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Variation in Diet and Resources

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ABSTRACT. The diet of maned wolves (MW) was investigated during a general study of the ecology of the species in Noel Kempff Mercado National Park, Bolivia. Qualitative field records of scat contents were recorded from 2001–2007, and a quantitative analysis comparing wet and dry seasons was based on scat collections from 2008–2009. Like other studies, we found the diet to be composed of about half each of fruit and animal prey, with ratios that changed slightly with seasons. Prey included all small mammal species found on the savanna, and fruit eaten included a wide array of seasonally changing species, but frugivory was dominated by *Alibertia edulis*, present in 47% of all scats, and by *Solanum gomphodes*, in 18% of scats. Rodents declined by >90%, and a major prey species, *Cavia aperea* (cavies; over 60% occurrence), went to extinction in the study savanna from 2003–2006. No other species replaced cavies in importance, and their loss coincided with changes in maned wolf territory size and body condition. Savanna fires influenced the fruiting of major dietary taxa, which peaked in the diet 2–3 years following burns, but were almost absent in the first year postfire. We estimate daily energy consumption and foraging return based on the biomass of items enumerated in scats and the nightly distances MW traveled.

INTRODUCTION

Diet is the paramount characteristic of animals, as it is associated with nearly every aspect of ecology, from morphology to geographic range. The diets of MW (*Chrysocyon brachyurus*) in many localities have been studied by analysis of scats. Maned wolves are dietary opportunists that feed on fruit, small vertebrates, and invertebrates, according to local availability. All studies show a diet that varies closely around half of fruits and half of small animal prey (Aragona and Setz, 2001; Bueno and Motta-Junior, 2004, 2006, 2009; Dietz, 1984; Jácomo et al., 2004; Juarez and Marinho-Filho, 2002; Queirolo and Motta-Junior, 2007; Rodrigues et al., 2007; Santos et al., 2003; Silva and Talamoni, 2003). The frugivorous part of the diet is usually dominated by a single species:

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the giant fruits of *Solanum lycocarpum* (Solanaceae; “lo-beira” or wolf’s fruit); and the carnivorous part is usually dominated by either rodents and other small mammals or armadillos (summarized in Rodden et al., 2004; Rodrigues et al., 2007). Nonetheless, Bestelmeyer and Westbrook (1998) and Rodrigues et al. (2007) reported MW chasing and killing large prey in Emas National Park, Brazil (pampas deer, *Ozotoceros bezoarticus*).

We studied the behavioral ecology of a small population of MW on Los Fierros savanna, Noel Kempff Mercado National Park (NKP), Bolivia. For seven years we concurrently documented the relative numbers of rodents on trapping plots in maned wolf habitat (Emmons, 2009; Emmons et al., 2006a). Lilienfeld (2000) studied maned wolf food habits in NKP prior to our project, and because he found a diet like that recorded by others, we did not at first repeat a quantitative analysis of scats. Nonetheless, we recorded the grossly visible contents of scats encountered in the field, photographed many, and tried to identify dietary species. In 2004, our long-term small mammal trapping studies showed a large decline in rodent abundance (Emmons, 2009). Low rodent numbers persisted until yearly trapping ceased in 2007, and a key maned wolf prey species had disappeared. This plunge in prey density was an opportunity to observe the consequences for MW of a resource decline. Thus Castro (2010) undertook a quantitative analysis of maned wolf diet, with the double goals of describing the seasonality of diets and to discover how the diet had changed in the decade since Lilienfeld’s research.

Maned wolves are the only omnivores among the largest Canidae. Their tooth morphology is strongly indicative of this dietary omnivory and provides evidence of a millennial adaptation to this lifestyle (Van Valkenburgh, 1989; Chapter 1). Our ultimate aim in studying diet was to reach beyond the enumeration of dietary taxa to understand the costs and consequences of individual food choices for MW in a varying environment.

We first describe the taxonomic contents of the diet and evaluate its seasonal and interannual changes. We then estimate the daily consumption of individual food items and calculate their return per kilometer of daily travel, based on the ranging patterns reported in Chapters 2 and 3. We discovered much interannual variation in consumed taxa of both fruits and animal prey, which seemed to result from changes in the available resource base. We end by presenting some apparent consequences of resource changes on the spatial behavior of our study animals.

MATERIALS AND METHODS

Qualitative Analysis of Diet

We studied the diet from scats of a population of MW on the small savanna of Los Fierros in NKP. The scats were derived from few individuals and home ranges and so represent temporal samples from the same piece of habitat. The MW, study area, climate, and habitat are described in Chapter 1. From 2001–2007, 161 scats encountered in the field were picked apart *in situ*, examined qualitatively by eye, and their contents recorded and often photographed. We identified some ingested seeds and fruits, and a few were collected for reference. Tiny items, such as teeth of tiny mammals, were likely to have been missed, but not mammal hair. Although other species were identified, for this set of data we distinguish only caviies (Caviidae, *Cavia aperea*) from other rodents by their unique tooth morphology, relatively large bones, and distinctive, long, banded hair, often excreted in intact tufts. These qualitative data are scored only for presence/absence of an item or category in a scat and percentage of all scats examined in a given time that included that item. Researchers were usually in the field from September–November (late dry season) and sometimes in February–March (flooded season) or June–August; other months were not sampled for diet.

Quantitative Analysis of Diet

One hundred and thirty-five maned wolf scats were collected for quantitative analysis during 94 days of searches on the Los Fierros savanna in July 2008, October 2008, January 2009, and July and August 2009 (114 scats in the dry season; 21 in the wet season). Most were found by walking along tracks and transects across the savanna. A few were collected from trapped MW. Concurrent radio telemetry studies allowed us to be confident of the home ranges used by resident MW at any place on the savanna and the likely movement ranges of MW that were the sources of scats. Each collection had time, date, and GPS coordinates. Scats were field dried in the sun to prevent mold growth, washed carefully over fine mesh screens, and separated into identifiable components (fruits and seeds, bones, hair, feathers, feet, etc.). In the laboratory, scat components were identified by comparison with vertebrate, invertebrate, and herbarium specimens in the Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia (MNC); from the literature; and by consultation with specialists. We generally follow the mammal taxonomy of

Wilson and Reeder (2005) and for Caviidae, of Dunnun and Salazar-Bravo (2010a, 2010b). Lilienfeld (2000) reported maned wolf scats with *Solanum lycocarpum* (Solanaceae) from NKP, but M. Nee (pers. comm.) identified the species at Los Fierros as *S. gomphodes*, and noted that the “lobeira” is not known from Bolivia. Another giant-fruited species, *S. crinitum* (determined by Nee, pers. comm.), grew on the roadside at Los Fierros to at least 2007, but subsequently vanished. The two species grew together where MW often defecated, so some *Solanum* sp. identified in 2001–2007 scats could have been *S. crinitum*. Likewise, fruits identified as *Bromelia balansae* by Lilienfeld (2000) are now recognized as a new species, *B. ignaciana* R. Vázquez and Ibsch. During 2008–2009, fruiting plants were collected from the Los Fierros savanna and preserved for reference as herbarium specimens in MNK.

The biomass and numbers of prey individuals eaten were estimated by counting the minimum number in scats from hard parts such as incisor teeth, feet, tails, beaks, etc. Hair only was counted as one individual. For most mammal species, we used weights from voucher specimens from Los Fierros. To account for young in the population, we used 75% of adult weight to estimate prey biomass. Fruit numbers eaten were estimated by counting seeds in scats and dividing by the average seed numbers of intact fruits, following the methodology of Bueno and Motta-Junior (2004, 2009) and Rodrigues et al. (2007). Other details of the quantitative diet analysis are described in Castro (2010).

Relative numbers of rodents in the study area were monitored by annual captures on two, 17 ha trapping plots on the northern part of Los Fierros savanna (North Range maned wolf territory; Chapter 3). Each yearly sample was 10 days (1000 trap/nights) in September–October (Emmons et al., 2006a; 2006b; Emmons, 2009). Plot PA was in nonflooded Campo Cerrado (savanna woodland) that burned totally in 2003 and partially in 2007 (Figure 1.3). Plot PT was in seasonally shallowly flooded termite savanna that did not burn from 2000–2008. In 1999 the entire northern half of the Los Fierros savanna burned rapidly in a hot fire that carbonized nearly all woody vegetation (maned wolf North Range), but in the southern savanna (South Range) only small patches burned in the 15 yr before 2009, when nearly the entire savanna burned again (Figure 1.10).

Data Analysis

For quantitative analysis, fresh scats of <50 g mass, collected within the same territory, on the same day, and

containing the same items, were grouped into single feeding events to avoid pseudoreplication, as the same MW could have produced them from the same meals. This reduced the effective number of scats analyzed from 135 to 108. For comparability with other studies, we used (1) the crude percent of scats in the sample that included an item; (2) the number of items as a function of the number of total occurrences of all items in the sample, or frequency of occurrence; and (3) the minimum total number and biomass of items eaten, derived from countable hard parts (Dietz, 1984; Emmons, 1987; Motta-Junior et al., 1996). Biomass eaten was calculated with and without assigning an arbitrary mass representation for two fecal samples that included hair of marsh deer (*Blastocerus dichotomus*, 115 kg). Assigning to each scat with deer hair a large meal of 3 kg, assuming a canid capacity to gorge on meat when available, greatly inflates the percent of biomass eaten represented by prey, from 33% to 45%, based on the contents of only 1.5% of individual scats. Eleven occurrences of maned wolf hair, likely derived from grooming, are omitted from calculations.

