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Introduction: Study Site and Methods

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RESEARCH OVERVIEW

Although few outsiders know of its existence, a remarkable carnivore lives in the tropical and subtropical grasslands of southern South America. Maned wolves (MW) (Canidae: *Chrysocyon brachyurus* Illiger, 1815) combine distinctive physical and ecological features that place them in a unique category among living species (Moehlman and Hofer, 1997). This misfit among the large Canidae chiefly inhabits the Cerrado, a critically threatened South American Biome (Figure 1.1). We studied MW for 10 years in Noel Kempff Mercado National Park (NKP), Bolivia.

Our overall initial research goal in NKP was to describe the spatial assortment of mammal species among the diversity of habitats where Amazonian forest meets the tropical savanna complexes of the Cerrado (α and β diversity and habitat associations). By recording how species respond to increasing forest dryness and the transition to grassland, we set out to discover which species are the most robust to environmental stress (including climate change) and which are the most susceptible. We focused on the small mammal communities and on the maned wolf, a predator linked closely to small mammals by diet. MW are the largest endemic Carnivora of the southern grasslands, and as such, they may be indicators of the ecological integrity of such systems, as they are both primary and secondary consumers. In the end, temporal variation that we recorded during our research proved to be equally or more informative than spatial distribution (Emmons, 2009; Chapter 4). What we did not expect to observe during our study were severe climate phenomena that already exerted profound effects on all of our focal taxa (Emmons, 2009; Xu et al., 2011; Chapters 3–5).

A species is understood in the framework of its physical and social environment, and we aimed to discover how the unique suite of maned wolf physical adaptations might be fitted to the ecological conditions in the Cerrado. More

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FIGURE 1.1. Simplified diagram of major biomes of South America. The black area between the Chaco and Cerrado represents the Pantanal wetlands.

specific objectives of the research were to reduce multiple gaps in our knowledge of the behavior of individual MW. Among these objectives were basic questions: how far and fast, and when and where, do MW travel each day; when and how do they interact with other MW; what is their reproductive biology; how do floods and fires affect them; what are their diseases and causes of death; and might management improve their conservation prospects? In this monograph we group together what we have learned. Although each of the following chapters might stand alone, each is tied to the information in the others: movements cannot be understood without knowing the activity and diet, diet and ranging influence health and reproduction, and knowledge of diet and movements are required for understanding the social behavior and reproductive parameters. Together the information in these chapters aggregate into the holistic view of the species needed to understand its place among Mammalia.

This introduction gives a brief overview of our research. We describe the MW that were the object of our studies, the habitats they occupy, and the location and climate of the study area. We outline our methods for field research and analysis of data.

In Chapter 2 we describe how the circadian pattern of activity varies temporally, how many hours individuals spend traveling and resting in different seasons, and where they go when inactive. Our data suggest that temperature and water supply are critical issues for MW in the dry season. This routine knowledge is basic to understanding both habitat requirements and the energy balance of MW.

In Chapter 3 we extend the analysis of movements to describe the spatial patterns of landscape use, the size of ranges, and how individuals divide the landscape among themselves. The amount of space used by each animal, and how it shares space with others, is a fundamental property of its energetics, ecology, and conservation needs.

In Chapter 4 we analyze the diet qualitatively and quantitatively, and we estimate the calories represented by individual food items and the number of each item that a maned wolf needs to acquire each day based on the travel times and distances estimated in Chapters 2 and 3. We assess the changes in species in the diet after fires and following the decline to extinction of the dominant rodent prey from the study area after 2004 (Emmons, 2009), and we show some probable consequences of a prey decline on maned wolf ecology and behavior.

In Chapter 5 we summarize our limited data on social behavior and reproduction based on interactions surmised from proximity patterns of maned wolf telemetry locations. We also document long-distance calling behavior noted as we followed MW on foot with old-fashioned very high frequency (VHF) telemetry. We describe pair formation, estrus, parental behavior, and the fates of a few young born in the study area. Their social organization is the most fascinating aspect of canid biology, as it can rival in complexity that of primates and cetaceans. Our results hint that MW have more complex family lives than sometimes supposed.

In Chapter 6 we describe maned wolf health and mortality based on serology, ecto- and endoparasites, and tooth and skeletal lesions. Our study population is one of the few that is isolated from human-caused mortality (road kill, shooting, toxins), so our health survey exemplifies an "isolated" population in a pristine national park. Maned wolves that have never been in direct contact with domestic dogs and cats evidence frequent exposure to their pathogens. Infectious diseases are a wildcard that must be considered in conservation planning.

In Chapter 7 we give an overview of both range-wide and local conservation issues, and we list the known and likely threats to maned wolf survival. A summary of the existing published knowledge base uncovers little data on maned wolf population biology, probably because of the great difficulty of detecting and counting individuals. We map the distribution of the species in relation to protected areas and identified population subunits. From our findings in Chapter 7 and the preceding chapters we outline some recommendations for conservation and research.

In Chapter 8 we give an overview of our conclusions and develop some hypotheses about maned wolf functional morphology. We conclude with a list of unanswered questions about MW biology that we propose as fruitful subjects for future research.

The Maned Wolves

Measuring 90 cm in standard shoulder height (SH), MW are the tallest of wild Canidae (Table 1.1). For their

TABLE 1.1. Average measurements of females of the seven largest Canidae. No measurements of female Dhole (*Cuon alpinus*) seem available (nd, no data found). Maned wolves (MW) (indicated in bold) are the second heaviest species when females are considered, but because red wolves and African wild dogs have relatively heavier males, MW males are outweighed by three species. Maned wolves are the tallest, with the longest hind foot, but the head and body length ranks fourth, much shorter than that of similar-weight African wild dogs. Measurements in millimeters: shoulder height (SH); head and body length (HB); and hind foot length (HF). Data from current study (SH) and Jácomo et al. (2009; MW), Sillero-Zubiri et al. (2004; other species), Mech (1970; gray wolf, part), and Creel and Creel (2002; SH of *Lycaon*). Coyotes and gray wolves show great geographic size variation, and some populations are larger or smaller than tabulated. We measure SH as tip of the scapula to tip of the toes, leg of prone animal stretched. Jácomo et al. (2009) give much shorter measurements of "Height" (M:F 86:83 cm) than ours of SH (M:F 93:90 cm), so their measurement was taken differently. Jácomo et al. (2009) had a sample size tenfold greater than ours.

