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SMALL MAMMAL SELECTION AND FUNCTIONAL RESPONSE IN THE DIET OF THE MANED WOLF, *CHRYSOCYON BRACHYURUS* (MAMMALIA: CANIDAE), IN SOUTHEAST BRAZIL

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ABSTRACT: Data reported here are intended to describe patterns of predation by a solitary hunter, as well as to bring new insights into the predator-prey relationship in the Neotropical region. The goal of this study was to verify if there was small mammal selection in the diet of the maned wolf. Also, we attempt to test for a functional response in relation to the consumption of small mammals. The study was carried out in the Ecological Station of Itirapina (ESI), São Paulo, Brazil. Faeces collection and small mammal abundance survey by pitfall trapping were conducted simultaneously during 2000-2002. The maned wolf was selective in the consumption of small mammals. *Calomys tener* and *Oligoryzomys nigripes* (Muridae) were consumed less than expected by chance, whereas *Clyomys bishopi* (Echimyidae) was preyed on more than expected. We did not detect a clear functional response by this canid in the ESI to overall shifts in abundance of small mammals. However, prey switching was detected by an increase in diet diversity in the wet season when small mammals become less available.

Key words. *Chrysocyon brachyurus.* Prey selection. Prey switching. Small mammals.

INTRODUCTION

Predators may influence prey population dynamics (Craighead and Craighead, 1956; Erlinge et al., 1983) either selecting prey species or consuming higher proportions of a particular size or age class (Brown and Twigg, 1971; Roberts and Wolfe, 1974; Lay, 1974; Fast and Ambrose, 1975; Fulk, 1976; Marti, 1976; Boonstra, 1977; Marti and Hogue, 1979; Jaksic and Yañez, 1979; Longland and Jenkins, 1987; Dickman et al., 1991; Bellocq and Kravetz, 1994; Trejo and Guthmann, 2003). On the other hand, predators may be affected by prey density (Jaksic and Simonetti, 1987). Predator's reaction to fluctuation in prey levels might involve changes in the foraging behaviour. For example, predators might increase the consumption of a particular prey when they are abundant or switch to a different prey type when their abundances decrease (Korpimäki and Norrdahl, 1989; Jaksic et al., 1992; White et al., 1996).

Jaksic (1989 a, b) defines an opportunistic predator as the one that consumes all prey types in similar frequencies as their availability in its hunting site and whose diet composition better fit with prey abundance than with prey size. Conversely, a selective predator consumes one or all prey in different proportions than those present in the field and its diet fits better with prey size than with prey abundance.

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The functional response of predators to variation in prey abundance was reported in boreal forests of the Holoartic region (e.g. Korpimäki and Norrdahl, 1989; Dale et al., 1994), in a seasonal forest in Africa (e.g. Ray, 1998), and in subtropical areas (Jaksic et al., 1980, 1992; Silva et al., 1995; Branch et al., 1996) (see Marti, 1987, and Jaksic and Simonetti, 1987 for reviews). Although some authors have emphasized the need for additional studies on patterns of predation in Neotropical region (Jaksic and Yañez, 1979; Jaksic et al., 1981; Meserve et al., 1987; Jaksic et al., 1992), few studies on functional response, selection and prey vulnerability to mammalian carnivorous have been conducted in this region (e.g., Meserve et al., 1987; Iriarte et al., 1989; Corley et al., 1995; Motta-Junior 2000).

The maned wolf *Chrysocyon brachyurus* is a large canid (20 to 33 Kg for adults) that inhabits mostly savannah-like and grassland habitats. Its distribution comprises central South America, including all over Paraguay, north eastern Argentina, north western Uruguay, extreme south eastern Peru and large parts of central and eastern Bolivia, and central and southern Brazil (Langguth, 1975; Dietz, 1984, 1985; Nowak, 1999). *Chrysocyon brachyurus* is included in the IUCN Red List as a "lower risk – near threatened" species (IUCN, 2003), whereas in the Brazilian official list it is considered a "vulnerable" species (Machado et al., 2005).

Except in the breeding season, the maned wolf is a solitary animal, being active mainly during the crepuscular-nocturnal period. Its home range extends from 21.7 to 115.0 km^2 (Dietz, 1984, 1985; Carvalho and Vasconcellos, 1995). It is omnivorous, relying on fruits (mostly wolf's fruit *Solanum lycocarpum*) and small vertebrates (mainly small mammals) for most of its nutrition (Dietz, 1984; Motta-Junior et al., 1996; Motta-Junior, 2000; Aragona and Setz, 2001; Bueno et al., 2002; Juarez and Marinho-Filho, 2002; Santos et al., 2003; Bueno and Motta-Junior, 2004; Jácomo et al., 2004). Although several studies about its diet were recently published, only one reported on small mammal selection and functional response (Motta-Junior, 2000).