Kelly and Garton (1997) reported that whereas all hair was passed undigested when mice and rats were fed to coyotes (*Canis latrans*), a maximum of only 24% of teeth of mice and 52% of teeth of rats were recoverable from scats, and the rest were digested. Tallying the numbers eaten from hard parts in scats may thus underestimate prey numbers. Digestion of mouse bones and teeth by coyotes was enhanced by cofeeding of pure meat (Kelly and Garton, 1997), which is not an issue with MW. In contrast, feeding sporadically (as do MW *in situ*), decreased tooth digestion. Maximal recovery of teeth thus might be expected from maned wolf samples. Tiny teeth that we recovered from scats did not show much erosion, and all but two of our scat samples that included micromammal hair also included bones and/or teeth. We assume that there was little underestimation of prey from digestion of hard parts, but only feeding experiments can test whether maned wolf scat contents correctly estimate the number of micromammals eaten.

Energetics

The average total daily energy requirements of captive MW (in 12 × 45 m enclosures) are 525 kJ × kg^{0.75} (range: 501–674 kJ × kg^{0.75}; Barboza et al., 1994), that is, 5693 kJ/d for a 24 kg maned wolf or 1,360 kcal (range 1,297–1,745 kcal). The resting energy requirement (RER) would be the best baseline from which to estimate requirements,

but it is not available for MW. For dogs, Burger and Johnson (1991), report that resting energy expenditure (REE) is $678 \times M^{0.64}$ kJ/d, which for MW would be 1,205 kcal/d, or near the low end given by Barboza et al. (1994), of $501 \text{ kJ} \times \text{kg}^{0.75}$ or 1,297 kcal. The nutrient requirements of dogs are similar to those of MW (Barboza et al., 1994). We therefore chose the low end of the maintenance estimate as the “resting” value from which to calculate the costs of maned wolf travel and the benefits of items in the diet. Pregnancy generally costs canids and other mammals about 1.3–1.5 times as much as maintenance, while lactation about doubles energy requirements.

“The net cost of transport for a running animal is the same at any speed. . . . It means that the amount of energy that an animal uses to run 1 km is almost the same whether it runs very fast or at a leisurely pace.” (Biewener, 2003:208). This curiosity makes it fairly easy to calculate the energy expenditure of mammals when their basal expenditure is known. There is an exception if an oxygen debt is incurred that is repaid after travel ceases (Biewener, 2003) but because MW travel many hours at fairly standard rates (Chapters 2, 3), they are unlikely to be generating oxygen debt, especially because animals generally

choose to travel at the intermediate speeds of a given gait, where travel costs are minimal (Biewener, 2003). The generalized incremental cost of locomotion (ICL) for mammals is estimated at

$$\text{ICL (kJ/km)} = 10.678 \times M^{0.70}$$

or 99 kJ/km for a 24 kg maned wolf (23.6 kcal) (Goszczyński, 1986).

RESULTS

FOOD CLASSES AND SEASONALITY

Maned wolves at Los Fierros had a diet nearly equally divided between animal prey and fruit. It varied about 10% either way in terms of percent of scats with items, percent frequencies of items, and in estimated biomass represented in a scat, depending on the years, seasons and sampling (Tables 4.1, 4.2, 4.3). The species-rich list of items eaten included at least 30 plant and 51 animal taxa (Table 4.3; and other observations). The estimated overall

TABLE 4.1. Occurrence of food items in scats. The percentages of total maned wolf scats found on Los Fierros savanna that contained fruit or prey types, by grouped years (*N* scats). Years 2001–2007 are from qualitative field inspection of scats, when small or rare items may have been overlooked; other data are from quantitative analysis (Castro, 2010; Lilienfeld, 2000). Both species of caviés that Lilienfeld (2000) identified are combined (see text). As methods differed, quantitative and qualitative samples are not strictly comparable. However, the differences are significant between qualitative data from 2001–2004 and 2005–2007, in numbers both of scats with caviés, or those with all mammals (X^2 , $p < 0.05$); and likewise, there is a significant difference between the quantitative sets from 1997–1999 and 2008–2009 (X^2 , $p < 0.01$). Years 1997–1998 from Lilienfeld (2000), 2001–2007 from Emmons (unpublished), and 2008–2009 from Castro (2010).

Years (N)	Fruit	All mammals	Caviés	Armadillo	Birds	Reptiles	Fish	Invertebrates
1997–1998 (51)	100.0	86.3	74.5	10.1	13.7	17.6	0	37.3
2001–2004 (106)	97.0	69.8	45.3	5.6	0.0	0.9	0	0
2005–2007 (58)	97.0	29.3	8.6	3.9	8.6	3.5	3.5	5.7
2008–2009 (108)	99.0	73.0	0	0	31.0	21.0	2.0	60.0

TABLE 4.2. Summary of overall occurrence and frequency among 520 items in 108 scats analyzed quantitatively in 2008–2009 (Castro, 2010) and numbers of species identified. Data exclude 11 occurrences of maned wolf hair presumed from grooming.

	Fruit	Mammals	Rodents	Birds	Reptiles	Fish	Invertebrates
Occurrences	205	137	95	37	23	2	116
Frequency	0.394	0.263	0.183	0.071	0.044	0.004	0.223
Minimum taxa	26	15	12	5	6	2	20

TABLE 4.3. Taxon list of items from 108 maned wolf scats collected in 2008–2009, with number of scats in which found (*N*), frequency of occurrence (FO) among all items eaten by season, the raw percentage of scats in which item was found, by season, and the percent of total estimated biomass consumed (modified from Castro, 2010) Dashes indicate none identified.

Food Item	Wet season (15)			Dry season (93)			Percent of total biomass consumed
	<i>N</i>	FO	Percent of scats	<i>N</i>	FO	Percent of scats	
Fruit							
Rubiaceae							
<i>Alibertia edulis</i>	4	0.062	26.7	79	0.17	84.95	21.69
<i>Genipa americana</i>	–	–	–	2	0.004	2.151	1.43
Solanaceae							
<i>Solanum gomphodes</i>	2	0.031	13.3	22	0.047	23.66	10.83
Bromeliaceae							
<i>Bromelia ignaciana</i>	5	0.077	33.3	2	0.004	2.151	1.96
Annonaceae							
<i>Duguetia furfuracea</i>	–	–	–	5	0.011	5.376	2.21
<i>Annona coriacea</i>	1	0.015	6.7	1	0.002	1.075	2.10
<i>Annona nutans</i>	1	0.015	6.7	4	0.009	4.301	1.22
Icacinaceae							
<i>Emmotum nitens</i>	–	–	–	6	0.013	6.452	0.97
Polygalaceae							
<i>Moutabea longifolia</i>	4	0.062	26.7	–	–	–	0.55
Menispermaceae							
<i>Abuta grandifolia</i>	–	–	–	1	0.002	1.075	0.18
Hippocrateaceae							
<i>Salacia elliptica</i>	2	0.031	13.3	2	0.004	2.151	0.70
Malpighiaceae							
<i>Byrsonima sp.</i>	–	–	–	1	0.002	1.075	0.02
Moraceae							
<i>Brosimum gaudichaudii</i>	1	0.015	6.7	1	0.002	1.075	0.19
<i>Brosimum acutifolium</i>	–	–	–	17	0.036	18.28	
Melastomataceae							
<i>Miconia albicans</i>	–	–	–	1	0.002	1.075	0.04
<i>Clidemia capitella</i>	1	0.015	6.7	0	–	–	0.00
Sapotaceae							
<i>Chrysophyllum gonocarpum</i>	1	0.015	6.7	0	–	–	0.01
Indet. 1	–	–	–	9	0.019	9.677	5.51
Indet. 2	–	–	–	4	0.009	4.301	0.12
Indet. 3	2	0.031	13.3	2	0.004	2.151	0.01
Indet. 4	1	0.015	6.7	1	0.002	1.075	0.06
Fabaceae				1	0.002	1.075	0.04
Arecaceae							
<i>Mauritiella armata</i>	6	0.092	40	4	0.009	4.301	–
<i>Euterpe precatoria</i>	–	–	–	1	0.002	1.075	1.41
Arecaceae 2	1	0.015	6.7	0	0	0	0.12
Poaceae spp.	–	–	–	7	0.015	7.527	0.01
Subtotal fruit	32	0.492		173	0.371	–	51.38
Mammals							
Echimyidae							
<i>Proechimys longicaudatus</i>	4	0.062	26.7	9	0.019	9.677	6.97
<i>Mesomys hispidus</i>	–	–	–	1	0.002	1.075	0.30
Cricetidae							
<i>Holochilus brasiliensis</i>	1	0.015	6.7	7	0.015	7.527	4.26
<i>Pseudoryzomys simplex</i>	1	0.015	6.7	7	0.015	7.527	1.44
<i>Juscelinomys huanchacae</i>	–	–	–	2	0.004	2.151	0.48
<i>Necomys lenguarum</i>	3	0.046	20	13	0.028	13.98	1.91
<i>Oecomys sydandersoni</i>	–	–	–	10	0.021	10.75	0.98
<i>Oligoryzomys microtis</i>	2	0.031	13.3	5	0.011	5.376	0.40