Species	Mass, kg	SH	HB	HF	HF/HB
Maned wolf, *C. brachyurus*	**24.6**	**900**	**1068**	**292**	**0.27**
Gray wolf, *Canis lupus*	39	700	1150	279	0.24
African wild dog, *Lycaon pictus*	24	700	1265	241	0.19
Red wolf, *Canis rufus*	24.3	662	1073	222	0.21
Ethiopian wolf, *Canis simensis*	12.8	nd	919	187	0.20
Dhole, *Cuon alpinus*	11.5	nd	nd	nd	nd
Coyote, *Canis latrans*	10.1	570	824	180	0.22

height they are lightweight (25 kg), with little muscle mass. Adult females are slightly lighter than males (females, 24.6 kg, standard deviation (SD) 3.2; males, 26.6 kg, SD 3.6) but overlap with males in size range, and males and females average the same body length (Dietz, 1984; Jácomo et al. 2009). This handsome canid has thick, rust-red body fur highlighted by a pure white throat and ear linings, and a pale to white tail tip and eyebrows. These contrast with pitch-black legs, muzzle, lower throat, and mane (see Frontispiece). The dorsal pelage and its mane of long black hairs on the neck and shoulders are raised in excitement or alarm, and the tail is fluffed, exaggerating the apparent body size (Kleiman, 1972). The fox-like head has a narrow pointed muzzle and exceptionally large ears. The mouth is framed by black lips, but the upper lip has a narrow white band under the nose ("Got Milk?"); perhaps this is a target for pups to solicit regurgitation. The two center toe pads of the feet are joined at the base to form a single unit that along with shape, distinguishes the tracks of pups from those of foxes (Pocock, 1927; a character shared with the bush dog, *Speothos venaticus*). Long legs and a short back mandate a pacing gait (ipsilateral legs move together), and normal maned wolf travel is at a walk, with head held lower than the salient shoulder blades, and outsized ears pointed forward (Frontispiece). Maned wolves are calm and even timid, but to their peril, when free, they are generally unafraid of humans. The species occupies tropical and subtropical mesic savannas of Argentina, Brazil, Bolivia, Paraguay, and Peru, with most of the current range in the Cerrado ecoregion, but including drier parts of the Beni and Pantanal flooded grasslands, and humid grasslands of subtropical Argentina (Quierolo et al., 2011). They are considered Threatened or Endangered in all of their range countries, but Near Threatened by International Union for Conservation of Nature Red List (IUCN, 2009).

The behavioral ecology of MW was first studied with radio telemetry by Dietz (1984), in the Brazilian Cerrado. Free-living MW are rarely visible, and Dietz complemented his field studies with behavioral observations of captive individuals at the Smithsonian Conservation Biology Institute (formerly Conservation Research Center), which has maintained the Association of Zoos and Aquariums (AZA) Studbook and a breeding program for nearly 40 years. Dietz described MW as socially monogamous, solitary-living canids that share exclusive pair territories (we follow Reichard and Boesch [2003] for definitions of monogamy). Dietz' (1984) basic findings have been confirmed (Jácomo et al., 2009), but surprisingly little new has been added to his outline of their socioecology. Maned wolves are omnivores, with a diet of about half each of fruit and small vertebrate prey (Dietz, 1984; Rodden et al., 2004; Rodrigues et al., 2007). Their home range size varies from about 25 to 100 km^2 (Dietz, 1984; Jácomo et al., 2009). Diet and home range sizes have been well documented in multiple populations (Jácomo et al. 2009; Rodden et al., 2004; Rodrigues et al., 2007), but only a few details are recorded of the interactions or life histories of free-ranging individuals in any part of their range (Melo et al., 2007, 2009). Current knowledge of the species was summarized in Rodden et al. (2004), and recent important additions include Melo et al. (2007, 2009), Coelho et al. (2007, 2008) Rodrigues et al. (2007), and Jácomo et al. (2009).

Seven species of living Canidae can weigh over 15 kg (Table 1.1), and MW are the only omnivore among these. All but the coyote normally live in packs, and the heaviest all cooperatively hunt prey larger than themselves, making MW an ecological outlier. Their dentition shows MW to be morphologically adapted to their diet of relatively little meat and relatively more plant matter (which requires molar crushing to release cell contents; Table 1.2; Van Valkenburgh, 1989).

TABLE 1.2. Relative tooth morphology of canid species (from Van Valkenburgh, 1989). The first two species are omnivores; the last four are the most carnivorous of living Canidae. Canine shape is the ratio of cross sectional width/cross sectional length.

Species	Canine shape	m1 relative blade length	Relative molar grinding area
Maned wolf, *Chrysocyon brachyurus*	63.7	0.57	1.08
Crab-eating zorro, *Cerdocyon thous*	59.4	0.59	0.99
Gray wolf, *Canis lupus*	53.6	0.72	0.66
Dhole, *Cuon alpinus*	58.8	0.74	0.66
African hunting dog, *Lycaon pictus*	64.2	0.72	0.57
Bush dog, *Speothos venaticus*	72.4	0.72	0.55

Of 12 Canidae examined, MW have the largest relative molar grinding area, and of 31 total Carnivora, only omnivores and invertebrate feeders, such as bears, badgers, and procyonids, have greater molar grinding surfaces than MW (Van Valkenburgh, 1989). Similarly, the relative blade length of the lower first molar, used for slicing meat, is shorter in MW than in any other of the 12 Canidae. Even the sympatric crab-eating zorro (*Cerdocyon thous*) (following Macdonald and Courtenay [1996], we use the term "zorro" for South American foxes to distinguish them from other fox lineages) has teeth with slightly more meat-eating architecture than those of MW (Table 1.2). These features show MW to have an ancient evolution as omnivores, and it is unlikely that their current habits are a switch from greater carnivory in the recent past. We thus view their current ecology as reflecting an ancient adaptive suite.