The goal of this study was to verify if the maned wolf selects small-mammal prey in southeast Brazil. Also, we attempted to test for a functional response and prey switching in relation to the consumption of small mammals. Data reported here were intended to describe patterns of predation by this solitary hunter as well as to bring new insights into the predator-prey relationship in Neotropical region.

MATERIAL AND METHODS

Study area

The study was carried out in the Ecological Station of Itirapina - ESI (2 300 ha, 22º15' S; 47º49' W), São Paulo State, southeast Brazil. This Ecological Station comprises Cerrado (savannah-like) vegetation and it is one of the last remains of natural savannahs and grasslands in São Paulo State (Parker and Willis, 1997; SEMA, 2000). The physiognomies include grassland (locally named "campo limpo"), grassland savannah ("campo sujo", and "campo cerrado"), savannah ("cerrado sensu stricto") (see Coutinho, 1978) and small patches of marshes and gallery forests. The ESI is surrounded by plantations of *Pinus* sp., *Eucalyptus* sp., *Citrus* sp., and by pastures. According to Köppen (1948), the climate is Cwa with well distinct wet (October to March) and dry (April to September) seasons. A general description of the Cerrado biome can be found in Eiten (1994). The Cerrado is the second most important Brazilian hotspot, largely threatened by the expansion of pastures and agriculture (Ratter et al., 1997).

Faeces collection

Roads and trails were walked and driven on each month from February 2000 to July 2002 in order to search for faecal samples. Faeces were taken to the laboratory to be washed in water through a fine (1 mm) mesh screen (Emmons, 1987; Motta-Junior et al., 1996) or in a washing machine (e.g., Springer and Smith, 1981; Uresk and Sharps, 1986). Afterwards, they were oven dried (50ºC) during 24-48 hours, stored and individually examined.

Prey identification

Prey remains of teeth and bones were identified to the most detailed taxonomic level possible by comparison with a reference collection of the study site. Pairs of mandibles were used to count the minimum number of individual animals consumed (Emmons, 1987). The prey biomass consumption was estimated by counting the number of individuals in faeces and then multiplying this number by the mean body mass of each prey species, obtained at the study site by pitfall trap surveys (Emmons, 1987; Motta-Junior et al., 1996).

Prey availability

Three sets of pitfall traps were installed in three different physiognomies of Cerrado to survey small-mammal abundance ("campo sujo", "campo cerrado" and an ecotone "campo sujo"/forest gallery). Each set consisted of two lines separated by 100 m with four buckets (100 l) each, 15 m apart, connected by a plastic drift-fence (45 cm length and 0.5 cm high). A total of nine sets or 18 lines with 72 buckets (four buckets/line) were checked three days per month, from February 2000 to July 2002, resulting in 6 480 pitfall (bucket)-nights. All captured rodents were identified, sexed, weighed, ear-tagged with numbered monel tags, and then released. Only first captures were considered to obtain the small mammal frequencies in the field.

Boonstra and Krebs (1978), Iriarte et al. (1989), Jaksic (1989 a, b) and Dickman et al. (1991) highlighted the influence of sampling methods on prey capturability and on studies of prey selection. Traps should be as efficient as the predators in capturing different prey species, besides revealing the real prey composition and abundance in the environment. Some authors have suggested that the use of pitfall traps could avoid such potential methodological biases (Boonstra and Krebs, 1978; Korpimäki and Norrdahl 1989; Dickman et al., 1991). These traps are more efficient than cages in capturing smaller and younger individuals, and may invoke a more faithful picture of prey community.

Data analysis

The diet of the maned wolf was evaluated in relation to changes in prey availability along the years, using the Spearman correlation coefficient (r_s) (Zar, 1984; Silva et al., 1995). To provide adequate sample sizes for analyses, diet data were pooled in two or three-month periods, however avoiding the combination of different seasons. At least eight faeces per period were collected in the study area (mean ± standard deviation = 24.5 ± 10.5 faeces/period). The food-niche breadth was calculated for each group of months defined above using the standardized Levins measure (B_{st}) (Krebs 1999). Small mammal abundance in the diet was compared to their availability in the environment using *G* test (Jaksic, 1979, 1989a; Zar, 1984), and employing Bonferroni confidence intervals according to Byers and Steinhorst (1984). In all tests, a statistical significance of 0.05 was considered.