(continued)

TABLE 4.3. *Continued*

Food Item	Wet season (15)			Dry season (93)			Percent of total biomass consumed
	N	FO	Percent of scats	N	FO	Percent of scats	
Mammals							
<i>Euryoryzomys nitidus</i>	2	0.031	13.3	10	0.021	10.75	1.93
<i>Cerradomys maracajuensis</i>	–	–	–	6	0.013	6.452	0.90
<i>Cerradomys scotti</i>	1	0.015	6.7	7	0.015	7.527	1.62
<i>Akodon</i> sp.	1	0.015	6.7	3	0.006	3.226	0.44
Didelphidae							
<i>Gracilinanus agilis</i>	1	0.015	6.7	4	0.009	4.301	0.27
<i>Marmosa murina</i>	–	–	–	1	0.002	1.075	0.09
Indet.	3	0.046	20	31	0.067	33.33	5.29
Cervidae							
<i>Blastocerus dichotomus</i>	–	–	–	2	0.004	2.151	17.19
Canidae							
<i>Chrysocyon brachyurus</i>	–	–	–	11	0.024	11.83	–
Subtotal mammals	19	0.292	–	129	0.277	–	44.47
Birds							
Caprimulgidae	–	–	–	5	0.011	5.376	0.44
Emberizidae	3	0.046	20	19	0.041	20.43	0.81
Psittacidae	–	–	–	1	0.002	1.075	0.12
Columbidae	–	–	–	1	0.002	1.075	0.35
Indet.	1	0.015	6.7	7	0.015	7.527	0.84
Subtotal birds	4	0.062	–	33	0.071	–	2.56
Reptiles							
<i>Typhlops</i> sp.	–	–	–	7	0.015	7.527	0.21
Teiidae	–	–	–	8	0.017	8.602	0.39
Colubridae	–	–	–	4	0.009	4.301	0.56
<i>Mabuya</i> sp.	–	–	–	2	0.004	2.151	0.05
<i>Boa constrictor</i>	–	–	–	1	0.002	1.075	–
Indet. (1)	–	–	–	1	0.002	1.075	–
Subtotal reptiles	–	–	–	23	0.049	–	1.21
Fish							
Callichthyidae	–	–	–	1	0.002	1.075	0.01
Doradidae	–	–	–	1	0.002	1.075	0.01
Subtotal fish	–	–	–	2	–	–	–
Invertebrates							
Orthoptera	–	–	–	8	0.017	8.602	0.04
Isoptera	1	0.015	6.7	6	0.013	6.452	0.02
Diptera	–	–	–	4	0.009	4.301	0.00
Hymenoptera	–	–	–	3	0.006	3.226	0.01
Vespidae	–	–	–	5	0.011	5.376	0.00
Apidae	–	–	–	21	0.045	22.58	0.14
Formicidae	2	0.031	13.3	16	0.034	17.2	0.05
Gryllotalpidae	–	–	–	2	0.004	2.151	0.00
Blattidae	–	–	–	1	0.002	1.075	0.00
Cimicidae	–	–	–	1	0.002	1.075	0.00
Scarabaeidae	4	0.062	26.7	25	0.054	26.88	0.07
Passalidae	1	0.015	6.7	2	0.004	2.151	0.00
Histeridae	–	–	–	1	0.002	1.075	0.00
Cucurliionidae	–	–	–	1	0.002	1.075	0.00
Brentidae	–	–	–	1	0.002	1.075	0.00
Elateridae	–	–	–	3	0.006	3.226	0.01

(continued)

TABLE 4.3. *Continued*

Food Item	Wet season (15)			Dry season (93)			Percent of total biomass consumed
	N	FO	Percent of scats	N	FO	Percent of scats	
Invertebrates							
Carabidae	1	0.015	6.7	2	0.004	2.151	0.01
Cicadidae	1	0.015	6.7	1	0.002	1.075	0.00
Araneae	–	–	–	1	0.002	1.075	0.00
Ixodidae	–	–	–	2	0.004	2.151	0.00
Subtotal invertebrates	10	0.154	–	106	0.227	–	0.35
Subtotal animal prey	33	0.508	–	293	0.629	–	48.61
Total 531 items	65	1	433.3	466	1	501.1	99.99

TABLE 4.4. Seasonal occurrences of general categories in diets of MW at Los Fierros, excluding MW hair; numbers of occurrences (*N*) of items by season and seasonal frequencies of occurrences, from Castro (2010). The frequency of occurrences of general groups in the diets were independent of sampling season ($G = 7.19$; $df = 5$; $p > 0.05$).

	Fruit	Mammals	Birds	Reptiles	Fish	Invertebrates
Wet season, <i>N</i> (65)	32	19	4	0	0	10
Percent frequency	49	29	6	0	0	15
Dry season, <i>N</i> (455)	173	118	33	23	2	106
Percent frequency	37	26	7	5	0.4	23

average biomass represented in each scat in 2008–2009 was 312.3 g.

Maned wolf diets varied little by season in major groups consumed (Tables 4.3, 4.4). Occurrence in the dry season was 37% fruit and 63% prey, with biomass 63% fruit and 36.7% prey; while in the wet season, occurrence was 51% fruit and 49% prey, with biomass 54.5% fruit and 45.5% animal prey (Tables 4.3, 4.4; Castro, 2010). In the dry season, fruit thus had fewer occurrences relative to prey but more relative biomass, than in the wet season, and vice versa. In all sampling efforts, fewer fruit species were eaten in the wet season than in the dry season: 14:21 in 2008–2009 quantitative sampling (Castro, 2010), 7:21 in 2001–2007 qualitative sampling, and 6:10 in 1996–2007 quantitative sampling (Lilienfeld, 2000). Too few wet season scats were quantitatively analyzed for much inference about specific prey taxa or seasonal

patterns, but qualitative field examination provided additional taxon data.

ANIMAL PREY

All 12 small mammal species that we captured trapping on the Los Fierros savannas were found in maned wolf scats if we include two casually noted scats with *Kunsia tomentosus* remains (Muridae; L. Emmons and F. Del Aguila, pers. obs.; Emmons et al., 2006a; Emmons, 2009). They ate three scansorial taxa and some from forest, which can be found on ecotones. No species was too small for pursuit, including 20 g *Oligoryzomys microtis*. Only 4 of 272 scats (1.5%) included large mammals: two of marsh deer (*Blastocerus dichotomus*; 2008) and one each of collared peccary (*Pecari tajacu*; 2001) and capybara (*Hydrochoerus hydrochaeris*; 2005). Fish were notably

scarce. Yearly, when grasslands dry, fish are crowded into shrinking pools and make easy prey for foxes, ocelots, raccoons, and water birds. Our samples underrepresent months of fish die-off (June–July) but do include them. All listed invertebrates had been ingested, most notably the wasps and nest carton in five scats (Table 4.3).

When we began our study, one species dominated the prey of MW, *Cavia aperea* (white-toothed cavy; Table 4.1). Lilienfeld (2000) studied maned wolf diets at two sites in NKP, including our study area. His data for Los Fierros (1997–1988, both seasons combined), shows a higher percentage of scats with cavia than we found in 2001–2004 (Table 4.1). Six years earlier, in 1991, Emmons (pers. obs.) inspected about 20 maned wolf scats on the road across Los Fierros savanna. Although not quantified, nearly all included the remains of cavia, and most also included dermal bones of armadillos (*Dasypus* spp.). She saw many cavia and collected a voucher specimen (Emmons, 2000a). Cavia were thus a mainstay of MW for at least the decade prior to our study. Both cavia and armadillos were absent from the 2008–2009 quantitative analysis of scats (Tables 4.1, 4.3).

Captures on trapping plots recorded a steep decline in rodents on Los Fierros savanna from 2001 to 2004, with little recovery by 2007 (Figure 4.1; Emmons, 2009). Most

notably, cavia were not trapped after 2003. Contents of scats showed that cavia increased from 40% to 64% occurrence in 2001–2002, mirroring the rise in captures on trapping plot PA; followed by a steady decrease to zero after 2006 (Table 4.1, Figure 4.1B). Field observations confirmed the progressive disappearance of cavia from 2004 to 2006, when we saw the last feces and tracks in the southern part of the North Range maned wolf territory (Chapter 3). As cavia decreased in scats, there was an increase both in birds and in other rodents/small mammals in scats (Table 4.1, Figure 4.1B). There may be a trend for more scats without visible prey when fewer cavia were recorded, in both 2001 and 2007 (Figure 4.1B); however, the rank correlations are not significant for these series.