Their distinctive teeth were the basis for classification of a 5–4 Ma old jaw fragment from North America as the earliest known *Chrysocyon*, *C. nearcticus* (Tedford et al., 2009; Wang et al., 2008). The earliest known South American *C. brachyurus* fossils are much younger, from the Early Pleistocene of Bolivia (Ensenadan, 1.2–0.8 Ma; Berta, 1987). Slater et al. (2009) recently clarified the evolutionary relationships of South American Canidae by DNA analysis. Their hypothesis shows the nearest recent relative of MW to be the mysterious Falkland Island wolf (*Dusicyon australis*), which was found by Europeans in 1690 and extinct by 1876, extirpated by shepherds. The closest living species to MW is the bush dog (Slater et al., 2009; Wayne et al., 1997), with an estimated divergence time from MW of 10 Ma (compared with 6.7 Ma for *D. australis*; Slater et al., 2009). If confirmed, these early dates imply that the diversification of South American genera occurred in North America, prior to the arrival of Canidae on the South American continent (Slater et al., 2009), as is also suggested by the fossil record (Berta, 1987; Wang et al., 2008).

The Cerrado Habitat

The Cerrado ecoregion crosses South America in a diagonal belt south of the Amazon rain forests, in a band of about 1.9 million km^2 of tropical dry forests interdigitated with a complex mosaic of wet and dry savannas and shrublands (Figure 1.1). A quarter of the area of Amazonian rain forests, Cerrado is the second largest biome in South America. Annual rainfall is moderate but strongly seasonal, with 4–6 months of little rain. El Niño Southern Oscillations (ENSO) cause rapid interannual shifts in severity of drought and flooding. Monthly and annual average temperature excursions are much higher than in the evergreen rain forests, and daily temperatures can rise 20°C between dawn and afternoon. Cerrado soils are often acidic, with low cation exchange capacity and high aluminum saturation (>40%), which makes them toxic to many plants (Gottsberger and Silberbauer-Gottsberger, 2006). Moreover, Cerrado grasslands are fire-adapted ecosystems and frequently burn. The biota is thus challenged by environmental extremes, although to a lesser degree than those of the southern deserts or Chaco. Half or more of the area has been deforested for agroindustry.

The Cerrado flora is well known. With high β diversity and local endemism it is the richest tropical savanna region in the world for vascular plants, with estimates of 6,700 to 10,000 species (Bridgewater et al., 2004; Klink and Machado, 2005). The fauna, in contrast, is poorly studied. For mammals, the region has been supposed to be depauperate (Klink and Machado, 2005). In 1986, 100 nonvolant mammal species were listed, 11 of them endemic (Redford and Fonseca, 1986). By 2002, the list had grown to about 200 species of Cerrado mammals (143 nonvolant), 18 of them endemic (one a bat; Marhino-Filho et al., 2002). However, by 2011, this still seems significantly underestimated, with about 34 mammalian species now recognized as endemic to the Cerrado and related habitats (Emmons, unpublished list) from a total of at least 230 species (IUCN, 2009). At 46% of the richness of Amazonian rain forests on 25% of its landmass, the fauna now appears species rich in all orders except Primates. Our incomplete inventories record 91 species of nonvolant mammals and 72 species of bats in NKP (some of them Amazonian; Emmons et al., 2006a, 2006b). Most of these are small-bodied taxa.

The modern Cerrado fauna includes only the survivors/successors of an extinction event that eliminated at least 72 taxa of Pleistocene/early Holocene megafauna (>44 kg; de Vivo and Carmignotto, 2004; Martin and Klein. 1984), leaving it nearly empty of large mammals (>20 kg). There are but three endemic, large-bodied species restricted to open habitats of the humid southern tropical grasslands: the maned wolf and two large deer (marsh deer, *Blastocerus dichotomus* Illiger; 100 kg; pampas deer *Ozotoceros bezoarticus* L.; 35 kg). All three are declining and listed as Near Threatened or Vulnerable (IUCN Red List). Other large taxa found in open Cerrado habitats are ubiquitous throughout all tropical lowlands of the continent (jaguar, puma, tapir, capybara, peccaries, giant armadillo, and giant anteater). The causes of Pleistocene extinctions are beyond the reach of our research, but in Chapter 8 we speculate on reasons for the persistence of MW.

