-values are reported 2-tailed, unless stated otherwise.

TABLE 1.—Comparison of biometric measurements for adult maned wolves (*Chrysocyon brachyurus*) from Emas National Park, Brazil. Shown are number of individuals for which measurement is available (*n*), mean ($\bar{X}$, standard deviation (*SD*), and *t*- and *P*-values from *t*-test. An asterisk (*) indicates significant differences between males and females.

Measurement	Sex	*n*	$\bar{X}$	*SD*	*t*	*P*
Weight (kg)	Male	44	26.68	3.59	2.490	0.015*
	Female	29	24.63	3.22		
Circumference head (cm)	Male	44	38.78	3.11	1.924	0.058
	Female	29	37.43	2.65		
Circumference neck (cm)	Male	44	30.94	2.31	3.733	0.000*
	Female	29	28.95	2.11		
Circumference thorax (cm)	Male	44	55.66	3.77	4.019	0.000*
	Female	29	52.36	2.83		
Length head (cm)	Male	44	28.08	1.83	1.649	0.104
	Female	28	27.46	0.88		
Length body (cm)	Male	44	106.58	11.26	0.251	0.802
	Female	29	106.02	5.25		
Length tail (cm)	Male	44	44.06	12.33	0.623	0.535
	Female	29	42.58	4.10		
Total length (cm)	Male	44	150.64	8.18	1.085	0.281
	Female	29	148.59	7.38		
Length ear (cm)	Male	44	15.56	1.57	0.274	0.785
	Female	29	15.47	0.80		
Width ear (cm)	Male	42	9.19	0.72	1.771	0.081
	Female	26	8.86	0.82		
Height (cm)	Male	44	85.61	4.45	2.571	0.012*
	Female	29	83.00	3.91		
Length hind foot (cm)	Male	44	28.11	1.33	3.141	0.002*
	Female	29	26.79	2.26		

TABLE 2.—Mean home-range size (area $\bar{X}$) with standard deviation (*SD* (area)) for maned wolves (*Chrysocyon brachyurus*) in Emas National Park, Brazil, classified as resident adults (*n* = 37), transient adults (*n* = 8), and juveniles (*n* = 5), estimated with the fixed kernel (KER) and minimum convex polygon (MCP) for 50% and 95% of the locations.

Group	$\bar{X}$ locations	$\bar{X}$ duration (months)	Home-range estimator	Area $\bar{X}$ (km^2)	*SD* (area)
Resident adults (*n* = 37)	60	21	MCP50	15.09	14.10
			MCP95	67.69	43.48
			KER50	13.78	8.34
			KER95	80.18	53.03
Transients (*n* = 8)	29	29	MCP50	35.20	35.42
			MCP95	145.35	75.34
			KER50	28.60	17.01
			KER95	188.12	112.96
Juveniles (*n* = 5)	45	11	MCP50	8.96	9.30
			MCP95	97.70	150.62
			KER50	17.35	20.65
			KER95	209.68	331.11

RESULTS

Between September 1995 and July 2007 we accumulated 18,003 trap-days at 128 different sites inside the Emas National Park and 17 sites on the surrounding farmland. As a result, 84 maned wolves, 74 adults and 10 subadults, were caught 475 times (captures and recaptures) and 72 individuals were fitted with radiocollars. Number of adult males (*n* = 44) and adult females (*n* = 30) did not differ significantly from 1:1 (*P* = 0.130). Adult body mass and morphological measurements showed significant sexual dimorphism in 5 of the 12 measures taken: body weight, neck circumference, thoracic circumference, height, and length of hind foot (Table 1).

Home range.—For 45 adult individuals (23 males and 22 females) and 5 subadults (1 male and 4 females) we accumulated ≥10 independent locations for the proposed analyses. A total of 2,661 locations were accumulated among these individuals, with the mean number of locations per maned wolf being 53.22 (*SD* = 51.68), collected over a mean monitoring period of 21 months (*SD* = 14).

The incremental area curves for 8 adults did not show any tendency toward an asymptote, indicating transiency for these individuals (Fig. 2). Duration of monitoring for both groups was similar (*t* = −1.5, *d.f.* = 43, *P* = 0.241), but transients had significantly larger home ranges than residents (Table 2) for 50% and 95% of the locations for the KER and 95% of the locations for the MCP estimators (−3.978 ≤ *t* ≤ −2.403, 7.68 ≤ *d.f.* ≤ 43, 0.023 ≤ *P* ≤ 0.044), based on estimates of home-range size from significantly fewer locations (*t* = 2.95, *d.f.* = 42.89, *P* = 0.005).

