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The Maned Wolves of Noel Kempff Mercado National Park

Edited by
Louise H. Emmons

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ABSTRACT

Emmons, Louise H., editor. The Maned Wolves of Noel Kempff Mercado National Park. *Smithsonian Contributions to Zoology*, number 639, xii + 135 pages, 60 figures, 37 tables, 2012.—We studied the behavioral ecology of maned wolves (Canidae: *Chrysocyon brachyurus*) for 10 years in Cerrado habitat of Noel Kempff National Park, Bolivia. Most data were collected by GPS-collar technology, which yielded over 37,000 locations in 27 collar deployments on 10 individuals. The eight chapters introduce the study area and methods (1) and describe daily and seasonal activity (2); movements and ranges (3); diet and energetics (4); social interactions and reproduction (5); disease exposure, morbidity and mortality (6); maned wolf conservation (7); and finally, we synthesize the results in an overview of maned wolf behavioral ecology, with hypotheses about the unique form and function of this atypical canid (8). Activity was temperature related and sharply nocturnal in the dry season but partly diurnal in the rainy season. Adult home ranges were 40–123 km^2, with strong seasonal variations in land use. Maned wolves averaged 14 km/night travel in dry months and 7 km/night during wet months. Breeding pairs shared territories with contiguous borders, which did not overlap with neighboring pairs. Young females twice stayed until adulthood on natal territories, as presumed helpers, and acquired the territory upon disappearance/death of the adult females. Females were the holders of territories into which males moved to form pairs. Young males all emigrated. By 8 years old, maned wolves showed extreme tooth wear, and dental disease was a major cause of morbidity. Habitat loss is the chief conservation issue for the species, but drought-related resource loss appears to be reducing the study area population.

RESUMEN

Emmons, Louise H., editor. Los Lobos de Crin de Parque Nacional Noel Kempff Mercado. *Smithsonian Contributions to Zoology*, número 639, xii + 135 páginas, 60 figuras, 37 tablas, 2012.—Estudiamos la ecología de los lobos de crin (Canidae: *Chrysocyon*) durante 10 años en el Parque Nacional Noel Kempff, Bolivia. La mayoría de los datos fueron colectados por la tecnología GPS-de-collar, que generó más de 37.000 ubicaciones en 10 individuos. Los ocho capítulos dan a conocer el área de estudio y métodos (1), y describen la actividad diaria y estacional (2), movimientos y rangos (3), dieta y energética (4), interacciones sociales y reproducción (5), exposición a enfermedades, morbilidad y mortalidad (6), conservación del lobo de crin (7) y, finalmente, sintetizamos los resultados con información general de la ecología y comportamiento del lobo de crin, con hipótesis acerca de la singular forma y función de este atípico cánido. La actividad estuvo relacionada con la temperatura y fue claramente nocturna en la estación seca, aunque en parte diurna en la temporada de lluvias. El área del territorio de adultos fue de 40–123 km^2, con marcadas variaciones estacionales en el uso del hábitat. El desplazamiento promedio fue de 14 km/noche en los meses secos y 7 km durante los meses húmedos. Las parejas reproductoras compartieron territorios con límites contiguos, los cuales no se superpusieron con el de las parejas vecinas. Una hembra joven permaneció en dos ocasiones hasta la edad adulta en su territorio natal, se supone como "helper" y adquirió el territorio, a la desaparición/muerte de las hembras adultas. Las hembras fueron las dueñas de los territorios, en los que los machos se trasladaron para formar parejas. Los machos jóvenes emigraron. A los 8 años de edad, los lobos de crin mostraron desgastes extremos de los dientes, y las enfermedades dentales fueron una importante causa de morbilidad. La pérdida de hábitat es la amenaza principal para la conservación de la especie, pero la sequía relacionada con la pérdida de recursos parece estar reduciendo las poblaciones del área de estudio.

Cover images from L to R: Maned wolf male M3 sitting in long grass; view during the wet season of the great Huanchaca tableland, a major feature of Noel Kempff Mercado National Park; and maned wolf youngster F9 with mane ruffled. All photos: L. H. Emmons.

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Contents

Figures

Tables

Preface

Our investigations into the lives of maned wolves ("borochi" in Bolivia) began as infatuation at first sight, which engendered an unanticipated side branch to a research project on mammal communities in Noel Kempff Mercado National Park. This branch grew until it became a main trunk of the project. We began with an intentionally arduous method. We used hand-held antennas and receivers to follow maned wolves that carried old-fashioned VHF radio collars. We followed the wolves on foot (or tried to) from when they stirred from their daytime rest in the late afternoon to when they settled back to sleep through the day. We did not see them, nor try to, for fear of altering their behavior. As we triangulated the signals through the night, we tracked along beside them on a maze of narrow paths in the grass. We mirrored their movements, sensed their pace, rested during their rests, smelled their passage, and heard their deep barks and the faint answering calls of their companions. When later in the study we turned to GPS telemetry, we often missed the moonlit grasslands, cold starlit nights, and dawns emerging through the ground fog, but mostly we missed feeling the presence of the wolves and the exhilaration when suddenly they materialized from the tall grass beside us. We continued to follow so few animals year after year, always under trying and occasionally nearly impossible logistical difficulties, because we acquired a nonscientific connection to the animals and passionately wanted to know their individual stories.