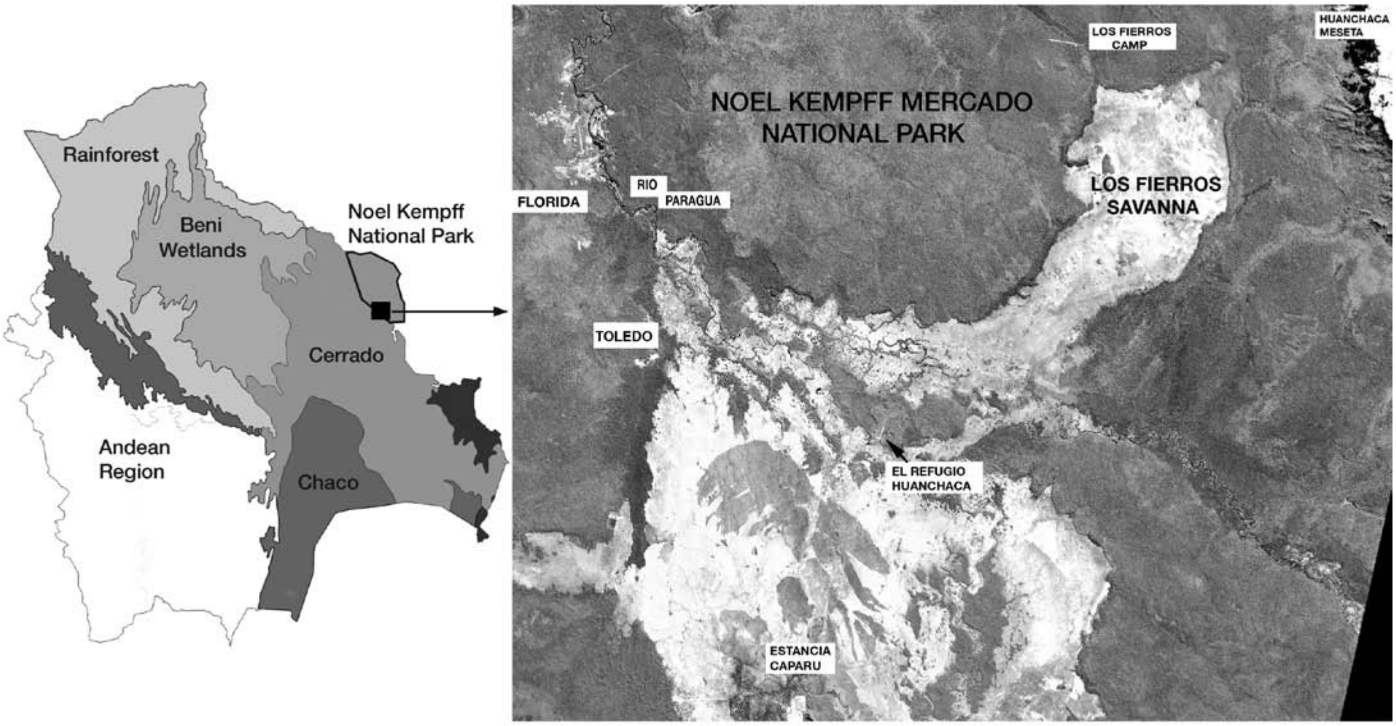

FIGURE 1.2. Location of the study area. The pale areas in the satellite image are grasslands; the darker matrix is forest. The park boundary is along the river that dissects the image diagonally from upper left to lower right. The finger of grassland from the river in the center of the image and up to the right is Los Fierros savanna, where we studied the maned wolf population. The southern half of the savanna within the park is part of the El Refugio Huanchaca (ERH) Biological Station. The sharp-edged, dark areas in grasslands south of the park are fire-scars on cattle estancias. Bolivia map after Navarro and Maldonado (2002).

The Study Area in Noel Kempff Mercado National Park

Parque Nacional Noel Kempff Mercado, Santa Cruz Department, Bolivia, is a 1.523 million ha IUCN World Heritage site. A third of NKP is open savannas, in fragments separated by forests (Figure 1.2). The park was established to protect the massive Huanchaca tableland ("Meseta"), which rises 500 m above the plain of the adjacent lowlands (120 km × 30 km, 900 m maximum elevation). We studied MW in the 21,883 ha Los Fierros savanna near Los Fierros camp (14°33.24′ S; 60°55.40′ W; elevation 220 m). The southern half of the savanna is in El Refugio Huanchaca Biological Station (ERH; Figure 1.2), a privately managed property partly within the park. Noel Kempff Park is on nutrient-poor soils of the Brazilian Shield geological formation and spans a transition zone between tall Amazonian humid forests, semideciduous and deciduous forests, dry upland Cerrado savannas, and seasonally flooded savannas (Killeen and Schulenberg, 1998). Habitat nomenclature has been developed in Brazil for the major Cerrado plant formations, as defined by Gottsberger and Silberbauer-Gottsberger (2006).

Dry Ground Habitat Types

Cerradaõ. Dense woodland with >60% tree cover and canopy >7 m tall and a shaded woody and herbaceous understory. This mainly occurs on forest "islands" in Los Fierros savanna and on the slopes of the Huanchaca Meseta.

Cerrado *sensu stricto*. A low canopy (<7 m) woodland and scrub with >40% canopy cover. This habitat is widespread on the northern part of the Meseta.

Campo Cerrado. Savanna woodland with 10–40% canopy cover over a continuous layer of grasses (Figure 1.3). This is the principal maned wolf habitat type on never-flooded areas of Los Fierros savanna. Its local

FIGURE 1.3. Campo Cerrado, Los Fierros savanna, under a pall of late dry season smoke. This habitat never floods and is the home the endemic rodent *Juscelinomys huanchacae*. The blackened trunks are evidence of the frequent fires in this zone, which is part of the PA rodent trapping plot (Chapter 4) (photograph by L. H. Emmons).

name is "pampa arbolada." The Spanish term "pampa" is equivalent to the Portuguese and Spanish "campo" (field), both terms are used for natural and anthropic savannas.

Campo Sujo. Open grasslands with scattered shrubs and few low trees. This covers many open areas on top of the Meseta, along with **Campo Rupestre**, which is similar, but on a rocky substrate.

Wet Ground Habitat Types

Hummock Campo. Also "Campo de murunduns," an open grassland matrix studded with small humps of high-ground formed around termite mounds topped with trees and woody shrubs. When the grassland is shallowly flooded from about February to April, the hummocks become dry ground islets surrounded by water. From August to late December or early January, there is no standing water in the grassland. This is the major maned wolf habitat of the northern half of Los Fierros savanna and locally called "pampa termitero" or "termite" savanna, a term we use herein (Figures 1.4 and 1.5). Its fringing forests are Cerradaõ on the north and Amazonian humid forests on the east and west.

