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Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil

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Abstract

Four species of canids occur in the Cerrado of central Brazil. Three of them, the maned wolf *Chrysocyon brachyurus*, the crab-eating fox *Dusicyon thous* and the hoary fox *Dusicyon vetulus*, were studied in Emas National Park between 1996 and 1999 to investigate niche separation. The diet of the three species was studied to understand niche breadth and degree of overlap. Habitat and activity patterns were used as second and third ecological parameters to define niche dimensions, and were estimated using camera-trap data. The maned wolf is the largest species, weighing *c*. 21 kg, and is about three times larger than the crab-eating fox and six times larger than the hoary fox. The major ecological differences between the three species were found in their food niche and habitat use, where crab-eating fox presented higher differences from the hoary fox (Pianka's index of niche overlap $(O) = 0.405$). Despite differences in niche breadth, habitat use between the hoary fox and the maned wolf were more similar, explaining their larger overlap, in comparison with habitat use by the crab-eating fox. Activity patterns among the species showed less divergence. The three species presented two activity peaks, one in the dusk–night period and another in the morning period. These data permit a better understanding of the ecological separation of the three Cerrado canids that enables their coexistence.

Key words: diet, habitat, activity, competition, niche separation, canids, Cerrado, *Chrysocyon brachyurus*, *Dusicyon thous*, *Dusicyon vetulus*

INTRODUCTION

The family Canidae evolved in North America and subsequently radiated to South America, Eurasia and Africa. In South America, they are represented by seven genera and 11 species (Berta, 1987). Extinction of large South American canids at the end of the Pleistocene followed the extinction of their large herbivore prey base. The present pattern of canid distribution in South America may be explained by assuming that a group of species of generalized grassland canids colonized suitable grassland habitats along the Andes, reaching the southern pampas and Patagonian grasslands as well as spreading over the Brazilian highlands (Langguth, 1975). The current high diversity of South American canids is, at least in part, the result of an opportunistic strategy of feeding on small prey as well as on fruit and grains (Berta, 1987).

Differences between sympatric species in the use of trophic, temporal and spatial niches have been frequently used to describe and explain community structure (Jaksic, Schlatter & Yanez, 1980; Greene & Jaksic, 1983; Konecny, 1989; Sunquist, Sunquist & Daneke, 1989; Rabinowitz & Walker, 1991; Jaksic, Feinsinger & Jimenez, 1993; Marti *et al*., 1993). The segregation of these niche dimensions may permit the partitioning of resources and thus the ecological coexistence of species. Whether competitive interactions, stochastic effects or other historical and structural factors cause their divergence is unknown (Underwood, 1986).

Variation in the body masses of sympatric carnivore species, with similar morphology and foraging strategies, has a strict relation with the body masses of their prey (see Carbone & Gittleman, 2002). The basic idea is that large species specialize in larger prey and that body mass differences evolve to reduce competition (Rosenzweig, 1966). Sometimes, however, differences in body mass alone are not sufficient to allow coexistence. Rabinowitz & Walker (1991), studying a carnivore community in Thailand composed of 21 species, found that variation in factors such as habitat and activity patterns may determine the coexistence of species with similar food habits. Johnson & Franklin (1994), studying two species of the genus *Dusicyon* in Chile, found that the selection

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of microhabitat determines their coexistence. Kruuk *et al*. (1994), studying the ecological separation between three sympatric river otters in Thailand, found that the variation in the use of microhabitat and the specialization of some food items are the major factors allowing these species to coexist.

Four canid species are found in central Brazil: the maned wolf *Chrysocyon brachyurus*, the hoary fox *Dusycion vetulus*, the crab-eating fox *Dusicyon thous* and the bush dog *Speothos venaticus*. The first two are practically endemic to the Cerrado biome, a landscape dominated by grassland with scattered brushes and shrub trees. Except for the study by Juarez & Marinho-Filho (2002), the available literature on three species of canids is limited to descriptive information about their general biology, with no further consideration to community level structure or ecological features (Langguth, 1975; Brady, 1979; Bisbal & Ojasti, 1980; Dietz, 1984; Strahl, Silva & Goldstein, 1992; Dalponte, 1997).

Our study was carried out in Emas National Park (ENP) between July 1994 and July 1996 and from March 2002 to March 2003, and our aim was to elucidate the basic ecological differences between the maned wolf, crab-eating fox and hoary fox using a comparative analysis of their diets, habitat use and activity patterns.