In the absence of cavia, no species dominated animal prey. In 2008–2009, the most numerous mouse in the savanna, *Necromys lenguarum* (Emmons, 2009), was eaten the most often (14.8% of all scats, 2% of biomass), but heavier rodents predominated in consumed biomass, including *Proechimys longicaudatus* (12% of scats, 7% of biomass) and *Holochilus brasiliensis* (7% of scats; 4.3% of biomass; Table 4.3). The raw percentages of food categories in scats show an apparent overall decline in mammalian prey that parallels the decline in rodents on Los Fierros savanna from 2001–2007 (Table 4.1). In 2010,

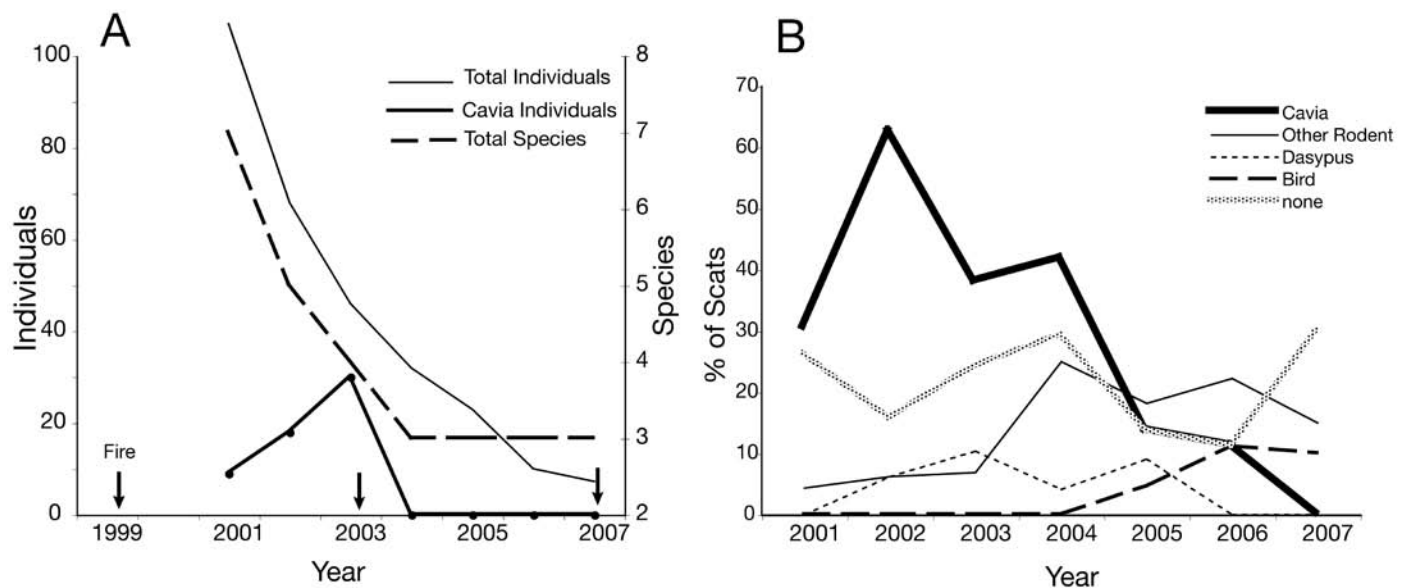


FIGURE 4.1. (A) Rodent captures over 7 years on trapping plot PA in nonflooded habitat in Los Fierros savanna, per 1000 trap nights in yearly samples. Total individuals (thin line), total species (broken line), and individuals of *Cavia aperea* (heavy line). Arrows indicate years when the plot burned. The same pattern of decline occurred on a seasonally flooded plot that did not burn after 1999 (Emmons, 2009). (B) Changes in percentages of scats that included the most common prey types, from qualitative field inspection, 2001–2007. None, scats without prey.

we again trapped plot PA and two new plots in Pampa Termitero. Numbers of *N. lenguarum* had everywhere increased considerably, but it was the only species captured on the new plots. Plot PA remained species poor, with but three species, unchanged since 2004 (Figure 4.1A).

FRUGIVORY

Almost all scats included seeds or other fruit parts (Tables 4.1–4.3). Frugivory was highly skewed in favor of a few species: in 2008–2009, 77% of all scats included *Alibertia edulis* (Rubiaceae), or 16% of 520 occurrences of all dietary items; while 5% were of *S. gomphodes*, and 3% of *Brosimum acutifolium*. Over all years and seasons, *A. edulis* was present in 47% of scats, and *S. gomphodes* in 18%. The fruit taxa identified in scats from 2001 to 2007 varied both intra- and interannually (Figure 4.2; Tables 4.3–4.5). The most commonly eaten fruit overall was *A. edulis*; except in March, when *Bromelia ignaciana* (Bromeliaceae) predominated. The percentages of scats that included particular fruit species varied between years for every taxon (Table 4.5).

Most fruits eaten by MW are from small trees and woody shrubs that grow on dry ground: in Campo

Cerrado, on hummocks around termite mounds in lightly flooded savanna, or on roadside banks. The ground bromeliad, *B. ignaciana*, especially favors termite hummocks. One of the only fruit sources that grows directly on flooded ground is the small palm *Mauritiella armata*. In termite savanna, all the grassland matrix is flood prone, while the woody plants that supply fruit are on high points without grass, so there is a two-phase habitat matrix, with rodents in the grassland and fruits on hummocks. Two fruit species eaten by MW grow in forest surrounding the savanna. Fallen fruits of *Cecropia* spp. were eaten along a 3 km road through forest between the savanna and Los Fierros camp, where MW may also have traveled to feed on fruits of planted guava and cashew nut. *Brosimum acutifolium* is a forest tree with fruits much used by spider monkeys in NKP (Wallace, 2005). We never found a *B. acutifolium* tree that MW used, and it appeared in the diet only after 2004.

The major dietary fruits (*A. edulis*, *S. gomphodes*, and Annonaceae) are characterized by few fruits per plant that ripen one by one over many weeks or months. Most fruits of *A. edulis* are parasitized by insects and do not ripen or are above the reach of MW where they are eaten by bats and birds. Frugivory is thus characterized by a daily

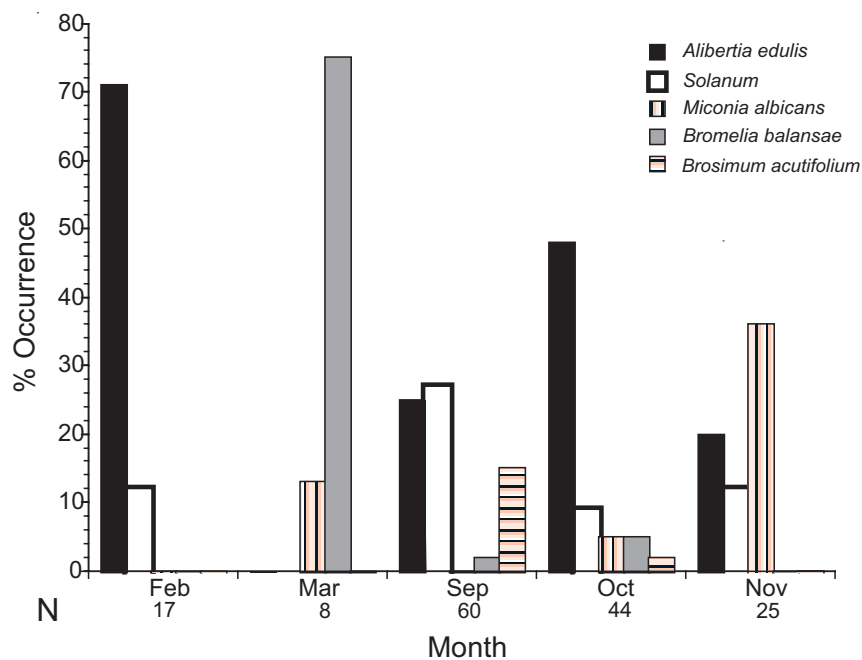


FIGURE 4.2. Percent of total scats in which the dominant six fruits occurred from 2001–2007, by month. Number below month is number of scats examined. Only seven months are represented.

TABLE 4.5. Percentages of total field-inspected scats in which fruit species occurred, by year, in the months from September to November. In descending order of percent occurrence in total sample of scats. *N*, number of scats in yearly sample. Years marked with asterisks are two years after large fires that burned half (2003) to all (1999) of the northern savanna where most scats were collected.