Considering the MCP, mean home-range size for all resident adults was 67.69 km^2 (*SD* = 43.48) for 95% and 15.09 km^2 (*SD* = 14.10) for 50% of the locations. For the KER, these values were 80.18 km^2 (*SD* = 53.02), and 13.78 km^2 (*SD* = 8.34), respectively. Although mean home ranges of subadults were larger that those of adults (Table 2), the difference was not significant. Likewise, we did not find significant differences in home-range size between sexes, estimators, or seasons. Number of locations only showed significant correlation with home-range size for the 50% and 95% MCP for resident adults (0.337 ≤ Pearson correlation ≤ 0.547, *n* = 37, 0.0001 ≤ *P* ≤ 0.041).

Home-range overlap.—In 2003, 28 individuals (8 adult males, 13 adult females, 3 transients, and 4 juveniles) were radiotracked. We identified 5 potential male–female pairs based on an overlap of at least 0.75 of the 95% KER ($\bar{X}$ = 0.75), at least 0.50 of the 50% KER ($\bar{X}$ = 0.44), or both. Considering the 95% KER, we identified 8 male–male, 15 female–female, and 30 nonpair male–female dyads. Nonpair male–female dyads showed a mean overlap of 0.23 (*SD* = 0.23), female–female dyads of 0.21 (*SD* = 0.22), and male–male dyads of 0.19 (*SD* = 0.20). Differences in overlap among the 3 means was not significant (Kruskal–Wallis test, χ^2 = 0.404, *d.f.*= 2, *P* = 0.817). For the 50% KER, we identified 3 male–male, 3 female–female, and 10 nonpair male–female dyads. Female–female dyads showed overlap of 0.08 (*SD* = 0.06), whereas range cores of male–male dyads showed an overlap of 0.07 (*SD* = 0.05). The average overlap in range cores of nonpair male–female dyads was 0.19 (*SD* = 0.12). A Kruskal–Wallis test was not performed because of small sample size.

In the analyses of overlap, resident adults formed dyads with an average of 5.67 other adults, independent of sex, considering their 95% KER home ranges. Transients formed

dyads with an average of 10 other adults. Sample size was too small to perform statistical comparison of these values.

Interaction.—For the 5 potential mating pairs, the mean coefficient of association (Cole 1949) was 0.28 ($SD = 0.19$) during the day and 0.33 ($SD = 0.20$) during the night. Mean index of interaction (Kenward et al. 1993) was 0.72 ($SD = 0.32$) during the day and 0.86 ($SD = 0.13$) during the night (Table 3). We found no significant differences in either index between daytime or nighttime (Cole: Mann–Whitney $U = 9$, $z = -0.731$, $P = 0.465$; Kenward: Mann–Whitney $U = 11$, $z = -0.314$, $P = 0.753$).

DISCUSSION

Home-range size.—This is the 1st study to estimate home-range size and spatial organization of maned wolves based on a large sample, both in terms of individuals monitored, and in terms of locations obtained per individual. We are therefore confident that the mean Kernel home-range estimates obtained in our study, with 80.18 km^2 for 95% of the locations and 13.78 km^2 for the 50% core for resident adults, reliably reflect maned wolf home ranges. This value is considerably larger than the 38.14 km^2 estimated by Melo et al. (2007), using the 95% KER for data from global positioning system telemetry of a pair of maned wolves. However, their monitoring was restricted to a 6-month period. Other studies investigating home-range size of maned wolves report mean MCP (percentage of locations not stated) values of 30–75 km^2 for 3–6 individuals (Carvalho and Vasconcellos 1995; Dietz 1984; Rodrigues 2002). In general, long-term monitoring can result in larger home ranges, for example, if range shift is not accounted for. However, all adults considered in our estimates showed range stability and were classified as residents. Range stability over various years also has been shown for red foxes (*Vulpes vulpes*—Tsukada 1997). Locations collected over a longer time frame also give more realistic home-range estimations (Harris et al. 1990).

We did not find home-range size to differ between seasons. Food availability and the species' foraging strategy are expected to play an important role in determining home-range size (Sandell 1989). The resource defense hypothesis states that distribution of food sources has a stronger influence than their abundance (Macdonald 1983). An increase in home-range size with increasing resource dispersion has been reported for various carnivoran species, including red foxes (Geffen et al. 1992; Lucherini and Lovari 1996) and arctic foxes (*Vulpes* [formerly *Alopex*] *lagopus*—Eide et al. 2004). In Emas National Park, the maned wolf exhibits a typical omnivorous diet comprised of at least 32 items consumed according to their availability (Jácomo et al. 2004). Its ability to forage for typical seasonal food sources (e.g., Aragona and Setz 2001) should allow it to maintain a similar home-range size across seasons.