RESULTS

Eleven potential small mammal prey species and 1 223 individuals were captured in ESI during the study period. *Calomys tener* (83.0%) was the most abundant, followed by *Oligoryzomys nigripes* (12.7%) and *Clyomys bishopi* (2.2%). The remaining species comprised only 2.1% of the total individuals captured (**Table 1**).

The study was based on a total sample of 252 faeces. *Clyomys bishopi* and *C. tener* were the most abundant rodents found in the faecal samples (**Table 2**). Although some other rodent species, such as *Oxymycterus delator* and *Nectomys squamipes*, were present in the study area, they were not found in the collected faeces during the study period.

Although the maned wolf consumed more small mammals in the dry season, when they were more abundant in the study area (**Tables 1** and **2**), we did not detect a functional response by this canid in ESI to shifts in the abundance of the small mammals. The whole assemblage data showed a negative non-significant correlation. (r_s= -0.018, p=0.957, **Fig. 1**). The association between abundance in the field and consumption by the wolves for each prey species also was not significant. The mean B_{st} was higher in the wet season (0.57 ± 0.14; n=5 periods) than in the dry season (0.37 ± 0.09; n = 6) (Mann-Whitney test, U=3, p=0.0285). Also, there was no significant correlation, neither between B_{st} and small mammal abundance in the field (r_s=-0.020, p=0.959, n= 11) nor between B_{st} and small mammal consumption by the wolves (r_s=0. 209, p=0.537, n= 11) (**Fig. 1**).

Table 1

Small mammal species captured in ESI from February 2000 to July 2002. Figures represent number and percentage of captured individuals in both seasons, for a total sample effort of 6,048 trap/nights, evenly distributed between seasons.

Species (mean weight ± standard deviation, nº of individuals)	**Wet season**		**Dry season**		**Total**	
	Nº	%	Nº	%	Nº	%
Calomys tener (10.6 ± 4.8, n=377)	404	85.2	607	81.0	1011	82.7
Oligoryzomys nigripes (11.1 ± 4.9, n=41)	49	10.3	101	13.5	150	12.3
Clyomys bishopi (208.7 ± 65.2, n=10)	10	2.1	17	2.3	27	2.2
Bolomys lasiurus (23.7 ± 14.6, n=3)	6	1.3	2	0.3	8	0.7
Oryzomys subflavus (52.0 ± 17.1, n=3)	1	0.2	4	0.5	5	0.4
Oxymycterus delator (54.0, n=1)	0	0.0	1	0.1	1	0.
Nectomys squamipes (juvenile -11.0, n=1)	0	0.0	2	0.3	2	0.2
Cavia aperea (281.0, n=1)	1	0.2	0	0.0	1	0.1
Opossums (*Cryptonanus* sp., *Gracilinaus* sp., *Monodelphis kunsi*)	2	0.4	5	0.7	7	0.6
Total	**474**		**749**		**1223**	

Table 2

Small mammals preyed on by the maned wolves in ESI from February 2000 to July 2002 as assessed by analysis of faeces. Figures are number of prey individuals and percentage.

Species	**Wet season**		**Dry season**		**Total**	
	Nº	%	Nº	%	Nº	%
Calomys tener	7	16.7	44	36.4	51	31.3
Oligoryzomys nigripes	0	0.0	6	5.0	6	3.7
Clyomys bishopi	19	45.2	40	33.1	59	36.2
Bolomys lasiurus	0	0.0	2	1.7	2	1.2
Oryzomys subflavus	0	0.0	1	0.8	1	0.6
Cavia aperea	4	9.5	12	9.9	16	9.8
Didelphis albiventris	1	2.4	1	0.8	2	1.2
Unidentified rodent	11	26.2	15	12.4	26	16.0
Total	**42**	**100**	**121**	**100**	**163**	**100**
Number of faeces	**94**		**158**		**252**	

According to the overall analysis, the maned wolf was selective in relation to the consumption of small mammals ($G = 245.76$; d.f. = 2; $p << 0.001$). *Calomys tener* and *O. nigripes* were consumed less than expected by chance, whereas *C. bishopi* was preyed on more than expected (**Table 3**).

Both in the wet season (G=75.87; d.f.= 1; p <0.001) and in the dry season (G=57,0; d.f.=1; p <0.001), the maned wolf selected small mammal species (**Tables 4** and **5**). *Calomys tener* was always consumed in lower proportions, while *C. bishopi* was invariably consumed more than expected by chance.