Species	Percent of scats						
	2001*	2002	2003	2004	2005*	2006	2007
<i>Alibertia edulis</i>	45	4	30	17	74	58	24
<i>Solanum gomphodes</i>	7	4	0	22	0	42	76
<i>Brosimum acutifolium</i>	0	0	0	11	32	0	24
Annonaceae all species	0	19	0	0	0	42	35
<i>Miconia albicans</i>	17	19	0	0	5	0	0
<i>Cecropia</i> sp.	0	0	20	11	0	0	0
<i>Bromelia ignaciana</i>	0	12	0	0	0	0	0
Discoid seed indet.	0	0	0	17	0	0	0
<i>Emmotum nitens</i>	0	0	0	0	0	8	6
<i>Hancornia speciosa</i>	0	4	0	0	5	0	0
<i>Chrysophyllum</i> sp.	0	0	0	0	0	8	0
<i>Anacardium</i> sp.	0	4	0	0	0	0	0
<i>Astrocaryum</i> sp.	0	4	0	0	0	0	0
<i>Dipteryx alata</i>	0	0	0	0	0	8	0
Fabaceae	0	0	0	0	0	0	6
<i>Ficus</i> sp.	0	0	0	0	0	0	6
<i>Vismia</i>	3	0	0	0	0	0	0
Indet. 4	0	0	0	0	0	8	0
Indet.	7	8	10	11	0	8	24
None	3	4	0	0	11	17	0
<i>N</i>	29	26	10	18	19	12	17

search of hundreds of plants. We watched a maned wolf at dawn zigzag directly from hummock to hummock across grassland, lifting its muzzle to sniff *A. edulis* treelets in an apparent olfactory search for fruits, but eating none.

ENERGETICS

We assume that the taxon-rich, omnivorous diet provides MW with all required nutrient classes, such as proteins, lipids, minerals, and vitamins, and that consequently, meeting energy demands is the limiting dietary factor. Below we consider only caloric content in estimating dietary costs and benefits.

As the baseline for maintenance without travel, we use the minimum energy requirements of captive MW, or 1,297 kcal per day (Barboza et al., 1994). The average nightly wet season travel distance of 9.0 km theoretically costs 212 kcal (January–June; 37 data sets of 5 MW, based on hourly fixes; Chapter 3); while the dry season average

travel of 13.13 km should cost 310 kcal above resting requirements (July–December, 5 MW, 55 data sets; Goszczynski, 1986). On this basis, the overall average calculated costs are 1,580 kcal per day: wet season costs are about 1,509 kcal per day, and dry season costs are about 1,607 kcal. The travel cost difference between the month of minimum average nightly travel (April, 7.9 km; Table 3.2) and the month of maximum travel distance (November, 14 km per night; Table 3.2) is about 144 kcal. However, as animals not traveling might be sleeping (with lowered metabolic rate), shorter trajectories could be associated with additional energy savings.

On artificial diets in captivity, MW produce 3–4 scats per day (Childs-Sandford, 2005; M. Rodden, pers. comm.). We find no data on transit times for fruits or rodents through maned wolf digestive tracts, but for beads ingested with artificial diets in early morning, the median excretion time of 92% of ingested beads was 14.1 hours, (eight individuals tested once each; M. Rodden

TABLE 4.6. Estimated caloric contents of various maned wolf food items; kcal per unit of an individual fruit or prey, number of units needed for the energy to travel 1 km (= 23.6 kcal, see Materials and Methods), and number of units needed for half of the average daily energy expenditure based on 12 km of travel (1,580 kcal, see text); and double that amount during lactation (fruit data from Gottsberger and Silberbauer-Gottsberger [2006], Motta-Junior and Martins [2002], Leung [1968], and Martins [2006]; animal data from Dierenfeld et al. [2002], Hill et al. [1984], Leung [1968], and Vitt [1978]). *Solanum lycocarpum*, *Annona crassiflora*, and *Psidium guajava* (guava) are items reported in the diet elsewhere (e.g., Lilienfeld, 2000; Rodrigues et al., 2007), which we use to estimate energy values for congeners or similar items for which we lack data. Here n/a, not available.

Item	Weight, g	kcal/ 100 g	kcal per unit	Units per km travel	Units per 50% daily kcal	Units per 50% daily lactating
Fruit						
<i>Alibertia edulis</i> *	30	60	18	1.31	43.89	87.78
<i>Genipa americana</i>	130	81.7	106.2	0.22	7.44	14.88
<i>Solanum gomphodes</i> †	300	41.1	124.2	0.19	6.36	12.72
<i>Bromelia ignaciana</i>	18.3	51	9.2	2.57	85.87	171.74
<i>Annona coriacea</i>	218	n/a	n/a	n/a	n/a	n/a
<i>Hancornia speciosa</i>	30	60	18	1.31	43.89	87.78
<i>Annona crassiflora</i>	650	52	532	0.04	1.48	2.97
<i>Psidium guajava</i>	45	64	29	0.81	27.24	54.48
Animal Prey						
<i>Dasybus septemcinctus</i> ‡	1500	201	3015	0.008	0.26	0.52
<i>Cavia aperea</i> §	300	216.7	651	0.04	1.21	2.43
<i>Proechimys longicaudatus</i> §	250	200	500	0.05	1.58	3.16
<i>Necomys lenguarum</i> ¶	42	171	72	0.33	11.10	22.19
Snakes	n/a	140	n/a	n/a	n/a	n/a
Bee and wasp larvae	n/a	254	n/a	n/a	n/a	n/a
Grasshoppers	n/a	170	n/a	n/a	n/a	n/a
Termites	n/a	356	n/a	n/a	n/a	n/a

*Estimated based on values for *Psidium guajava* (guava).

†Based on value for *S. lycocarpum* (Martins, 2006): in many publications, that value has been given as 345, or 10 times the true value.

‡Based on *D. novemcinctus*, parts eaten by humans (Hill et al., 1984)

§Based on value for domestic cavies.

¶Based on value for *Microtis* spp.

pers. comm.). The beads were excreted in a median number of three scats collected within 24 hours of feeding. If passage times *in situ* for small, indigestible items (seeds, rodent teeth) are similar to those for beads *ex situ*, and a similar number of 4 scats is produced per day, then the estimated caloric values of items in the diet, and the estimated caloric return of feeding on specific items, can be combined with the analyzed contents of scats to estimate daily energy consumption (Table 4.6). Scats examined in 2008–2009 included an overall average of 4.8 items eaten per scat: 1.9 items of fruits, 1.8 items of vertebrate

prey, and 1.1 invertebrates (Table 4.3) for an estimated biomass of 312.3 g eaten per scat. Dry season scats included 4.9 items versus 4.3 items in the wet season. Of these, fruits included 2.1 items (wet season) and 1.9 items (dry season); while for vertebrate prey, scats included 1.5 items (wet season) and 1.9 items (dry season; Castro, 2010). A daily production of four scats of our sample should thus represent on average 1,249 g of ingested foods and include 19 items, of which 7.6 are fruit and 7.2 are vertebrate prey. In the dry season, this sums to an estimated 1.48 items eaten per kilometer traveled, excluding

invertebrates (0.35 vertebrate prey and 0.57 fruits); while in the wet season, the number is 1.9 items per kilometer (0.68 vertebrate prey and 0.95 fruits), based on 4 scats/d and distances taken from hourly fixes (an underestimation of actual travel, see Chapter 3).

Lean small mammal prey are nearly alike in caloric value per gram (about 1.8 kcal per gram wet weight; Hill et al., 1984; Dierenfeld et al., 2002). If whole prey is consumed, the return per unit is a simple product of prey mass: a single cavy would provide 40% of all daily caloric needs, but 10 *Necromys* would be needed to achieve this amount (Table 4.6). A biomass of 625 g of prey (half the mass in 4 scats \times 1.8 kcal/g) would yield about 1,124 kcal, or 71% of estimated daily requirements. Caloric values of fruit pulps are lower (Table 4.6), and they vary greatly in water content. Most fruits seem to yield 0.5–0.6 kcal/g, so 646 g \times 0.5 would yield 312 kcal, or only 20% of daily requirements. The average value represented by four daily scats is thus estimated at 1,436 kcal, from the estimated 1,492 g of consumed biomass.

CONSEQUENCES OF A RODENT DECLINE

Expressed as biomass, the decline of rodents on our trapping plots was catastrophic, to 2% of maximal values in Termite Pampa (plot PT, 2001) and to 6.5% in Campo Cerrado (plot PA, 2003; Figure 4.3). The three MW that

were captured in years both during and after the rodent crash, gradually lost body weight (Figure 4.3), which for two males stabilized at 2–3 kg lighter after the decline of rodents in 2006. Female F3, with the longest record, was nonparous when she was heaviest in 2003–2004, but she was reproductive in subsequent years and continued to lose weight. The mean weight for these three MW stabilized at 26 kg in 2006–2008. Concurrent with the rodent declines, the number of maned wolf territories on the northern part of the savanna decreased from two to one, reducing the number of breeding pairs on Los Fierros savanna by a third (Chapters 3, 5). Associated with loss of a territory was an increase in territory size of pairs on the North Range from about 50 to 80 km² (Figure 4.3C; 10 data sets from four MW, 2001–2008). Although the territorial boundary with the neighboring pair on the South Range changed little after 2004, the northern territory continued to increase through 2009, largely by expansion into formerly little-used parts of the savanna (Figure 4.3C). Linear regression on average 95% kernel home range (KHR) size of adults on the North Range, by year, gives: $N = 6$, $R^2 = 0.947$; $p < 0.001$). There is a significant negative correlation between the percent of scats that included *Cavia* and the average 95% KHR size of the MW on the North Range (Pearson correlation coefficient, -0.86 ; Kendall tau -0.79 , $p < 0.03$). Coincident with the decline in rodent biomass was a fire that burned half of the northern savanna in 2003. This