Pampas de bajíos (Navarro and Maldonado, 2002). Open grasslands more deeply flooded seasonally than termite pampas (above), with water 0.5–1 m deep. These

FIGURE 1.4. Termite savanna (pampa) or Hummock Campo of Los Fierros savanna from the air, showing regular spacing of termite mounds topped by woody vegetation. The Huanchaca Meseta, major feature of Noel Kempff Mercado National Park (NKP), fills the background. Pozo Matt (PM) waterhole is in the clump of tall trees, 2/3 down the image, in a pale streak directly below the point of the wing. This grassland matrix is lightly flooded in the wet season (photograph by L. H. Emmons).

open grasslands include larger islands of tall forest. The Los Fierros savanna slopes downward, with increased depth of flooding, from north to south (Figures 1.6 and 1.7). The southern half is Bajío pampa, and most of its fringing forests and forest islands are likewise flood prone. Along the river, there are some permanently wet open marshes.

The geology, habitats, flora, and fauna of NKP are described in Killeen and Schulenberg (1998) and the mammals in Emmons et al. (2006a, 2006b). All savannas in NKP support maned wolf populations (Rumiz and Sainz, 2002). The Los Fierros study savanna is separated on the southeast by a river, open marshes, and gallery forest from larger, flood-prone Bajío grasslands (Figure 1.6) and Campo Cerrado on cattle estancias, and on the northeast by 9 km of forest from a large pristine Campo Sujo savanna on top of the Huanchaca tableland (Figure 1.2). The adjacent grasslands have maned wolf populations that can interchange with the study groups. One all-season road crosses 10 km of the Los Fierros pampa, and a 25 km dry season-accessible track penetrates its length. To follow MW with VHF telemetry, we made a network of footpaths marked for radio-tracking at GPS-mapped 100 m intervals.

FIGURE 1.5. Maned wolf F3 (with piloerection) in termite savanna or hummock campo, showing structure of grass and shrubs relative to the size of a maned wolf (photograph by L. H. Emmons).

Climate and Seasonality

Rainfall was measured at ERH with a garden gauge (1995 onward) and temperature with a max-min thermometer or digital home weather station (2003 onward). In July–August 2009, hourly climate variables were taken with a Kestrel® weather logger placed under a shade roof in the grassland of Los Fierros savanna. Rainfall and water availability in the NKP savannas are highly variable (Figure 1.8). Annual rainfall averages 1.4 m (range, 2000–2010 1.2 to 1.8 m), with a strong dry season from May to October and a rainy season from November to March (Figure 1.8A). Standing water normally covers parts of the landscape from January or February to May, but in 2009, water remained until July. Ground flooding is temporally displaced about three months after the beginning and end of the rains (Figure 1.8A). By mid-August, there is little to no surface water on the Los Fierros grasslands and most streams and waterholes are dry. The savannas are both fire and flood maintained: without these events, woody plants overgrow and shade out the grasses. Over the years of the study, annual rainfall did not show any overall trend (Figure 1.8B), but dry season rainfall (July–September) showed a gradual and striking decline, from a maximum of 172 mm in 2002 to 20 mm in 2010 (Figure 1.9). There was exceptionally high late wet season rainfall in 2008 and 2009, which caused deeper and later flooding of the savanna, followed immediately by a catastrophic