METHODS

Study area

Emas National Park is situated in central Brazil in the extreme south-west of Goiás State (18°19′S, 52°45′W) and is one of Brazil's most representative Cerrado reserves. Its 132 000 ha protects large tracts of grassland plains (97%), small patches of shrub fields Cerrado (*sensu stricto*) (1%), marshes, and riparian forest (2%). About 1500 mm of rain falls during the September to May wet season (IBDF/FBCN, 1981). There is virtually no rain the rest of the year, when daylight temperatures reach 39 °C and may drop as low as − 1.5 °C at night. At least 13 endangered mammal species are found in the Park, which is considered to be one of the best sites for observing large Cerrado fauna (Erize, 1977; Redford, 1983). Emas is centred in one of the most productive agricultural areas of central Brazil, where soybean and cornfields are the main activity that fragments the regional landscape.

Scat collection and analysis

Scats from the 3 canids were collected along dirt roads in Emas Park, sun dried and stored in plastic bags. At the beginning of the study the identification of the scats was achieved by comparing a scat reference collection made from zoo specimens and their association with tracks. Later, familiarity of the researchers in identifying the scats in the field enabled the species to be identified. For instance, maned wolves produce much larger scats than the other two species studied, varying from 22 to 36 mm ($n = 134$) in diameter, and they usually deposit them in conspicuous sites. Latrines are also commonly found. Crab-eating foxes and hoary foxes, in contrast to the maned wolf, do not usually deposit their scats in conspicuous sites. Although the crab-eating fox is twice the weight of a hoary fox, their scat diameters can overlap. The scat diameter of crab-eating fox varied from 13 to 20 mm, while those of hoary foxes ranged from 11 to 18 mm. However, the scats from these 2 species present considerable physical differences in shapes, with those of crab-eaters being much more segmented than those of the hoary fox.

Scats were washed in a sieve under running water. They were later dried and food items were separated macroscopically, according to the methodology described in Putman (1984) and Reynolds & Aebischer (1991), into the following categories: mammal bones, bird bones, reptile bones, hair, feathers, scales, insect parts, fruit parts, inorganic material. Animal parts were identified with the aid of a reference collection of animal parts previously obtained from the field and museum collections. Plant parts not identified were sent for identification at the Botanic Department of the Universidade Federal de Goiás.

Activity patterns and habitat use

Information on activity patterns was obtained using camera trapping between March 2002 and March 2003 (Carbone *et al*., 2001; Silveira, Jácomo & Diniz-Filho, in press). Eighty-two infrared-triggered cameras were distributed across the study area close to animal trails and were set to work on a continuous 24 h basis. Photographic rates for each species were given by the number of photographs for that species divided by the total number of hours of camera trapping. The exact time of the photo-trapped species was also printed on the photograph, allowing the number of records for the species to be counted in the following time categories: morning (05:00–11:00); afternoon (11:01–17:00); dusk (17:01–18:00); and night (18:01–04:59). The relationship between the number of records and these periods of activity was tested for independence by a chi-square test. For better visualization of their activity patterns, the classes of periods were presented as percentages of the total records per species.

The same 82 camera-traps used in the activity study were moved across 113 distinct sites among the 3 major habitats of Emas Park: the grassland, comprising 96% of the Park's area, the Cerrado (*strictu sensu*) characterized by shrubs and scattered short trees, covering 2% of the area and, forest, distributed along the streams and rivers, making up 1% of the Park. The camera-traps were placed in these habitats in proportion to their extent in the study site. Differences in the average photographic rates among habitats, for each species, were tested using single classification analysis of variance (ANOVA), but due to non-normality and heterocedasticity in data, the F-statistics were tested under randomization procedures in ECOSIM 7.0 (Gotelli & Entsminger, 2001).

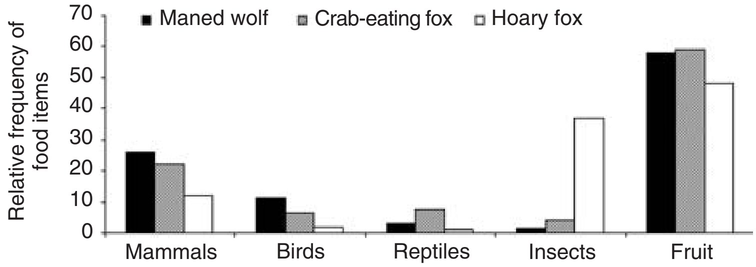

Fig. 1. Relative frequency of food items consumed by maned wolf *Chrysocyon brachyurus*, the crab-eating fox *Dusicyon thous* and the hoary fox *Dusicyon vetulus* in Emas National Park, Central Brazil.