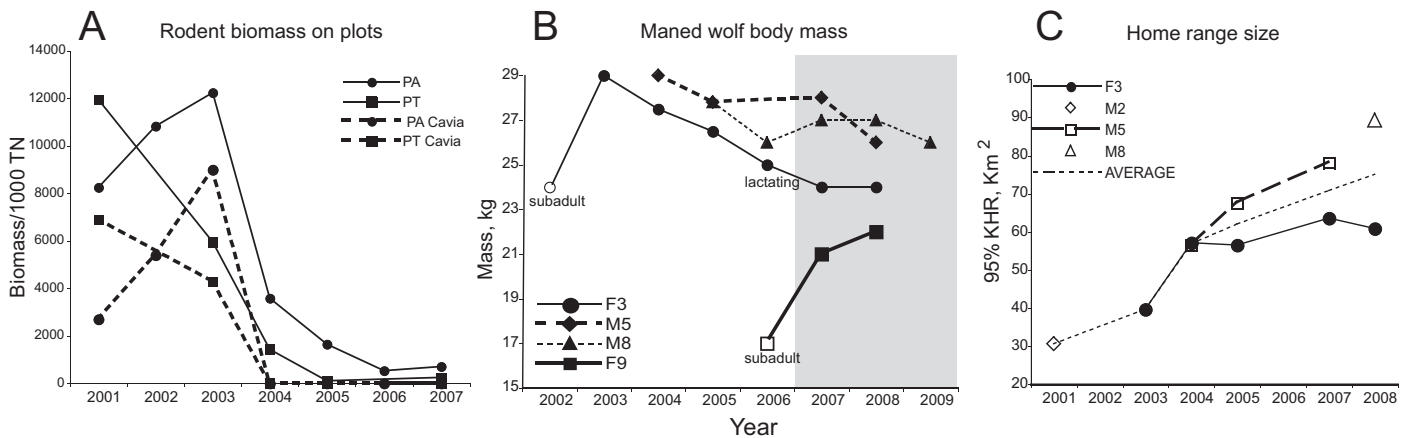


FIGURE 4.3. Rodent biomass and maned wolf weights and range sizes. (A) Biomass of rodents captured in 1000 trap nights on two trapping plots on the North Range (solid lines) and biomass of cavies (broken lines) on each plot. Plot PT (square symbols) was not trapped in 2002 or 2006. Biomass estimated at 0.75 of adult mass of a species. (B) Mass at yearly captures of four MW caught more than twice as adults. Subadults, open symbols; adults, solid symbols; males, broken lines; females, solid lines. Shaded area includes years following the total disappearance of cavies. (C) 95% kernel home range sizes and average (thin dotted line) of five territorial adults on the same territory (North) in successive years (10 data sets, > 600 fixes each, plotted by year when GPS data set was initiated).

would have reduced 2004 fruit production (Table 4.3) and perhaps directly killed rodents.

DISCUSSION

ANIMAL PREY

Our work confirms the results of most other studies, which show rodents as the chief prey taxa of MW (Table 4.3 Aragona and Setz, 2001; Belentani et al., 2005; Bueno and Motta-Junior, 2004, 2006, 2009; Dietz, 1984; Jácomo et al., 2004; Juarez and Marinho-Filho, 2002; Motta-Junior et al., 1996; Silva and Talamoni, 2003; Queirolo and Motta-Junior, 2007). At some sites, cavies were important components of the diet (Bueno and Motta-Junior, 2004; Motta-Junior et al., 1996), but in others they were not (Dietz, 1984; Rodrigues et al., 2007). Lilienfeld (2000) reported both *Cavia aperea* and *Galea* sp. (yellow-toothed cavies) in maned wolf diets, both from our study area and from Mangabalito on the far side of the park. We captured *Galea* c.f. *leucoblephara* at Mangabalito in 2000, but we did not identify it at Los Fierros (Emmons et al., 2006a). Because *C. aperea* vanished from Los Fierros between 2004 and 2006 (Emmons, 2009), possibly *Galea* also went extinct there, but earlier, between 1998 and 2001. However, there are no specimens to vouch for any *Galea* presence at Los Fierros. *Galea* spp. live in burrows that could shelter them from fires (J. Dunnun, pers. comm.); but burrows would exclude them from flood-prone areas of the Los Fierros savanna. *Cavia aperea* do not burrow (Asher et al., 2004), and they never occupied the deeply flooded southern parts of the savanna, although they lived in shallowly flooded zones, where we saw them sheltering on brushy hummocks surrounded by a few centimeters of standing water.

MW hunted prey in all savanna habitats, and all but one micromammal species known from Los Fierros savannas were identified in their scats. The prey species live in drier grasslands (*C. aperea*, *Juscelinomys huanchacae*, *Cerradomys scotti*, *K. tomentosus*); wet grasslands (*H. brasiliensis*, *Pseudoryzomys simplex*, *Cerradomys maracajuensis*, *O. microtis*); all grasslands (*N. lenguarum*); woody parts of dry grasslands (*P. longicaudatus*); forest islands in wet grasslands (*Oecomys sydandersoni*); or roadside brush, forests, and forest edges (marsupials *Marmosa murina*, *Gracilinanus agilis*, and rodents *Mesomys hispidus*, *O. microtis*). *Euryoryzomys nitidus* is a forest species, but we trapped rare individuals in all five sampled grasslands (Emmons et al., 2006a). We captured no marsupials and no wet grassland species in 15,312 trap nights

on the two trapping plots on the northern savanna (Emmons, 2009), and no species of dry grasslands in 1,030 trap nights in a Bajío savanna, where we caught all rodents of wet grassland and some marsupials eaten by MW. Maned wolves thus have wider habitat latitude than do their rodent prey.

Armadillos are reported as maned wolf prey in nearly all studies (Rodden et al., 2004), but in parts of central Brazil, they are the primary prey taxon in biomass, especially *Dasyus septemcinctus* (seven-banded armadillo; Rodrigues et al., 2007; Santos et al., 2003). The high energetic value of even the smallest Los Fierros armadillo (*D. septemcinctus*), enough for two days of nutrition, makes them the most valuable of all common maned wolf prey. We found them in 10% (2003) and 9% (2005) of scats (Figure 4.1), while Lilienfeld (2000) reported them in 15% of dry season scats, when they likely dominated prey biomass, as each armadillo is equivalent to about five cavies. Armadillos were sporadic in maned wolf diets at Los Fierros; they were absent after the destructive fire of 1999 and again after 2005 (Figure 4.1). Perhaps they were affected by whatever caused the rodent declines (Table 4.1; Emmons, 2009). As burrowers, small armadillos are susceptible to high levels of flooding, as occurred in 2008–2009 (Emmons, pers. obs.). Maned wolves prey on at least three other armadillo species (Rodrigues et al., 2007), and we found a carapace of *Euphractus sexcinctus* (5 kg) with tooth marks consistent with maned wolf predation.

A few records of large mammal prey (>10 kg) are found in nearly all studies of maned wolf diet (Rodden et al., 2004). Our 266 samples (2001–2009) included two scats with marsh deer hair, one with capybara and one with collared peccary. Rodrigues et al. (2007) state that MW “commonly” pursued pampas deer at night (*Ozotoceros bezoarticus*, 30–40 kg adult), but in their study, one of 328 scats included brocket deer hair (*Mazama* sp.), and none included pampas deer. Bestelmeyer and Westbrook (1998) saw a female maned wolf pursue, kill with a throat bite, and feed on a yearling pampas deer in Emas Park. The maned wolf then regurgitated meat to her pup. Nevertheless, in the same park a year earlier, Jácomo (1999) found pampas deer remains in only 0.2% of 1,673 maned wolf scats, compared with a 65% presence of rodents in the same sample. Motta-Junior et al. (1996) found remains of juvenile red brocket deer in two of 304 scats (*Mazama americana*). There are now no pampas deer on Los Fierros savanna, but the larger marsh deer (*Blastoceros dichotomus*, about 100 kg) is numerous, and there are a few grey brockets (*Mazama gouazoubira*, 15 kg). The deer we found in two scats may have been scavenged, as in one case, there

was an old carcass nearby. Jaguar and puma are common at Los Fierros, and we found the scat with capybara hair a day after campesinos reported one killed by jaguar about a kilometer away (they likely scared it off the kill). In Emas Park, where MW have been seen to scavenge on road kill (Rodrigues et al., 2007), surveys censused 540 vertebrate road kills in one year (Fischer et al., 2003). Carcasses or mutilated survivors could give MW a taste for deer, which might subsequently entrain predation. A curious feature of the NKP ecology is that only vultures seem to visit most carrion, and there are no bone scavengers.