DISCUSSION

The diet of the maned wolf in the ESI was described in detail in Bueno et al. (2002). Small mammals represented 22.5% in terms of frequency of occurrence (total of 1 054 occurrences), 45.8% of the number of ingested animals (total of 507 individuals) and 16.2% of the ingested biomass estimated (total of 185,323 g).

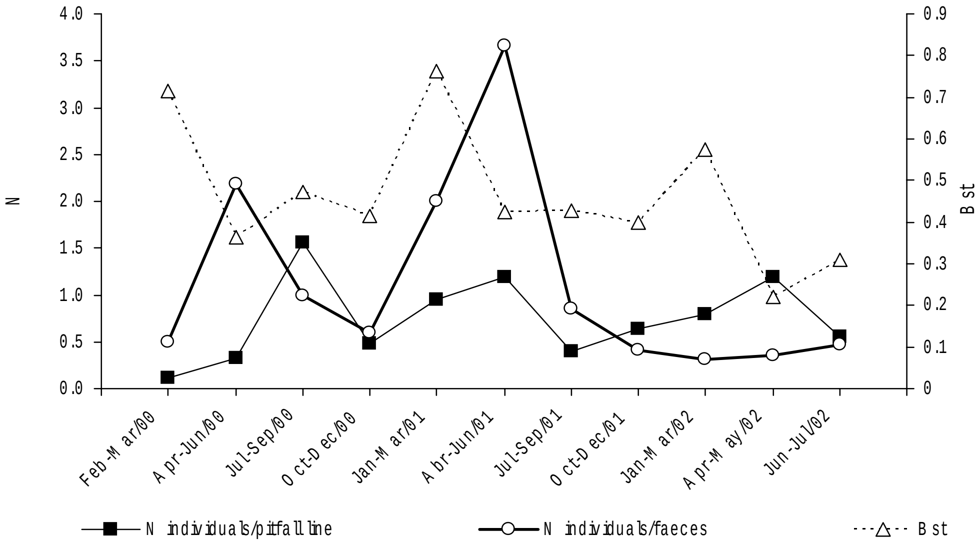

Fig. 1. Number of small mammals in the field (individuals per pitfall line), number of small mammals per faecal sample and Levins standardized food niche breadth (B_{st}), in relation to groups of months

Table 3

Bonferroni confidence intervals used to evaluate prey selection by the maned wolf in the ESI, southeast Brazil, from February 2000 to July 2002.

Species	Observed usage proportion (P_i)	Expected usage proportion (P_{io})	Bonferroni Confidence Interval for P_i	Selection
Calomys tener	0.421	0.830	0.298= p_i =0.544	-
Olygoryzomys nigripes	0.049	0.130	0.005= p_i =0.103	-
Clyomys bishopi	0.487	0.023	0.362= p_i =0.611	+
Bolomys lasiurus	0.016	0.007	0.000= p_i =0.047	=
Oryzomys subflavus	0.008	0.004	0.000= p_i =0.030	=
Oxymycterus delator	0.000	0.0008	0.000= p_i =0.000	-
Nectomys squamipes	0.000	0.002	0.000= p_i =0.000	-
Opossums	0.016	0.006	0.000= p_i =0.047	=

(+) Proportion of consumption was higher than proportion in the environment; (-) proportion of consumption was lower than proportion in the environment and (=) proportion of consumption was similar to the proportion in the environment.

The high consumption of small mammals by the maned wolf was reported mainly in the dry season when they are more abundant (Dietz, 1984; Motta-Junior, 2000; Bueno and Motta-Junior, 2004; Jácomo et al., 2004). However, we did not find any functional response in this study. Motta-Junior (2000) also reported this lack of functional response in relation to small mammals by the maned wolf elsewhere. The lack of significant results occurred probably because the maned wolf included many individuals of *C. bishopi* in its diet during the wet season, despite having reduced its overall consumption of small mammals in this period (**Tables 1** and **2**). This species comprised almost 50% of all small

Table 4

Bonferroni confidence intervals used to evaluate prey selection by the maned wolf in the dry season in ESI, southeast Brazil, from February 2000 to July 2002. Abbreviations for selection results as in **Table 3**.

