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Diet of adults and cubs of *Lycalopex gymnocercus* in Pampas grassland: a validation of the Optimal Foraging Theory?

Diego F. Castillo, Diego E. Birochio, Mauro Lucherini & Emma B. Casanave

GECM — Lab. Fisiología Animal, Depto. Biología, Bioquímica y Farmacia, UNS, Argentina (corresponding author's e-mail: diefcastillo@gmail.com)

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We compared the diet of adult Pampas foxes (*Lycalopex gymnocercus*) and their cubs in a Pampas grassland area of Argentina by analysing 152 scats (adults: 92, cubs: 60). We used an Index of Relative Importance (IRI) to determine the contribution of prey items to the diet. IRI scores for rodents, hares and birds were higher for cubs, whereas adults consumed grasshoppers and larvae more often than cubs did. Fruits and carrion of ungulates were consumed only by adults. Both the number of items per scat and diet diversity were smaller for cubs than adults. We conclude that the Pampas fox behaves as a typical central place forager, with fruits and insects being probably consumed on the spot (with low foraging costs) and rodents, birds and hares being brought to the den for the cubs.

Introduction

Food utilization is an important aspect in the study of carnivore ecology, since trophic resources dominate several aspects of their biology (Macdonald 1983, Bekoff *et al*. 1984).

The Marginal Value Theorem (MTV) developed by Charnov (1976) describes the behaviour of rate-maximizing animal foraging in an environment consisting of well-defined resource patches separated by empty space. There are two main concerns: how long the animal spends foraging within a patch and how long it spends looking for the next patch. The optimum foraging strategy is to abandon each patch when the rate of return of prey items falls to the average rate of return for all of the patches available to the animal. The concept of central place foraging is a special case of the MTV and predicts that a central place forager, i.e. an organism collecting food and carrying it to the same place (e. g. a den), should consume small prey at the capture site, and bring larger prey to its offspring (Orians & Pearson 1979).

The Pampas fox (*Lycalopex gymnocercus*; formerly *Pseudalopex gymnocercus*) is a medium-sized canid. It is one of the most widespread South American mammals and is found in Bolivia, Paraguay, Brazil, Uruguay and Argentina (Redford & Eisenberg 1992), particularly in Chaco, Monte and Pampas ecoregions (Diaz & Lucherini 2006).

There are several studies about the diet of Pampas foxes in the Pampas grassland of Argen-

tina (Castillo 2002, Farias & Kittlein 2007, Birochio 2008, Varela *et al*. 2008) that concur in defining *L. gymnocercus* as an omnivorous generalist, with a diet dominated by animal prey, particularly wild mammals and insects.

Pampas's foxes may form monogamous pairs. Pairs are frequently observed from mating until cubs leave the natal den (Lucherini *et al*. 2004). Usually cubs remain in dens until at least the age of 3 months and males provide food to them and females at den (Lucherini & Luengos Vidal 2008). Thus, Pampas's foxes may be expected to behave as central place foragers. Nevertheless, studies comparing the food habits of Pampas fox cubs and adults are absent.

The present study compared the diet of adults and cubs of Pampas foxes during the breeding season, in a protected area in the Pampas grassland of Argentina. We tested the prediction that during the rearing period adult foxes consume a greater proportion of abundant and less nutritive food items (e.g. arthropods and fruits), and carry more nutritive prey to their denning cubs. Additionally, we tested the related prediction that the number of items per scat and diversity of diet are smaller for cubs. Finally, we aimed to contribute to the knowledge on the food habits of this little-studied canid.

Materials and methods

Study area

We conducted our study at Parque Provincial Ernesto Tornquist (PPET), located in the central part of the Ventania mountain range (38°00´S, 62°00´W), southern Buenos Aires province, Argentina. This protected area has a surface of approximately 6700 ha and a maximum altitude of 1240 m. The climate is temperate with mean annual precipitation of 500–800 mm (Frangi & Bottino 1995). This area is a part of the Pampas ecoregion (Olson *et al*. 2001) and vegetation is characterized by native grassland (genuses *Stipa*, *Piptochaetium*, *Festuca* and *Briza*; (Cabrera 1976). Introduced plant patches (*Pinus*, *Cupressus*, *Acacia*, *Eucalyptus* and specimens of the *Rosacea* family) are also frequent (Zalba & Villamil 2002).

Dietary analysis

We determined diet composition of Pampas foxes by identifying food remains in scats. Because Pampas fox cubs are born between October and December and in February they are still living in the den and its immediate surroundings (Lucherini & Luengos Vidal 2008), we opportunistically collected scats between November 2000 and February 2001 to compare the diet between adults and cubs for the same period of the year. Fox scats were distinguished from those of sympatric carnivores on the basis of morphology, smell, associated footprints and ingested hairs (Manfredi *et al*. 2004). Fecal samples that could not be accurately attributed to foxes or cubs/adults were discarded. Scats of cubs were collected exclusively in the surroundings of three reproductive dens, whereas scats of adults were located singly far from dens, over bare or grassy soil, on vegetation, and along paths and could be easily distinguished from those of cubs based on their larger size.