The MW watched by Bestelmeyer and Westbrook (1998) chewed apart its deer kill and cached it in 10

separate pieces. Similarly, MW stole a series of our HB Sherman rodent live traps several times and cached them out of sight shoved under vegetation, dispersed in all directions many meters from our trap line. Inveterate cachers, they also took and hid objects such as a metal water dish and steel water bottle. Deer bones in the Los Fierros savanna were little scattered, sometimes with parts missing, but bones showed few or no marks of gnawing by rodents or other mammals, or evidence of caching. Skeletons we found of five MW and a few zorros were complete and scattered within a short radius, as if by vultures (Figure 4.4). The bones had no tooth marks, even on ribs, and a skeleton 82 days postmortem had all spine articulations



FIGURE 4.4. Skeleton of maned wolf F9, dead 84 days. The head is at left of big grass tuft, and the completely articulated spine is in grass at top left, to the right of a dark leaf. No bones had tooth marks. Note narrow spread of only 4–5 m, as if dispersed by vultures.

intact. Zorros and raccoons are ubiquitous and common and would certainly discover any large cadaver, but there was no evidence of mammalian scavenging. If MW at Los Fierros scavenged, they did so rarely and avoided conspecific cadavers.

Rodrigues et al. (2007:48) remark that pampas deer alarm at MW and “perceives the wolf as potential predator.” Marsh deer grazed the evergreen sward around the PM water hole (Chapter 3), where Emmons watched a deer and maned wolf meet. Only 10 m apart, ears cocked, they stretched out their muzzles toward each other, without signs of fear; and with no predatory movements by the maned wolf. The deer took several steps toward the maned wolf but then went back to grazing, and the maned wolf drank. If predation were commonplace, the maned wolf would have spooked deer from the water hole, but neither marsh deer nor giant anteaters avoided MW or alarmed noticeably at their odor. In contrast, zorros (*Cerdocyon thous*) made themselves scarce or hovered in the distance when MW were present.

We found wasps with their nests in 5 of 93 dry season scats, and bees in 21 (Table 4.3), items likewise reported in multiple scats by Dietz (1984) and Bueno and Motta-Junior (2004). The high caloric content of wasp larvae may be worth a few stings (Table 4.6), but other arthropods in the diet are unlikely to contribute significant nutrition.

FRUGIVORY

MW eat the same general fruit taxa throughout their geographic range (reviewed by Rodden et al., 2004; Rodrigues et al., 2007). The exceptional feature of frugivory at Los Fierros was the preponderance of *A. edulis* in the diet. Other maned wolf studies have been in dry grasslands, where *Solanum lycocarpum* strongly dominated diets and *A. edulis* was absent or nearly so (Rodrigues et al., 2007). The local importance of *A. edulis* may be due to flood-prone Los Fierros habitat, as the species was common on hummocks in seasonally flooded savannas, where *Solanum gomphodes* was rare. *Solanum lycocarpum* is favored by anthropic disturbance (Courtenay, 1994; Motta-Junior et al., 1996) and *S. gomphodes* may have similar ecology, as it seems more common on roadsides than in undisturbed NKP savanna. The predominance of the genus in maned wolf diets may indicate altered habitat (Motta-Junior et al., 1996).

Other studies of maned wolf diets report the dry season as the time of fruit scarcity and lowest dietary diversity of fruits (Motta-Junior et al., 1996; reviewed by Rodrigues et al., 2007). In our study area the wet season period of

deepest flooding (February–April) was the time of fewest dietary fruit species (Castro, 2010; Lilienfeld, 2000), as well as the least travel and smallest range area (Chapters 2, 3). It was also the period of all known-date adult maned wolf deaths at Los Fierros (Chapter 6), perhaps reflecting seasonal dietary and/or social stress.

Fires can influence the production of savanna fruits (Sanaiotti and Magnusson, 1995). Hot fires, as in 1999 (whole northern savanna), 2003 (half of northern savanna), 2007 (part of northern savanna), and 2009 (whole savanna) at Los Fierros, entirely remove the above-ground stems of many woody plants, which stump-sprout after burns (*A. edulis*, *M. albicans*). Other species have fire-resistant bark and lose only leaves and thinner branches (*S. gomphodes*, *Brosimum gaudichaudii*, various *Annona* spp.) but can also lose aboveground trunks if the fire is extremely hot. In the year after a burn, plants recover their woody vegetative parts and leaves, but with some exceptions (*Duguetia furfuracea*, *Bromelia ignaciana*), flower little (Figure 4.5). The second year after burns, fruiting may be especially abundant. *Alibertia edulis* peaked in scats two years after burns, in 2001 and 2005, with fewer eaten in the third and fourth years following burns (Table 4.5; Figure 4.2). We observed that after burns, *A. edulis* fruits were larger and had less insect damage (study in progress). Fire may benefit adapted plants by reducing insect predators as well as liberating nutrients as ash. Lilienfeld (2000) identified *A. edulis* in only 4% of 51 scats collected at Los Fierros in 1996–1997 (as “indet. D, marmelada”). He perhaps failed to identify the species, but a 1996 satellite image shows the entire northern half of the savanna carbonized; so it is more likely that few *A. edulis* fruited in those years. Annonaceae spp. peaked in scats only in the third year following burns (Table 4.6), but records are few. A fire-influenced pattern for *S. gomphodes* is unclear.

Miconia albicans is abundant on hummocks in termite savanna and its fruits ripen in October–November. It was important in the diet only in 2001–2002 (Table 4.5). In later years, its fruits did not ripen and dried up on the plants. Sanaiotti and Magnusson (1995) found that fire nearly eliminated next-year fruiting *M. albicans* and other savanna shrubs with bird-dispersed fruits, which masted maximally two years after burning. There is a hint of this in its presence in maned wolf scats (Table 4.5), but another factor, such as the decrease of dry season rainfall (Figure 1.9), seems to have affected fruiting after 2002.

The highest biomass fruits in the maned wolf diet, including *S. gomphodes*, *A. edulis*, *Annona* spp., and *G. americana* (Table 4.6), are soft pulped, too large to



FIGURE 4.5. A termite hummock with *Alibertia edulis* in Los Fierros pampa in October 2000, one year after the 1999 burn. The lush rounded foreground clump is new regrowth from the roots. The gray stems above the clump and in the background are woody stems killed by the fire, showing their former height. Another large-leaved species is in front of the *A. edulis* clump. The forest edge is in the background.

swallow whole, and dull yellow or brown when ripe, with scores or hundreds of small flat seeds. These fruits were broken by mastication before ingestion, as were the yellow, coriaceous *B. ignaciana* (Figure 4.6A). In contrast, the melostome *M. albicans* has clusters of small, juicy, blue-green, berries, which MW bit off and swallowed with little chewing, so that many berries were excreted nearly whole (Figure 4.6B). Too-large-to-swallow fruits may thus be better triturated and yield more of their nutrients than are berries that pass nearly intact through the gut (Figure 4.6). Seeds were passed whole, unbroken by mastication. As elsewhere (Motta-Junior and Martins, 2002) MW disperse these fruits on the Los Fierros savanna, but tapirs also eat and disperse all of them.

DENTAL ISSUES

The large molar surface area of MW should help to crush fruits for better assimilation than is usual for other Canidae (Table 1.2; Van Valkenberg, 1989), but by the age of about five years, our study animals had worn down the cusps of the second and third molars or premolars, and at about six years, these teeth were worn down to gum level (Figure 6.2). Ten-year-old zoo MW show almost no tooth wear (based on U.S. National Museum specimens). Likewise, free-living, wholly carnivorous gray wolves reach this stage of tooth wear only at 10–12 years (Gipson et al., 2000). The rapid tooth wear of *in situ* MW is almost certainly associated with frugivory. Acids and sugar in fruits,

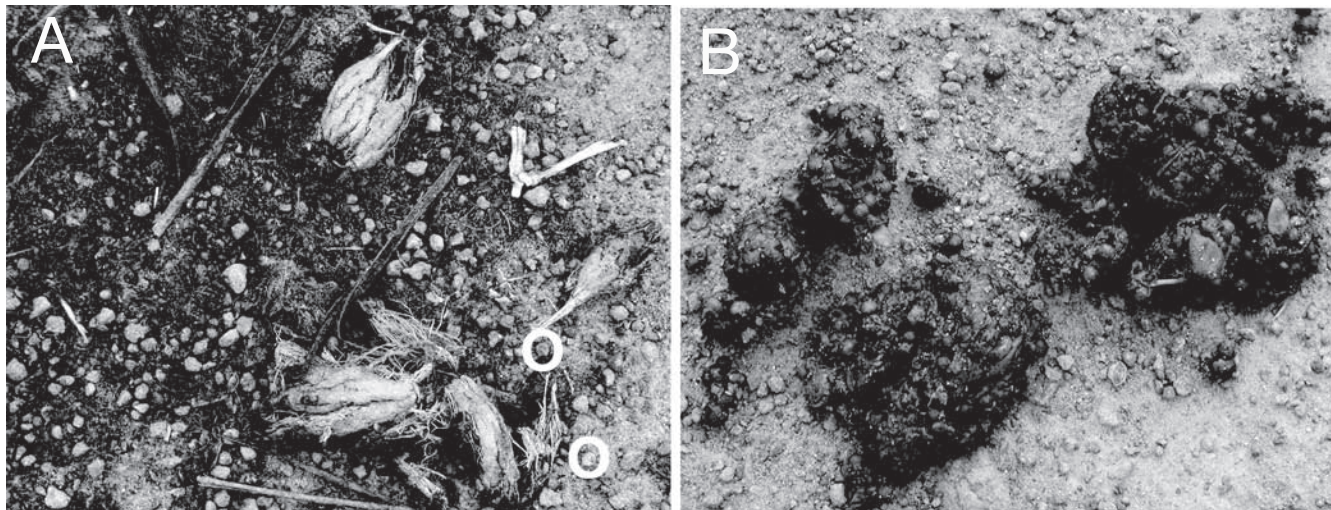


FIGURE 4.6. Fruits in maned wolf scats on road. (A) *Bromelia ignaciana*, crushed fruits, and rodent foot in old, rain-washed scat; two bromeliad seeds are circled. (B) *Miconia albicans* (nearly whole berries) and *Duguetia* sp. (leaf-shaped sheaths and isolated seed on right below mass).

and phytoliths of *B. ignaciana*, probably contribute both to decay and to erosion of tooth enamel, but we cannot exclude a genetic legacy of weak teeth or thin enamel.