Niche breadth and overlap

The food niche breadth was calculated for the maned wolf, crab-eating fox and hoary fox using the total number of items identified in the scats. Levins index (Krebs, 1998) was used as an exploratory measurement of niche breadth, given as: $B_A = (B - 1)/(n - 1)$, where B_A is the standardized Levins index by the number of items (n) e $B = 1/\sum p_i^2$, where p is the frequency of the item on the total sample (scats). To verify the seasonality effect on the breadth width, the Levins (B_A) index was also calculated by clustering the frequencies for the months between 1994 and 1996 that represented the dry season (June, July and August) and for the other months, which represented the rainy season. Values of B_A close to 1.0 indicate that the resources are used in similar frequencies (equidistributed), while diet concentration in 1 or a few items will generate B_A values close to 0.

The food niche overlap was calculated using the total number of items identified in the scats of the 3 species. The Pianka index between species 1 and 2 (O_{12}) (see Pianka, 1974; Krebs, 1998; Gotelli & Entsminger, 2001) is given as

$$O_{12} = O_{21} = \frac{\sum_{i-1}^{n} p_{2i}\, p_{1i}}{\sqrt{\sum_{i-1}^{n} \left(p_{2i}^2\right)\left(p_{1i}^2\right)}}$$

where p_i is the frequency of the ith item in the diet. This index was used as a measure of pairwise overlap and is in fact a correlation between species along the abundance of items, so that values close to 1.0 indicate equal use of resources in their relative abundances. The significance of the overlap was tested using randomization procedures in ECOSIM 7.0 (Gotelli & Entsminger, 2001).

RESULTS

A total of 2123 scats from the three canids were collected. The scats were analysed macroscopically and 39 food items were identified to the lowest taxonomic level possible. However, as some identifications were limited to the level of order, the total number of identified food items represents an underestimate of the total number of food items (species) consumed by the canids.

Diet description

Maned wolf

From 1673 maned wolf scats, 38 items were identified. Twenty of these items were grouped in the animal category, representing 42%, and 18 in the plant category, representing 58% of the animals' diet (Table 1). These categories were later divided in five classes, with the following percentages: mammals (26%), birds (11.3%), reptiles (3.1%), insects (1.6%) and plants (58%) (Fig. 1). For the animal items, rodents were most frequently found, corresponding to 24% of the total, followed by Tinamidae birds with a frequency of occurrence of 8%. For the plant items, the maned-wolf fruit *Solanum lycocarpum* had a frequency of occurrence of 18% and was the most important item, followed by *Annona* spp. (11%), and species of dwarf coconuts (10%).

Crab-eating fox

From 177 crab-eating fox scats that were analysed, 18 items were identified. Five items were animal matter, representing 41% of its diet and 13 plant matter, representing 59% of its diet (Table 1). The items were clustered in five classes with the following percentages: mammals 22.5%, birds 6.6%, reptiles 7.6%, insects 4.3%, and plant matter 59% (Fig. 1). In the animal category, rodents had the highest frequency at 22%, followed by snakes at 8% and Tinamidae birds at a frequency of occurrence of 6%. Within the plant items, dwarf coconut was the most frequent at 29%, followed by *Annona* spp. at 5%, and bromélia at a frequency of occurrence in the scats of 3%.

Hoary fox

From the 273 hoary fox scats that were analysed, 16 items were identified. Six were classified in the animal category, representing 52% of its diet, and 10 as plant origin, comprising 48% of its diet (Table 1). The items were

Table 1. Percentage of animal and plant items found in the scats of the maned wolf *Chrysocyon brachyurus*, crab-eating fox *Dusicyon thous* and hoary fox *Dusicyon thous* in Emas National Park