Scats were dissected, and the contents separated into mammals, birds, reptiles, invertebrates, anthropogenic refuse, and plant material. Scats were washed in a 0.5-mm sieve under a stream of hot water and all items such as hairs, feathers, bone fragments, teeth, and insect chitin were separated (Reynolds & Aebischer 1991). Each item was then identified through comparison with reference materials.

The diet of the Pampas fox was described by using three different methods based on both frequency and volumetric analyses; *viz*. Frequency of Occurrence (FO, expressed as percentage of the total number of scats), Numerical Frequency (NF, expressed as percentage of the total number of occurrences of all food items) (Corbett 1989, Reynolds & Aebischer 1991, Paltridge 2002, Posluszny *et al*. 2007) and Percentage Volume (PV, percent dry volume of each prey in scats through visual estimation) (Elmhagen *et al*. 2000, Angerbjörn *et al*. 1999). In order to minimize individual biases of the three methods used to estimate the diet of the Pampas fox, we used the Index of Relative Importance (IRI) (Pianka *et al*. 1971, Paltridge 2002, Home & Jhala 2009) to determine the importance of different prey items in the diet of adults and cubs [where IRI

= (NF + PV) × FO]. The IRI scores for the different prey items obtained were subjected to re-sampling with 1000 iterations using R 2.7.1 (R Development Core Team 2008) to generate means and bias-corrected 95% confidence intervals and compare the diet of adults and cubs.

The niche breadth was estimated by measuring the Levins' index *B* (Levins 1968):

$$B = \frac{1}{\sum p_i^2}$$

were p_i is the proportion of records in food category i.

Results

We collected 152 scats (adults: 92, cubs: 60) and identified 12 different prey items. We found significant differences in scat measurements between adult and cubs. Scats of adults had, on average (± SD) greater weight (adults = 7.35 ± 5.9 g, cubs = 1.94 ± 0.9 g; $U = 672$, $n_{cubs} = 60$, $n_{adults} = 91$, $p = 0.001$), volume (adults = 7.71 ± 5.4 ml, cubs = 2.84 ± 1.9 ml; $U = 381.5$, $n_{cubs} = 28$, $n_{adults} = 83$, $p = 0.001$), and diameter (adults = 1.68 ± 0.3 cm, cubs = 1.02 ± 0.1 cm; $U = 52.5$, $n_{cubs} = 21$, $n_{adults} = 52$, $p = 0.001$).

The percentages of scats containing more than one food category were 90 and 71.6, in adults and cubs, respectively. The mean number of food items in feces (± SD) was higher for adults (3.8 ± 1.4) than cubs (2.1 ± 0.8; $U = 932$, $n_{adults} = 60$, $n_{cubs} = 92$, $p = 0.001$). Accordingly, the list of food items in adult scats was more diverse (Levins' index values were 3.8 and 6.9 for cubs and adults, respectively).

Coleoptera contributed the most to the adult fox diet (both Frequency of Occurrence and Numerical Frequency), followed by fruits of *Prunus* sp., Orthoptera, and large mammal carrion (horses, cows, sheeps). However, *Prunus* fruits comprised 36.2% in terms of Percent Volume and were more important than Coleoptera and carrion (Table 1). Pampas fox cubs fed mainly on vertebrates: rodent constituted the most represented prey, followed by birds. Hare (*Lepus europaeus*) remains were present only in cub scats. Also Coleoptera reached relatively high values. In contrast to adults, no fruit remains were found in cub fecal samples (Table 1).

The IRI scores for adults were the greatest for Coleoptera and Orthoptera in the category of invertebrates and *Prunus* sp. in vegetables. Within vertebrates, but with lower values, horse carrion followed by rodents presented the top

Table 1. Diet composition of adults and cub of Pampas foxes (*Lycalopex gymnocercus*) in Pampas grassland of Argentina. FO = frequency of occurrence NF = numerical frequency, PV = percentage of volume, and IRI = Index of Relative Importance (IRI). *n* indicates the number of scats. – = not found in the diet.

Item	Adults (*n* = 92)				Cubs (*n* = 60)			
	(%FO)	(%NF)	(%PV)	IRI	(%FO)	(%NF)	(%PV)	IRI
Vertebrates	63.0	17.0	19.7	2312.1	96.7	44.6	83.2	12358.3
Carrion	44.6	12.1	13.4	1133.7	–	–	–	–
Hares	–	–	–	–	15.0	6.9	11.2	272.6
Rodents	18.5	5.0	5.1	186.8	75.0	34.6	54.9	6713.0
Reptiles	3.3	0.9	0.1	3.1	–	–	–	–
Birds	8.7	2.3	1.1	30.5	51.7	23.8	17.0	2112.1
Invertebrates	93.5	25.3	35.4	5675.4	61.7	28.5	16.4	2770.3
Coleoptera	68.5	18.5	24.1	2916.1	56.7	26.1	13.8	2262.6
Orthoptera	63.0	17.1	8.7	1622.0	13.3	6.1	2.6	116.6
Larvas	13.0	3.5	2.5	79.2	1.7	0.8	0.01	1.3
Other invertebrates	6.5	1.8	0.1	12.4	1.7	0.8	0.03	1.3
Vegetables	92.4	25.0	44.9	6458.8	1.7	0.8	0.4	2.1
Prunus sp.	55.4	15.0	36.3	2842.2	–	–	–	–
Other fruits	21.7	5.9	3.6	207.0	–	–	–	–
Grass, leaves	66.3	17.9	5.0	1518.2	1.7	0.8	0.4	2.0