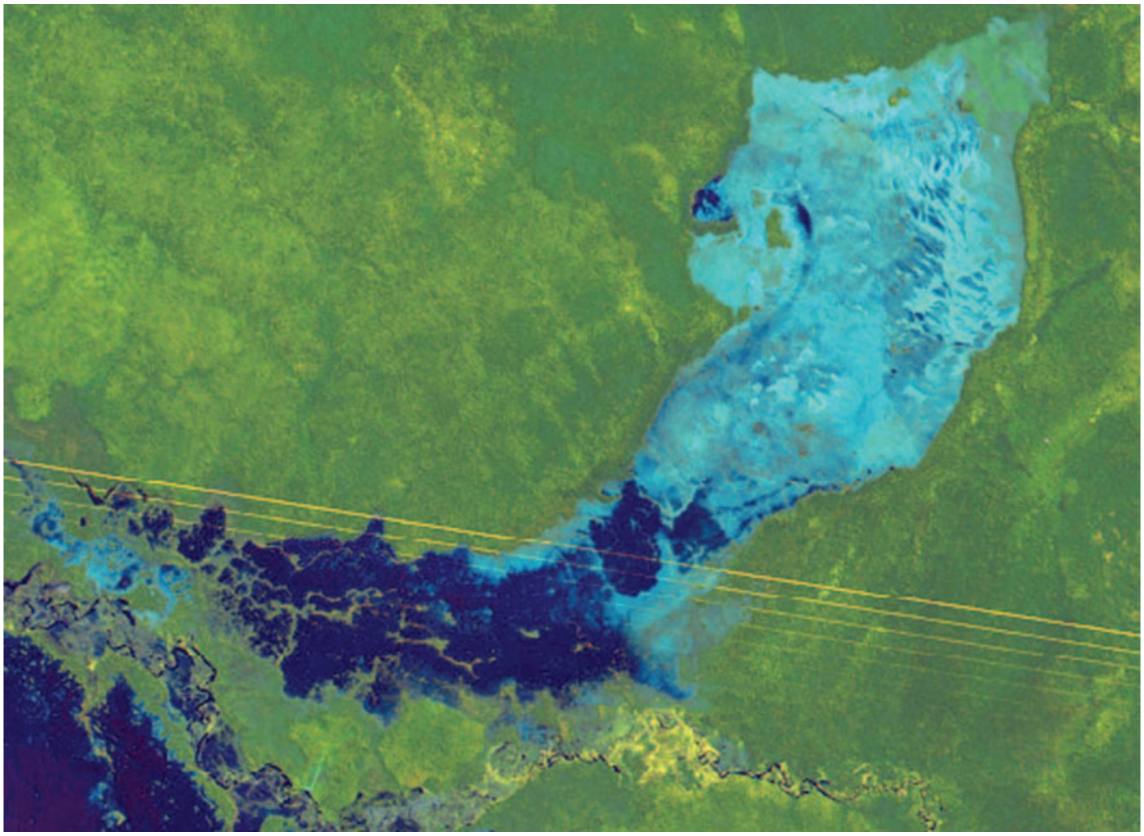

FIGURE 1.6. False color image of flooding in Los Fierros savanna 25 April 2008, during exceptionally high water levels. Darker blue indicates deepest flooding of Bajío savanna; palest blue more open, lightly flooded grasslands; olive tinge, shrubs and trees; intermediate blues, lightly flooded termite savanna; uniform olive, Campo Cerrado; green, closed canopy woodland and forest; yellow, marshland and swamp. Note progressive deepening of flooding from north to south, with drop in land elevation. The Río Paraguá-Tarvo runs along the lower edge.

FIGURE 1.7. Bajío savanna, ERH, at the beginning of February flooding. This savanna has tall-grass marshes in the wet season, with large islands of Campo Sujo, but no water at all in the late dry season. R. Choré and E. Bronson riding in to trap maned wolves (MW) from a tent camp (photograph by L. H. Emmons).

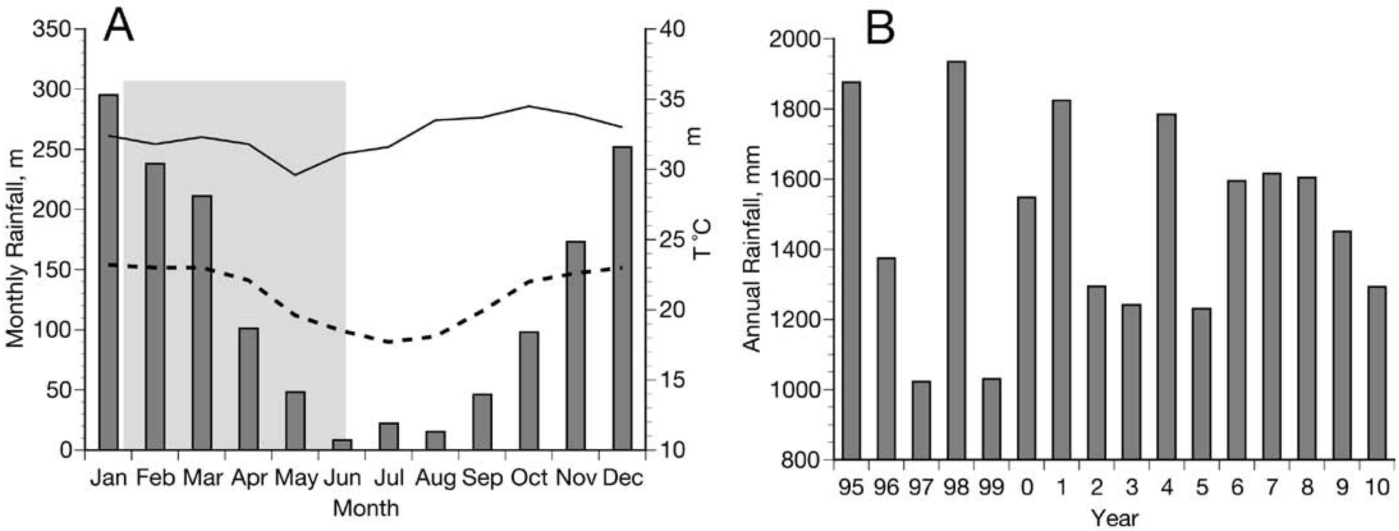

FIGURE 1.8. (A) Mean monthly rainfall (bars) and mean monthly temperature maxima and minima at El Refugio Huanchaca (lines, 2003–2010) and months when there is usually standing water on parts of the area (light shading) and (B) total annual rainfall (1995–2010).