	Maned wolf	Crab-eating fox	Hoary fox
Animal and plant items	Percentage of each item/number of total items ($n = 4540$)	Percentage of each item/number of total items (302)	Percentage of each item/number of total items (596)
Rodent	23.964	–	12.2
Nine-banded armadillo *Dasypus septemcinctus*	1.585	–	–
Hairy armadillo *Euphractus sexcinctus*	0.418	–	–
Naked tail armadillo *Cabassous unicinctus*	0.110	–	–
Pampas deer *Ozotoceros bezoarticus*	0.088	–	–
Agouti *Dasyprocta* spp.	0.022	–	–
Opossum *Didelphis albiventris*	0.066	–	–
Hoary fox *Dusicyon vetulus*	0.110	–	–
Grison *Galictis cuja*	0.044	–	–
Tinamidae birds	8.171	22.500	1
Unidentified large birds	0.176	5.600	–
Seriema *Cariama cristata*	0.352	–	–
Birds from the order Passeriformes	1.453	–	1
Psittacidae birds	0.528	–	–
Greater rhea *Rhea americana*	0.396	–	–
Curassow *Crax fasciolata*	0.044	–	–
Egg	0.176	–	–
Insects	1.651	4.300	3.700
Teju lizard *Tupinambis* spp.	0.638	–	–
Termites		–	33.000
Snakes	2.511	7.600	1.200
Maned-wolf fruit *Solanum lycocarpum*	17.973	1.600	3.300
Annonaceae 2 species	10.814	5.300	19.000
Annona spp. *Annona monticula*	1.497	0.300	0.300
Curcubittaceae – *Melancium campestris*	0.594	–	–
Miscellaneous fruits	0.066	7.900	–
Talisea angustifolia	0.418	–	–
Myrtaceae	2.466	2.600	2.000
Curriola *Poulteria* spp.	1.696	4.300	0.500
Parinari obtusifolia	5.286	1.600	2.300
Grass	3.237	0.300	0.200
Bromélia balansae	0.947	3.300	–
Hortia brasiliensis	0.550	–	–
Anacardium spp.	1.453	1.000	0.500
Byrsonima spp.	0.176	–	–
Diospyrus hispida	0.220	1.300	0.500
Rubiaceae	0.088	0.300	–
Palicourea sp.	0.022	–	–
Dwarf coconuts 3 species	10.044	28.800	19.300

grouped in five classes with the following percentages: mammals 12.2%, birds 2%, reptiles 1.2%, insects 36.6% and plant species 48% (Fig. 1). Among the animal origin items, only two species of termites (*Syntermes wheeleri* and *Conitermes* sp.) represented 33% of all animal items, followed by rodents, with 12% frequency in the scats, and

Table 2. Niche breadth (B_A) calculated for the maned wolf *Chrysocyon brachyurus*, the crab-eating fox *Dusicyon thous* and the hoary fox *Dusicyon vetulus* in Emas National Park from the total number of items identified in the scats of the three canids for the months that represent the dry season (June, July and August), and the rainy season (other months), between 1994 and 1996

	Niche breadth (B_A)		
Season	Maned wolf	Crab-eating fox	Hoary fox
Dry 1994	0.075	0.076	0.080
Rainy 1994–95	0.227	0.079	0.082
Dry 1995	0.158	0.116	0.076
Rainy 1995–96	0.178	0.121	0.118
Dry 1996	0.075	0.083	0.062
B_A overall	0.180	0.140	0.100

dwarf coconuts and *Annona* spp. with 19% frequency of occurrence each.

Food niche breadth and overlap

The food niche breadth (B_A) of the maned wolf, crab-eating fox and hoary fox in Emas National Park, calculated from the total number of items identified in the scats of the three species, can be found in Table 2. The maned wolf presented the largest niche breadth (overall $B_A = 0.180$), followed by crab-eating fox and hoary fox. The three species maintained this same difference ratio in the food niche breadth during the dry and rainy season (Table 3). In the dry season, niche breadths were smaller than in the wet season, and maned wolves tended to concentrate on a few available items, although this difference was not very obvious in the other two species.

Among the three canids, the maned wolf and the hoary fox presented the highest food overlap indices (Table 3), statistically significant at the 5% level after 5000 randomizations, followed by the crab-eating fox and the maned wolf.

Habitat use

Among the three major habitat types in the Park, 113 distinct sites were sampled proportionally for their availability. Seventy-eight cameras sampled the grasslands, 18 the Cerrado, and 17 the forest habitat. Significant differences in habitat use were found after 5000 randomizations of F-statistics, for maned wolf and hoary fox. Both species predominantly used the grassland habitat, while the crab-eating fox used all three habitats with similar rates, (although with large variances in grassland) (Fig. 2, Table 4).