Free-living MW have many slab fractures of the teeth (Furtado et al., 2007; Chapter 6). We have no evidence that MW crush large bones in our study area, but Motta-Junior et al. (1996) noted that armadillos, deer fawns, and *Tupinambis* lizards were eaten whole, and crushed fragments of crania and mandibles were found in scats. Fractured cheek teeth could also result from chewing fruits with large, hard pits (*M. armata*, *B. gaudichaudii*, *Emmotum nitens*, *Dipteryx alata*; Table 4.3) and/or tough fibrous fruits such as bromeliads. The canine teeth also had slab fractures, which are unlikely to be broken by frugivory. Armadillos seem the only commonly reported prey likely to fracture canine teeth, especially if MW bite the heavy braincase. Lilienfeld (2000) reported one scat with a tortoise (*Chelonoidis* sp.), but other studies with large samples report no chelonians in the diet (Bueno and Motta-Junior, 2009; Dietz, 1984; Jácomo, 1999; Rodrigues et al., 2007; Silva and Talamoni, 2003). Rapid tooth wear and molar damage may be major costs of frugivory that effect both morbidity and mortality (Chapter 6).

ENERGETICS

The estimation of daily food consumption from scats requires data on the related variables of both food item

passage times through the gut and the number of scats produced daily. Neither of these is recorded for *in situ* MW. Of beads added to food, 20% to 90% were passed by MW in the first scat after morning feeding (following a night's fasting), and almost all passed by the third scat, generally within the same 12 hours (M. Rodden, unpublished data). But the time between feeding to the first scat varied from less than 3 hours to over 10 hours, perhaps because defecation was delayed in sleeping individuals because experiments were done by day. Childs-Sanford and Angel (2006) measured the passage times of artificial maned wolf diets tagged with titanium dioxide dye and found transit times of 12 to 14 hours for 50%, and 48–47 hours for 97% excretion of ingested dye (again, fed in the morning). Titanium dioxide is a hyperfine powder, and peristalsis may move it more slowly than beads, which better mimic indigestible seeds or rodent bones. The passage times of native seeds through crab-eating zorros averaged 7.7 hours to 80%–91% recovery, with larger seeds passing more rapidly than smaller seeds (Varela and Bucher, 2006). In wolves (*C. lupus*), the passage time of prey was 8–56 hours, but no very small prey were fed. Hares of 1.4 kg produced only 1.2 collectible scats (Floyd et al., 1978). From these reports, it seems likely that undigested parts of fruit and small prey of MW are nearly or entirely excreted in scats within 24 hours of feeding, or at most, within 48 hours.

If four scats represent one day of foraging, as *ex situ* (Rodden, pers. comm.), our estimate of daily consumed

biomass sums to 1,249 g total, or 1,436 kcal if the diet is 50/50 prey/fruit. This is close to the theoretical calculated value of 1,580 kcal. If, instead, the biomass eaten is 60/40 prey/fruit, the total comes to 1,598 kcal: precisely the same as the 1,607 kcal per day theoretical value that includes the dry season travel average of 13.1 km per night. The wet season ratio of 45/55 prey/fruit yields 1,378 kcal, but the calculated requirements for maintenance plus 9 km average nightly travel are 1,509 kcal. Thus, in the wet season, there seems to be a caloric deficit in the estimated contents of scats. We reported that MW are active for averages of over 14 of the 24 hours during dry season months, but for only about 12 hours during wet season months (Chapter 2; Table 2.2). Two hours of extra rest would reduce wet season maintenance energy needs and account for some of the estimated deficit. We also expect some underestimation in our calculations of the biomass represented in scats: from guesswork in calculations of item weights, scat numbers per day, and energy values, or from failure to identify all items in scats. Nevertheless, the close correspondence between our estimates from scats and those from theoretical calculations of energy expenditure confer some confidence to both the methods of analysis and the completeness of identification of scat contents. During the months in 2008–2009 when we collected scats for quantitative analysis, one of the females was pregnant, but none was lactating. Because diets include many fruits and small prey, gleaned one by one over hours of foraging, we would expect the greater energy consumption of lactating females to be reflected in a greater number of scats produced per day rather than in a greater biomass representation per scat (in the absence of larger prey, such as armadillos). One more scat per day would balance the accounts. It would be informative to experiment *ex situ* on passage times of fruit, rodents, and armadillos fed at night to better calibrate diet analysis from field-collected scats.

Santos et al. (2003) estimated a consumed biomass per scat of 469 g, while Rodrigues et al. (2007) calculated 900 g/scat. In the former study, armadillos comprised 44% of consumed biomass, and in the latter, 37% of consumed biomass, while *C. aperea* was only 0.5%. Calculating consumed biomass from scats is problematic if (1) a prey item is too large to be eaten in one meal and is eaten in several (Ackerman et al., 1984; Marucco et al., 2008), (2) if only parts are eaten, (3) if scats are highly variable in the amount of a day's food they represent, or (4) if parts used to count ingested individuals are digested variably (Kelly and Garton, 1997). We cannot directly compare our findings of 312 g per scat with those of the above studies, where the consumed biomass was dominated by *Dasyopus*

septemcinctus (1.5 kg each, 27% of biomass eaten; 16% of scats; Rodrigues et al., 2007). Nonetheless, 900 g/scat exceeds the daily energy requirements, even of lactating females. If daily scat production was equivalent to one or two feeding events, the discrepancy is reconciled (i.e., analyzed scats are not independent; one armadillo in 2–3 scats). We grouped scats into events to avoid counting the same food item more than once. If consumed prey was partly regurgitated to young, assimilated biomass would be also overestimated.

The energetic consequences to MW of the rodent decline are clear (Table 4.6). It is reasonable to assume that the chance of a maned wolf encountering a savanna rodent decreased by 95%, in parallel with the number of individuals trapped. It is hard to imagine that this did not greatly affect all carnivores on the savanna, but the loss in body mass, increase in territory size, and reduction in territory number that simultaneously occurred among MW (Figure 4.3) are nevertheless correlations without proof of causation. A future reversal of these trends would help to support a causal hypothesis.

Maned wolves should obviously prefer to eat armadillos and larger rodents, such as cavies and *Proechimys*, and large fruits, such as *S. gomphodes* and *Genipa*, just three or four of which can satisfy their daily energy needs (Table 4.6). Instead, scats show that they apparently eat everything encountered, no matter how small, such as insects, tiny mice, and tiny berries. This implies a high unpredictability in meeting the daily requirements. The long, nonrepeating, nightly trajectories of MW and movements with few pauses (Chapters 2, 3) match the diet of small, highly dispersed, and unpredictable items, a score of which were required to meet the needs of each day at Los Fierros (four scats). The low reproductive rate may reflect the difficulty for MW of increasing their daily food intake (Chapter 5).

CONCLUSIONS

Ours is the first multiyear study to record the interannual variation of fruit and prey species eaten by MW, with a concurrent independent study by trapping of the rodent resource base. Our samples were small, but they point to unexpected levels of interannual variation in dietary fruit and prey that were coincident with changes in maned wolf home range size and body mass. Shorter projects would not have detected these changes. Mammalian prey declined in the study area, without reversal through 2007. Likewise, all fruit resources of MW were variable seasonally and unpredictable interannually, with production dependent on

chance fires and probably rainfall. The opportunistic omnivorous diet allows MW to survive extreme resource unpredictability on the temporal scale of their lifetimes, but only to a point: the combination of extreme events from 2003–2009 resulted in a population reduction of Los Fierros MW of as yet unknown duration (2011). Conservation of the heterogeneous matrix of woody fruiting plants and grassland rodent habitat is critical to maned wolf viability. The grasslands require fire maintenance to prevent the overgrowth of trees (Chapter 7), but woody fruiting plants cannot be burned more often than every three years without loss of fruit diversity and productivity. Our results suggest that maned wolf breeding populations might be doubled in optimal, compared to depleted, resource conditions. To maintain sustained resource levels, on the 100 km² scale of maned wolf home ranges, a patchwork rotation of a quarter of the habitat burned yearly, such that the other three quarters are in one, two, and three year stages of regeneration, would seem to be the best initial plan for maximal resource production. Much can be gleaned from

longitudinal analysis of scats, but experimental studies are needed to better define the variables used in calculations of energetics

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