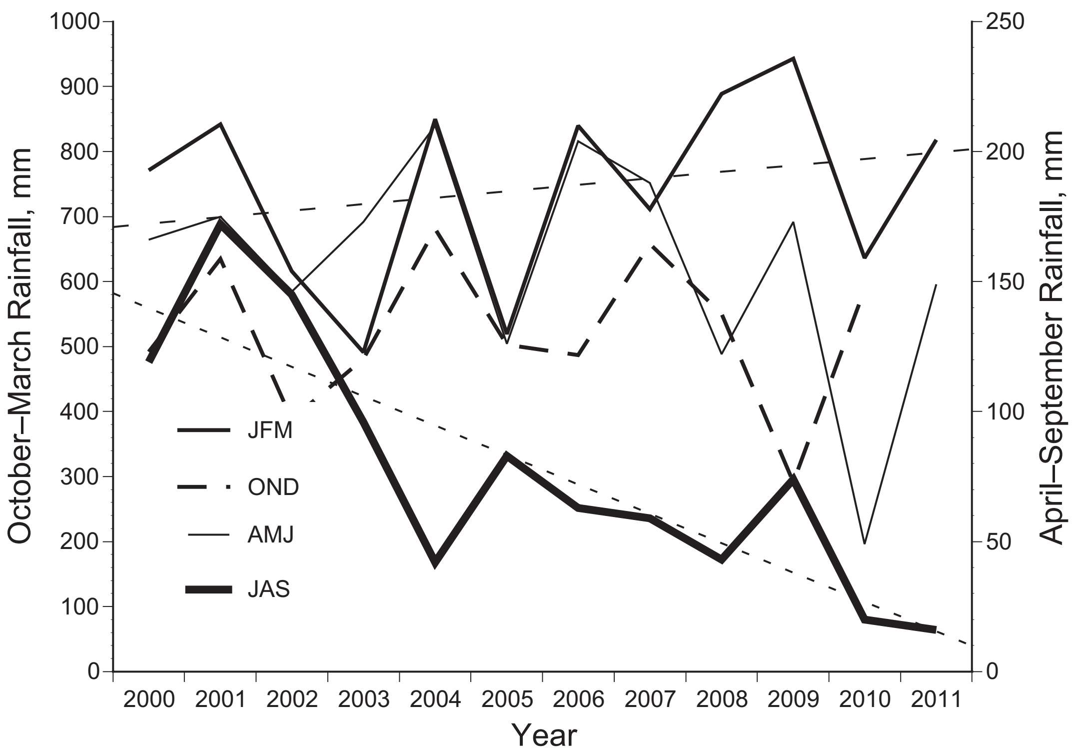

FIGURE 1.9. Rainfall trends by season during the study years, with drier seasons on the right axis. Linear regressions for the wettest (January–March) and driest (July–September) months are shown as dotted lines. Data from records kept at ERH.

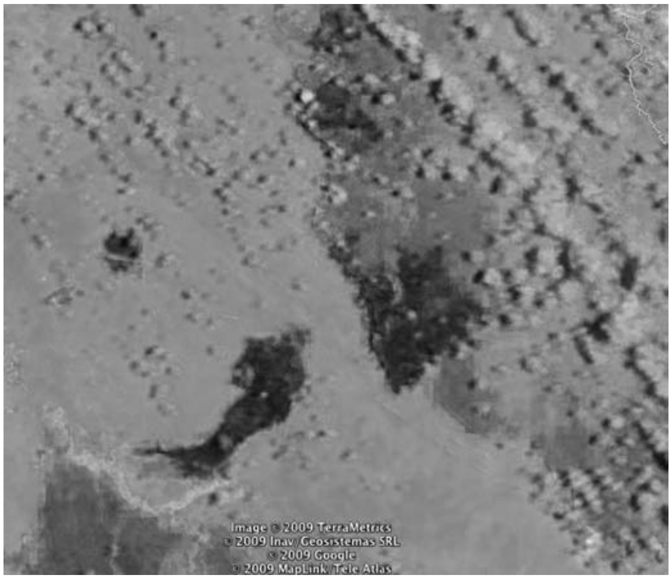

FIGURE 1.10. Fires of 2009. October 12 composite image from NASA Goddard Space Flight Center (GSFC), MODIS Rapid Response and Google Earth®. All darker areas are fire scars, except the isolated round spot on the left, which is a lake, and cloud shadows. The entire Los Fierros savanna appears carbonized (fingerlike black area on left lower quadrant). The adjacent edge of the Huanchaca Meseta (top to bottom diagonal on the right of the image) shows numerous fire scars of different ages, as does the savanna southwest of Los Fierros (darkest areas are the most recent fires, paler scars are from earlier ones; parallel lines of cirrus clouds and their shadows form diagonal structures). Fires in NKP can be monitored daily through NASA/GSFC, MODIS Rapid Response. Following this fire, two resident adult MW were not seen again (pair F3–M8).

drought (Figure 1.9, JFM; Xu et al., 2011). The northern half of the Los Fierros savanna burned in 1999, half of that burned again in 2003, and about a quarter in 2007. Lightning strikes sporadically burned a few hectares between 2003 and September–October 2009, when nearly the entire savanna burned during six weeks (Figure 1.10).

General Methods

Trapping and Radio-Tracking

The following methods apply to all chapters, but those specific to individual chapters are included therein. Field studies took place over several months yearly from 2001 to 2011, and the study is ongoing. We captured MW in wooden drop-door box traps (Dietz, 1984; less successful) or metal and hardware-cloth drop-door cage traps (more effective) baited initially with live chicks, but after 2007 with sardines and dried fatty beef ("charqui"). Lures of maned wolf urine dried on gauze and hung in the back of traps improved success. Three trap-shy individuals were free darted with a DanInject® rifle. Captured MW were immobilized with 100 mg of Telazol® delivered by a Telinject® or DanInject dart. If needed, anesthesia was supplemented by ketamine HCl. A veterinarian performed a physical examination and collected blood, urine, and fecal samples for analysis of pathogen exposure, health metrics, and genetic analysis. Deem and Emmons (2005) detail procedures. Captured MW were measured, weighed, photographed, marked with Rototag® ear tags, and fitted with VHF radio collars (ATS®) or archival GPS collars with scheduled drop-off (2003–10; Lotek®, ATS®, and Telemetry Systems®). We estimated age from tooth wear, compared with that of a known-age individual on the same study area and the wear trajectories of other individuals followed for multiple years. We captured 14 individuals a total of 55 times, but we immobilized captured individuals only once per field session. Procedures of capture and handling were approved by the Institutional Animal Care and Use Committees, National Zoological Park, and Department of Vertebrate Zoology (Smithsonian Institution).

MW were not generally wary, but they were rarely visible in the dense vegetation. Presence of individuals was photo documented with camera traps placed at points of maned wolf activity, especially at dry season water holes. We maintained several of these by digging them out as the water table dropped, and at one (Pozo Matt, PM) we observed visitors from a blind as well as with cameras (Emmons et al., 2005). We color coded radio collars with reflective tape for field and photo recognition (Frontispiece). MW are nearly size monomorphic, with inconspicuous external genitalia, and few unmarked MW can be identified on sight to either individual or sex, or in photos to sex (Frontispiece).