Activity patterns

In 157 968 camera-trap hours, the maned wolf was recorded 177 times, crab-eating fox 93 and the hoary fox 43 times. The relationship between records and periods of activity was statistically independent ($\chi^2 = 23.88$, $P = 0.0005$), indicating that the three species have different activity patterns. All three species concentrated most of their activity in the night period but varied their daily activity (Fig. 3). The activity of maned wolves had a more homogeneous distribution in time, presenting activity at all periods. Nevertheless, two activity peaks

Table 3. Pianka's food niche overlap (O) (below the diagonal) found for maned wolf *Chrysocyon brachyurus*, crab-eating fox *Dusicyon thous* and hoary fox *Dusicyon vetulus* in Emas National Park, calculated from the 40 food items identified in the scats of the three species. Above the diagonal are the type I errors of each comparison, obtained by 5000 random permutations in ECOSIM

	Maned wolf	Crab-eating fox	Hoary fox
Maned wolf	1.000	0.074	0.044
Crab-eating fox	0.438	1.000	0.182
Hoary fox	0.498	0.4053	1.000

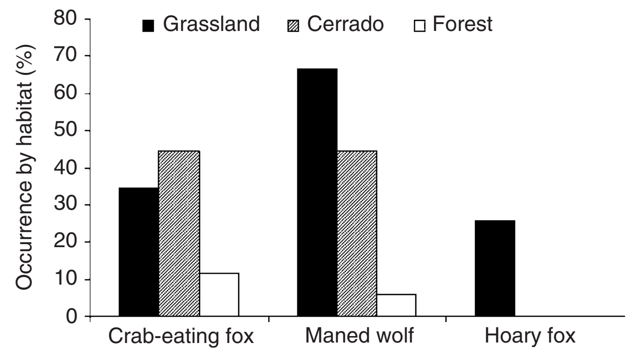

Fig. 2. Habitat use (%) by the maned wolf *Chrysocyon brachyurus*, the crab-eating fox *Dusicyon thous* and the hoary fox *Dusicyon vetulus* in Emas National Park, as determined by camera-trapping. Bars, percentage of occurrence of each species in the total camera-traps set at each habitat type: grassland ($n = 78$); Cerrado ($n = 18$); forest ($n = 17$).

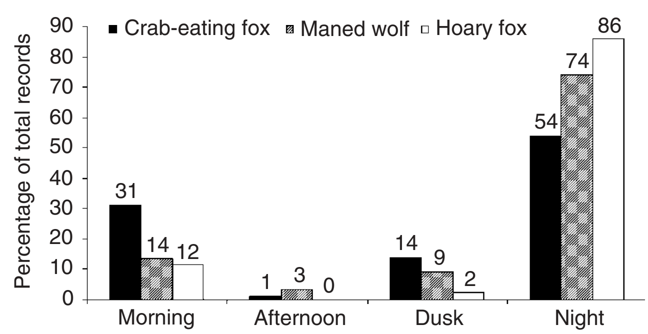

Fig. 3. Maned wolf *Chrysocyon brachyurus*, crab-eating fox *Dusicyon thous* and hoary fox *Dusicyon vetulus* activity patterns in the four periods in Emas National Park, as determined by camera-trap data. Hours were grouped in the following classes: morning (05:00–11:00); afternoon (11:01–17:00); dusk (17:01–18:00); and night (18:01–04:59).

Table 4. Average photographic rates (photographs/hours) and respective standard deviations for three canid species in three habitat types. F-statistics refer to difference among habitats for each species defined by a single classification ANOVA, with the associated type I error (P) obtained by 5000 randomizations in ECOSIM

Habitat	Camera-trap	Crab-eating fox	Maned wolf	Hoary fox
Grassland	78	0.000980 ± 0.002065	0.001498 ± 0.001973	0.000308 ± 0.000667
Cerrado	18	0.000178 ± 0.000557	0.000136 ± 0.000578	0.000010 ± 0.000007
Forest	17	0.000106 ± 0.001867	0.000600 ± 0.000777	0.000009 ± 0.000005
All habitats	113	0.000864 ± 0.001867	0.00146 ± 0.001763	0.000213 ± 0.000571
F-statistics		1.485	6.105	4.170
P		0.232	0.003	0.016

were observed, one in the morning and another at night. The crab-eating fox also presented two activity peaks, one in the morning and one at night but with some considerable activity during the dusk period. The hoary fox was the most nocturnal of all species, with a few records for the morning period.

DISCUSSION

In theory, the coexistence of carnivore species is possible because of their differences in size, morphology or behaviour, in such a way that the overlap along their niche dimensions can be diminished (Rosenzweig, 1966; Pianka, 1974). The adaptation of most South American canids to a carnivore–omnivore diet, with opportunistic feeding behaviour, may be explained, at least in part, by the lack of interspecific competition (Berta, 1987).