Species	Observed usage proportion (P_i)	Expected usage proportion (P_{io})	Bonferroni Confidence Interval for P_i	Selection
Calomys tener	0.468	0.820	0.327= p_i =0.609	-
Olygoryzomys nigripes	0.064	0.140	0.005= p_i =0.133	-
Clyomys bishopi	0.425	0.023	0.285= p_i =0.564	+
Bolomys lasiurus	0.021	0.003	0.000= p_i =0.061	=
Olygoryzomys subflavus	0.010	0.005	0.000= p_i =0.038	=
Oxymycterus delator	0.000	0.001	0.000= p_i =0.000	-
Nectomys squamipes	0.000	0.003	0.000= p_i =0.000	-
Opossums	0.010	0.007	0.000= p_i =0.038	=

Table 5

Bonferroni confidence intervals used to evaluate prey selection by the maned wolf in the wet season in ESI, southeast Brazil, from February 2000 to July 2002. Abbreviations for selection results as in **Table 3**.

Species	Observed usage proportion (P_i)	Expected usage proportion (P_{io})	Bonferroni Confidence Interval for P_i	Selection
Calomys tener	0.129	0.850	0.029= p_i =0.288	-
Olygoryzomys nigripes	0.000	0.110	0.000= p_i =0.000	-
Clyomys bishopi	0.838	0.022	0.663= p_i =1.013	+
Bolomys lasiurus	0.000	0.013	0.000= p_i =0.000	-
Oryzomys subflavus	0.000	0.002	0.000= p_i =0.000	-
Opossums	0.032	0.004	0.000= p_i =0.116	=

mammal individuals consumed in these months (**Table 2**).

However, prey switching –a concept closely associated with functional response– was observed. The maned wolf increased the consumption of fruits in the wet season (Bueno et al., 2002), when small mammals became less available (**Table 1**). According to White et al. (1996), prey switching enables the predator to survive and reproduce when their primary prey is scarce. When analysing the diet as a whole, and not only the consumption of small mammals, the higher values of B_{st} for the wet season may be understood by the fact that during these months, the maned wolf more often consumes food items other than small mammals, such as wild fruits (*Solanum lycocarpum* and *Campomanesia glabra*, among others) and other small vertebrates (Bueno et al., 2002). The maned wolf tends to show a more specialist diet during dry months, when small mammal abundance is higher and the predation is restricted to less rodent species, mostly *C. bishopi*. It also included higher proportions of *S. lycocarpum* fruits in its diet during drier months. Similar results were reported in Jácomo et al. (2004) for the maned wolf in central Brazil. White et al. (1996) and Jaksic et al. (1992) argued that if predators react functionally to fluctuations in densities of small mammals, then diet diversity might increase as mammals decline in abundance. This was reported in our study.

Among the rodents, the results showed strong preference for larger species. Such pattern was observed along the two-year study in the ESI. As a large mammalian predator, the high energetic needs of the maned wolf are fulfilled with the consumption of more profitable prey. The mean weights of the rodents in the environment are in **Table 1**. Differences in the selection between the two seasons may reflect prey availability.

The largest and most consumed rodent in ESI, *C. bishopi,* is a semi-fossorial and herbivorous species (Vieira, 1997, Bueno et al., 2004), that inhabits patches of savannah-like vegetation. A possible explanation to its high consumption in ESI may be related to its higher availability in this area. Enviromental conditions such as open vegetation also might contribute to the high rate of predation of this rodent species. It seems to be a vulnerable species above ground, with no display of erratic movements or bipedal leaps during escape (Bueno, 2003; see also discussions on locomotor adaptations to predation escape in Bartholomew and Caswell, 1951; Bartholomew and Cary, 1954; Kotler, 1984, 1985).

The genus *Calomys* was reported in the diet of the maned wolf by several authors (Motta-Junior et al., 1996; Motta-Junior, 2000; Bueno and Motta-Junior, 2004). Probably, these small sized rodents bring low benefits to such a large predator. On the other hand, they were very abundant, their bad hearing (relative small tympanic bulla, 12.38 ± 2.43 ml) and locomotion capabilities (Bueno, 2003; see Webster and Webster, 1971; Kotler, 1984, 1985 for the positive association between hearing and tympanic bulla size) might make them highly vulnerable to predation by maned wolves.

Morphological and behavioural components of both prey and predators may explain differential predation (Lay, 1974; Dickman et al., 1991; Castro and Jaksic, 1995). Selectivity may involve predator morphological limits in handling prey (Longland and Jenkins, 1987), as well as behavioural aspects of prey species (Jaksic and Marti, 1981; Kotler, 1985; Nashimura and Abe, 1988; Taylor, 1994). Handling time, rates of energy and nutrient intake, risk of injury as well as sensorial capabilities of prey and predator are involved in the process of selection (Endler, 1986). Differential predation may be a result of real selection by predators reflecting prey vulnerability. Future studies dealing with prey vulnerability could bring new insights to the understanding of predator-prey relationship (see Corley et al., 1995).

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