scores. In the cub diet, the IRI scores reached maximum for rodents, followed by birds and Coleoptera (Table 2).

The IRI scores were significantly different (non overlapping 95% CI) between cubs and adults for all items (except Coleoptera). Rodents, birds, hares were more important in the diet of cubs, while the rest of the items had greater values in the adult diet (Table 2).

Discussion

During summer, adults of *Lycalopex gymnocercus* had a generalist diet, including carrion (horses), insects, and fruits as main food items, while birds and reptiles were consumed in low proportions. This is consistent with studies from other regions that also reported that the Pampas fox behaved as a generalist (Crespo 1971, García & Kittlein 2005, Farias & Kittlein 2007). Contrasting with previous findings (Zapata *et al*. 1998, García & Kittlein 2005, Farias & Kittlein 2007), we did not record hares in the diet of adults.

Our data were in accordance with the predictions of the optimal foraging theory. The comparison of the diet between adults and cubs in Pampas foxes emphasized the importance of rodents in the diet of cubs. The IRI score of rodents for cubs was remarkably higher than that for adults. Additionally, we found hare remains exclusively in cub scats. Finally, the number of items per scat and diet diversity were smaller for cubs than adults. Similar results were found for the chilla (*Lycalopex griseus*) in Patagonia, where scats of cubs contained larger prey items than scats of adults (Zapata *et al*. 1998), as well as for foxes from other continents (Lindström 1994, Weber 1996, Home & Jhala 2009).

These findings are also relevant for the trophic behavior of Pampas foxes because small mammals are scarce whereas insects and fruits are abundant at PPET in summer (Birochio 2008). This implies that a greater effort is most likely needed to catch and consume rodents in comparison with insects and fruits.

Interestingly, insects such as beetles and grasshoppers also frequently occurred in cub scats, suggesting that they might be training their foraging skills in the vicinity of dens, as the adult foxes are unlikely to regurgitate or bring such food items to the dens (Lovari & Parigi 1995, Lanszki 2005).

We did not record any fruits in cub scats. Although fruits provide an easily obtainable source of energy and nutrients (Sovada *et al*. 2001, Kaunda & Skinner 2003, Silva *et al*. 2008), they are less protein-rich (important for growing cubs) than other food items such as small mammals (Ball & Golightly 1992, Willson 1993). In addition, the types of fruits occurring in our study area are small and with a large proportion of seeds in relation to fresh pulp (Biro-

Table 2. Comparison of IRI scores between adults and cubs of Pampas foxes (*Lycalopex gymnocercus*) using 95% Bootstrap CI. Asterisk (*) indicates significant differences (at $p < 0.05$) between pairs.

	Mean	95% CI
Carrion*		
Cubs	0	0
Adults	1150.59	661.3–1723.35
Hares*		
Cubs	293.22	50.68–689.92
Adults	0	0
Rodents*		
Cubs	6760.68	4879.22–8757.8
Adults	195.23	61.42–402.28
Reptiles		
Cubs	0	0
Adults	3.99	0–16.2
Birds*		
Cubs	2149.04	1256.19–3244.8
Adults	34.89	3.57–94.26
Coleoptera		
Cubs	2295.19	1469.46–3305.12
Adults	2944.78	2045.44–3894.65
Orthoptera*		
Cubs	124.78	16.49–307.53
Adults	1626.16	1107.16–2254.23
Larvas*		
Cubs	2.55	0–12.04
Adults	86.23	17.36–200.36
Other invertebrates		
Cubs	2.68	0–12.50
Adults	14.53	1.31–43.06
Prunus sp.*		
Cubs	0	0
Adults	2865.26	1827.23–4061.66
Other fruits*		
Cubs	0	0
Adults	213.43	72–420.93
Grass, leaves*		
Cubs	3.86	0–18.25
Adults	1531.25	1103.3–2009.27

chio 2008). However, we are aware that other possible explanations cannot be ruled out. In particular, adults could decide to bring partially succumbed prey to the den in order to simulate cubs to chase them.

We conclude that the Pampas fox appears to behave as a typical central place forager, with fruits and insects being probably consumed on the spot (with low foraging costs) and rodents, birds and hares being brought to the den for the cubs.

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