Data on home-range size for male and female maned wolves before this study are controversial. Dietz (1984) calculated the home-range sizes for pairs, but did provide data useful for comparisons between sexes. Rodrigues (2002) found females to have larger home-range sizes than males, and Carvalho and

TABLE 3.—Coefficient of association (C_A—Cole 1949), with >0.5 indicating spatial association, and index of interaction (I_I—Kenward et al. 1993), with values toward 1 indicating interaction, for 5 potential mating pairs of maned wolves (*Chrysocyon brachyurus*) monitored during 2003 in Emas National Park, Brazil, calculated for daytime locations (Day) and nightime locations (Night), together with number of times pair members were located simultaneously and geometric mean of distances observed between simultaneous locations.

	Day		Night	
	$\bar{X}$	SD	$\bar{X}$	SD
No. simultaneous locations	15	13	12	9
C_A	0.28	0.19	0.33	0.20
Distance observed (m)	970	1,029	572	569
I_I	0.72	0.32	0.86	0.13

Vasconcellos (1995) state that male maned wolves occupy larger home ranges than females, but in both cases the authors assumed that this could be an artifact of small sample size. We found no significant difference between home-range size of the sexes. In combination with a 1:1 adult sex ratio indicated by number of captures, our findings agree with the categorization of maned wolves as living in monogamous pairs. Although we observed sexual dimorphism in 42% of the body measurements we made, actual differences were small (Table 1). For example, mean body weight between the sexes differed only by approximately 2 kg, but this difference was statistically significant.

Home-range overlap.—One of the main characteristics of spacing pattern in a population is the extent of range overlap between individuals. Exclusive ranges should be expected when food resources are stable and uniformly distributed (Carr and Macdonald 1986; Sandell 1989), as we hypothesized for the maned wolves in Emas National Park. Monogamous pairs should be characterized by extensively overlapping home ranges (Geffen and Macdonald 1992), and we identified 5 maned wolf pairs exhibiting this characteristic. Dietz (1984) states that maned wolf pairs defend an exclusive area, whereas Rodrigues (2002) observed a high degree of overlap between maned wolves on the borders of their home ranges, but not in areas of intensive activities. Neither author provided any measure of overlap. In this sense, our study is the 1st to provide more substantial data on spatial organization of maned wolves.

We observed that both sexes shared their 95% ranges to some extent, with overlap being in the range of 0.20 independent of sex. Overlap decreased to around 0.08 in the 50% core areas for dyads of the same sex, but remained relatively high, at 0.18, for male–female nonpair dyads. Although our results for overlap in general indicate that home ranges are not entirely defended as territories, but have exclusive core areas (Crooks and Van Vuren 1996), the value for nonpair dyads does not fit into this picture. It could indicate that food abundance is higher than assumed, leading to relaxation of territoriality, as shown for arctic foxes (Eide et al. 2004) or red foxes (Macdonald et al. 1999), or some resources used by maned wolves could be heterogenously distributed. In both cases, maned wolves would exhibit more tolerance of the other,

rather than the same sex, indicating differential resource use and higher intra- than intersexual competition.

Although our results on overlap could be an artifact of failing to identify all mating pairs or transient individuals, the possibility of relaxed territoriality receives additional support from considerable overlap observed between home ranges of 2 distinct maned wolf pairs during a 2-month period in 2003. The crop fields that characterize the surroundings of the park—and constituted parts of these pairs' home ranges—present a constantly changing environment. Because maned wolves use these crop fields, it is possible that the different stages of the plantation cycle introduce temporal heterogeneity in food distribution or abundance in these areas. In Emas National Park, maned wolves were observed scent marking on clumps of grass and defecating on termite mounds, ant mounds, or on trails. This behavior suggests that territoriality is an important behavioral trait that affects the species' spatial organization in the park.

Dietz (1984) observed maned wolves traveling on the periphery of home ranges of pairs and hypothesized that the presence of nonterritorial individuals may explain why vacancies left by an individual's death or emigration are quickly filled. Using the lack of an asymptote in location-area curves as an indication of transiency, we identified 8 potentially transient adult individuals, which indeed showed larger home ranges. Transient red foxes also have been shown to roam over larger areas and occupy vacant territories (Dekker et al. 2001). However, occupation of territory vacancies is not restricted to transient individuals. In Emas National Park, we observed 1 female extending her range into the area of another female only 4 days after the latter female was road-killed. Rodrigues (2002) observed the same behavior in his study, where a female promptly expanded her home-range area after the death of another female.