Among the three canid species studied, the largest size and morphological divergences are between the maned wolf (23 kg) and the other two species, the hoary fox (4 kg) and the crab-eating fox (7 kg). These differences partially reflect on their diet breadth and overlap indexes.

The niche breadth found for the three species presented low indexes, with the largest niche breadth found for the maned wolf, followed by the crab-eating fox and the hoary fox. These low values indicate that these species use the resources in an unequally distributed way, consuming few resources with higher frequencies and a lot of species in lower frequencies. This is expected considering the large number of food items available.

The highest food niche overlap occurred between the maned wolf and the hoary fox where, out of the 16 food items consumed by the fox, 15 were also eaten by the maned wolf. Maned-wolf fruit was the most important plant item eaten by the maned wolf, with dwarf-coconuts and *Annona* spp. the plant items eaten most by the hoary fox. Among the animal items, termites were not eaten by the maned wolf. Maned wolves are approximately six times larger than hoary foxes, and have disproportionately long limbs that allow them to forage in tall grass, a habitat also used by the fox.

The second highest niche overlap occurred between the crab-eating fox and the maned wolf, although it was not statistically significant at the 5% level (but notice that type I error is *c*. 7%). In general, fruits and small mammals were items eaten most by both species, and in similar proportions. However, in contrast to the diet of the crab-eating fox, the diet of the maned wolf included larger prey items (> 1 kg). Similar overlap relations between the diets of the maned wolf and crab-eating fox were detected by Juarez & Marinho-Filho (2002), where consumption of larger prey items was restricted to the maned wolf. Motta-Junior, Lombardi & Talamoni (1996) described a similar diet for the maned wolf from another Cerrado site.

When comparing the diet of the maned wolf with the crab-eating fox it is possible to observe an inversion in the order of consumption of the bird species (family Tinamidae) and snakes, where the first group was consumed more frequently by the wolf and the second consumed more frequently by the fox. The crab-eating fox presented the highest frequency for the consumption of snakes within the three species. Of the 18 plant items eaten by the maned wolf, 14 (72%) were also eaten by the crab-eating fox, although the frequency order of these items in its scats varied. The maned wolf ate maned-wolf fruit, *Annona* spp. and dwarf coconuts (three species) more frequently, while the crab-eating fox ate dwarf coconuts and grasses. Dwarf coconuts were important in the diet of the crab-eating fox in ENP. Coconuts are also important items for the species in other localities (Motta-Junior, Lombardi & Talamoni, 1994; Facure, 1996; Facure & Giaretta, 1996). The crab-eating fox ate the highest proportion of plant items among the three species.

The crab-eating fox and the hoary fox presented the lowest overlap. Of the 18 items identified in the scats of the crab-eating fox, 14 (78%) were common in the diet of the hoary fox. Within the animal items, the major differences occurred in the insect category where the item 'termite' was exclusively eaten by the hoary fox and at a high frequency (36% of its diet). For the plant items, the order of consumption of species by the hoary fox was similar to that of the crab-eating fox (coconut, grasses and maned-wolf fruit). Differences were highlighted in the items *Bromelia balansae* and in a species of Rubiaceae that were eaten exclusively by the crab-eating fox.

The maned wolf and the crab-eating fox showed considerable diet overlap. Both species used all available habitats, but the hoary fox was mostly observed in drier grassland habitats, further from water sources. Activity patterns were the least divergent, as generally the three species had two activity peaks, one concentrated in the dusk–night period and another in the morning period. All three canids were active in the night period. The crab-eating fox was active in almost all periods of day and night. It was observed that in conditions of high air humidity and cloudy days the canids, especially the maned wolf and crab-eating fox, became active. Similar observations are stated by Juarez & Marinho-Filho (2002).

The ecological differences between the maned wolf, the crab-eating fox and the hoary fox in Emas Park were similar to those found by Juarez & Marinho-Filho (2002) in the Fazenda Pratudão, Bahia, Brazil. The maned wolf showed the most differences between the three species, probably as it was the only one to use larger food sources and marshes or tall grasses. Smaller ecological differences and higher competition were expected between the crab-eating fox and the hoary fox as they are similar in body mass and morphology. However, the specialization of the hoary fox for termites, which were not consumed by the crab-eating fox, and for the drier grassland habitat, which was less used by the crab-eating fox, may reduce interspecific competition. On the other hand, despite large morphological and body mass differences between the maned wolf and the hoary fox, they had a higher diet overlap that could be probably explained by similarities in their pattern of habitat use, as both species predominantly use the grassland habitat.

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