We tracked VHF-collared MW on foot and triangulated locations from GPS fixes or mapped markers on trails and roads. We tried to follow single MW for entire activity periods, with about three, three-point triangulations per hour for samples of three sequential nights, but sometimes MW traveled out of receiver range. Other collared individuals within range were located *ad hoc*. Archival GPS collars (require retrieval to download data) were programmed with several schedules: (1) all days with half-hourly locations (fixes) from 1800 to 0800 hours; hourly fixes at 0900, 1000, 1600, and 1700 hours, and no fixes from 1100 to 1500 hours (2003–2004 only); (2) hourly fixes daily from 1600 to 1000 hours the following date (because we thought MW to be nocturnal), for weekly three-night samples; (3) hourly fixes each hour for three-night (and day, 72 hours) samples (Wednesday–Saturday) of each week (all collars after 2005). Three collar deployments collected usable collar temperature data and "activity" at each fix. Data archived within GPS collars were recovered at recapture or after collar drop-off. The failure rate of GPS collars was high: almost 40% of 22 deployments resulted in truncated data, two of these because the collar housing was pierced by a maned wolf tooth mark, others because batteries failed and/or humidity entered the housings. About 90% of collar release mechanisms also failed to function. These problems caused data loss, so from 2009 we attached supplementary, 20 g ear tag transmitters to each collar to aid recovery when inbuilt VHF transmitters failed. We obtained 35,051 telemetry locations from 10 MW on Los Fierros pampa (Table 1.3).

Analysis of Field Data

Triangulation data from VHF radio-collared MW were hand-plotted onto maps (2001–2004: 1,411 locations), scanned, and rectified on a Landsat image with ArcGis (ESRI) or plotted with LOAS software (2005 onward). Maps were analyzed primarily with ArcView and ArcInfo GIS software (ESRI) and The Home Range Extension for ArcView (Rogers and Carr, 1998), Hawth's Tools (Beyer, 2004), or R-ade (Calenge, 2006). For hand-plotted data,

TABLE 1.3. Individuals captured, estimated ages, and telemetry collar deployments. Animal (M, male; F, female), data collection interval, number of fixes, number of complete nights of activity recorded, and number of weekly three-night samples where relevant. In "all days" data sets, fixes were taken every day at half hourly or hourly intervals. After 2005, GPS collars recorded locations on three sequential nights of each week. In cases with no GPS data, the capture date is given under Data start. A dash (–) indicates not applicable to data set.

Maned wolves	Estimated age, years	Home range zone	Data start	Data end	Total fixes	Total nights	Three-night samples
M2*	>8	N1	20 Oct 01	1 Jan 04	800	34	–
M4*	0.6	N1	23 Oct 02	24 Feb 03	243	8	–
F3*	1.2	N1	26 Sep 02	13 Oct 03	262	12	–
F3	2	N1	13 Oct 03	16 Jan 04	1847	95	All days
F3	3	N	9 Oct 04	1 Jan 05	3403	91	All days
F3	4	N	6 Oct 05	13 Jul 06	2900	121	45
F3	5	N	6 Jan 07	30 Jan 07	130†	24	–
F3	6	N	21 Sep 07	22 Nov 07	607†	36	9
F3	7	N	16 Jul 08	18 Oct 08	1008	41	14
M5	4	N2	4 Oct 04	7 Mar 05	4631	155	All days
M5	5	N	29 Sep 05	16 Dec 06	4606	192	64
M5	5.5	N	6 Feb 07	29 Mar 07	349†	19	6
M5	6	N	4 Oct 07	12 Jul 08	1112†	61	16
M6	>7	S	27 Sep 05	23 Feb 06	1514	–	21
F7	0.6	S	21 Oct 05	Lost	–	–	–
M8*	2	S	25 Oct 05	5 Sep 06	140	6	–
M8	3	S	5 Sep 06	7 Oct 06	428†	20	5
M8	4	S	25 Jul 07	26 Sep 07	635†	36	10
M8	5	N	9 Jul 08	18 Oct 08	1080	44	15
M8	5	N1	22 Oct 08	22 May 09	2249	–	31
F9*	1.5	S	18 Jul 07	7 Jul 08	–	–	–
F9	2.5	S	7 Jul 08	28 Aug 08	536†	23	8
F9	2.8	S	12 Oct 08	16 Apr 09	2131	69	25
M10*	0.8	S	16 Sep 06	Collar lost	–	–	–
F11	6	S	4 Feb 07	26 Mar 08	3784	201	59
F12	0.5	N1	16 Oct 07	NA	No collar	–	–
F13	3	All	16 Sep 10	14 Sep 11	2787†	88	22

*VHF transmitter.

†GPS collar failures.

we mapped only one location point (fix) if an animal was stationary, and we used all available points to calculate home range size. Activity periods (nights) are calculated from the first VHF or GPS fix after noon on a given date to the last fix before noon on the following date. Mean GPS PDOP (positional dilution of precision, a measure of probable fix accuracy) was 4.3 ± 1.2 (median 3.6, mode 2.7, range 0.5–25) for 4,612 fixes of a Lotek collar on M5 and 2.9 ± 1.2 (median 2.8, mode 2.5, range 0–6) for 3,402 fixes of an ATS collar on F3; other data sets were similar. To estimate the distance traveled by MW between successive GPS collar fixes, we considered all distances of <50 m from the previous fix to represent inactivity. For analysis, all such distances were converted to 0 m, so as to exclude random GPS errors around a stationary maned wolf from inflating travel. A collar stationary on the ground after a maned wolf death collected 869 fixes. Of these, 97% were ≤50 m from the geometric centroid of the cloud of fixes, despite the GPS antenna lying sidewise on the ground surface and partially covered with dirt (mean PDOP 5.0), which are adverse conditions for GPS location. For analysis of travel distances and rates, as well as rest and activity cycles, we use only GPS collar data. There was complete, hourly GPS data of weekly three-night samples of 9–14 months duration for three females and two males (F3, F9, F11, M5, M8; Table 1.3). These large data sets are used as exemplars for many analyses of temporal activities. To compare seasonal behaviors, the year is divided into quarters: January–March (JFM, ground flooded and much rainfall); April–June (AMJ, much surface water but little rainfall); July–September (JAS, almost no rain, surface water scarce to absent); and October–December (OND, some rain and ephemeral surface pools, no flooding).