Interaction.—For predators feeding on food items that are easily subdued by a single animal, as is the case for most food items consumed by the maned wolf (e.g., Jácomo et al. 2004), presence of a conspecific is likely to be disadvantageous (Sandell 1989). During foraging, individuals should therefore avoid each other, a behavior that has been observed for other solitary foragers like the red fox (Poulle et al. 1994), and Melo et al. (2007) provide some evidence for this avoidance in the case of the maned wolf. Because our study area was large, and maned wolves range over large areas, Cole's (1949) coefficient of association provided a coarse-scale measure of how often members of a pair are detected simultaneously (in our case, within 30 min) by radiotelemetry. Members of a pair were located simultaneously less often than alone, and when located simultaneously, showed a moderate degree of interaction, with mean distance between simultaneous locations consistently smaller than random but still >500 m, which should be sufficient to avoid interference with the mate's foraging success. Therefore, our results support the hypothesis by Dietz (1984) that, although sharing a common territory, members of a maned wolf pair live largely solitary lives, in the sense of not showing close spatial association with their mates. Contrary to that, we have observed maned wolves hunting ground birds

together. In contrast to Melo et al. (2007), we did not find closer association or interaction during daytime resting hours. Although the global positioning system collars used by Melo et al. (2007) yield much more exact data than regular VHF tracking, the restricted monitoring period (6 months) could be biased toward the period of parental care behavior. In captivity, male maned wolves have been observed providing food to offspring (Bartmann and Nordhoff 1984; Veado 1997), and sightings of males accompanied by young in the wild suggest that they are involved in cooperative rearing of the offspring (Carvalho and Vasconsellos 1995; Dietz 1984; Rodrigues 2002). This trait is typical of canids in general (Kleinman and Eisenberg 1973) and for most species is probably related to the necessity of food provisioning by males for the survival of young, and the role of males in territory maintenance (Kamler et al. 2003). We did not explicitly investigate aspects of parental care between maned wolves at Emas National Park, but we observed a radiotagged male regurgitating food to 3 pups after their mother died when hit by a car.

In summary, our findings support the description of maned wolf spatial organization as based on monogamous breeding pairs with home ranges largely overlapping between members of a pair, and a smaller number of transients, roaming over larger, nondefined areas. Although this resembles the typical population structure for canids feeding on homogenously distributed and low-abundance food sources (Geffen et al. 1996), we found some indication for relaxed territoriality. Overall, sociality between members of a breeding pair seems to be low, but our study focused on spatial organization of a maned wolf population and not on direct interaction between individuals. Because direct observations and results from Melo et al. (2007) indicate a potentially more social life, intrapair association and interactions of maned wolves, as well as interpair tolerance, remain to be studied in detail.

RESUMO

O lobo-guará (*Chrysocyon brachyurus*) é o maior canídeo da América do Sul, pesando até 30 kg. Apresenta uma dieta onívora, composta por frutas e pequenos vertebrados, e é um animal solitário na maior parte do tempo, formando casais monogâmicos, que defendem territórios comuns. Estas informações, porém, se originaram de um pequeno número de estudos realizados com amostragens limitadas. Neste estudo, lobos-guarás foram capturados no Parque Nacional das Emas, região central do Brasil, e monitorados através da técnica da radio-telemetria. Investigou-se a área de vida de 45 lobos-guarás adultos, assim como sua sobreposição e a interação entre os indivíduos de 5 casais. A extensão da área de vida dos animais adultos foi em média 80.18 km^2, considerando o método "fixed kernel" com 95% das localizações, e 13.78 km^2 com 50% das localizações. Considerando a área de vida estimada com 95% das localizações, observou-se uma sobreposição similar entre machos, entre fêmeas e entre os dois sexos, de aproximadamente 0.20, enquanto que com estimativas utilizando 50% das localizações, foi observada uma menor sobreposição e maior tolerância para a sobreposição

entre sexos opostos. Os indivíduos que formavam um casal foram mais freqüentemente localizados sozinhos do que juntos, e mesmo quando registrados juntos, mantiveram uma distância maior do que 0.5 km, independente do período do dia. Estes resultados estão de acordo com uma organização espacial baseada em casais monogâmicos com pouca interação social entre seus indivíduos.

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