Louise Emmons, August 2010

Acknowledgments

This project was a collaboration with the Museo de Historia Natural Noel Kempff Mercado (MNK), Santa Cruz, Bolivia. We are most grateful to the Dirección General de Biodiversidad (DGB) and the Servicio Nacional de Áreas Protegidas (SERNAP) of Bolivia for granting us permits to conduct our research in Noel Kempff Mercado National Park (NKP) and for otherwise facilitating our studies. The directors of MNK, M. Suárez and P. Herrera, encouraged and aided our collaboration. Kathia R. Rivero provided essential help with logistics and obtaining permits and was throughout an invaluable friend, as was Damian Rúmiz of Wildlife Conservation Society. Able field assistance was given by S. Angulo, A. Céspedes, J. M. Castro, S. Copetto, S. Cabrera, V. Chávez, P. Cuellar S., F. Del Aguila, F. Huaquipa, R. Peña F., N. Rocha, and L. Sainz; some field associates are coauthors. Essential logistical help and good company in the field were volunteered by the late B. Phillips, I. Phillips, R. Choré, and M. Choré of El Refugio Huanchaca. Fundación Amigos de la Naturaleza supported and encouraged our work in NKP. Gelguer Añez and the park guards of NKP and people of the community of Florida helped us in many ways. Steffen Reichle, Yuvinka Gareca, Alan Hesse, and Erika Cuellar gave us bed and board and logistical support in Santa Cruz. Melissa Rodden generously provided unpublished data and information from the Smithsonian Conservation Biology Institute (formerly, the Conservation Research Center) maned wolf breeding program and from her own encyclopedic knowledge. Matias Tobler kindly wrote scripts for R-Ade and gave us advice on geographic information system (GIS) analysis. For their generous financial support we thank The Douroucouli Foundation, The National Geographic Society, The Wildlife Conservation Society, The Amazon Conservation Association and W. Alton Jones Foundation, The Friends of the National Zoo, The Conservation Endowment Fund of the Association of Zoos and Aquariums, SeaWorld Busch Gardens Conservation Fund, the Maned Wolf Species Survival Plan, The Department of Animal Health of the National Zoological Park (Smithsonian), The Maryland Zoo, and Alan Weedon. Louise Emmons is indebted to the Smithsonian Institution, Division of Mammals, for their many years of support: they provided both the spatial home from which all research was launched and the intangible benefits of collegiality. Two anonymous reviewers made helpful comments that improved the manuscript. Acknowledgments specific to individual chapters are given therein.

FRONTISPIECE. Maned wolf male M8 on release with a new collar. Photograph by Louise Emmons.

1

Introduction: Study Site and Methods

Louise H. Emmons

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.

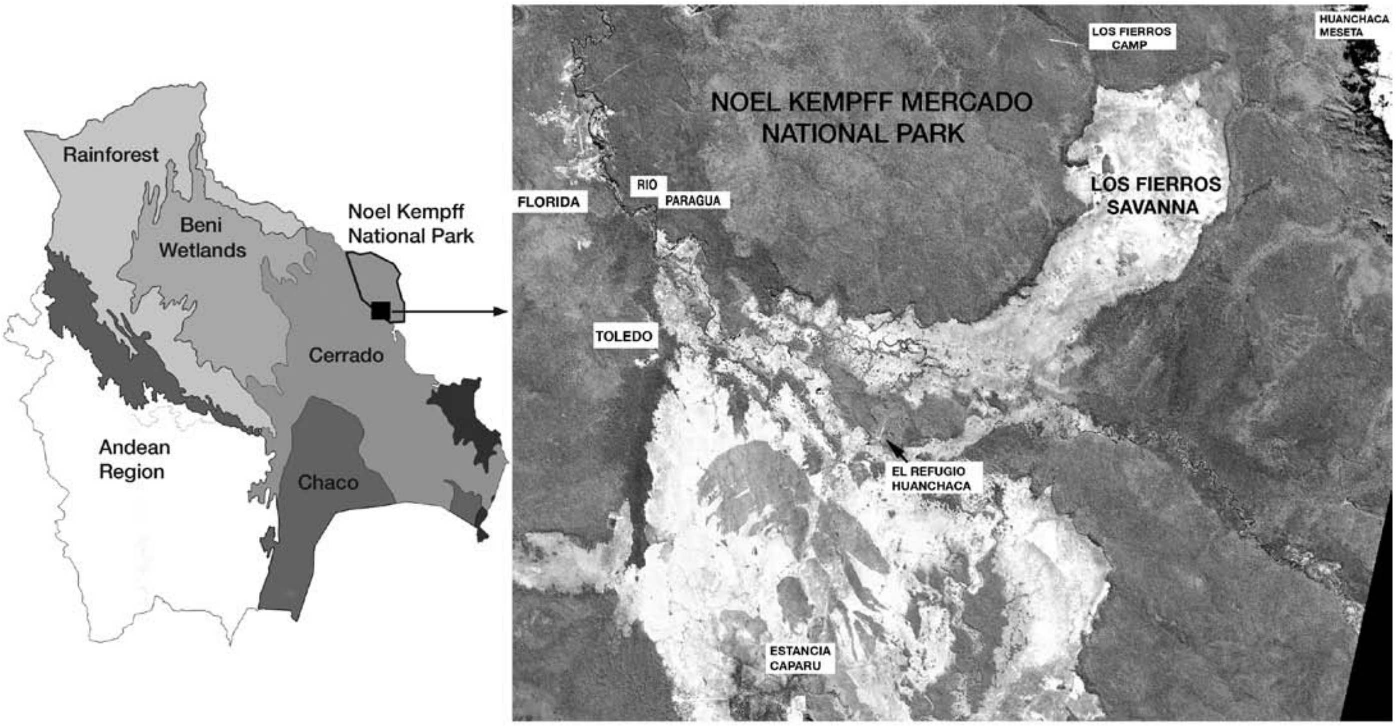

FIGURE 1.2. Location of the study area. The pale areas in the satellite image are grasslands; the darker matrix is forest. The park boundary is along the river that dissects the image diagonally from upper left to lower right. The finger of grassland from the river in the center of the image and up to 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 Cerrrado 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

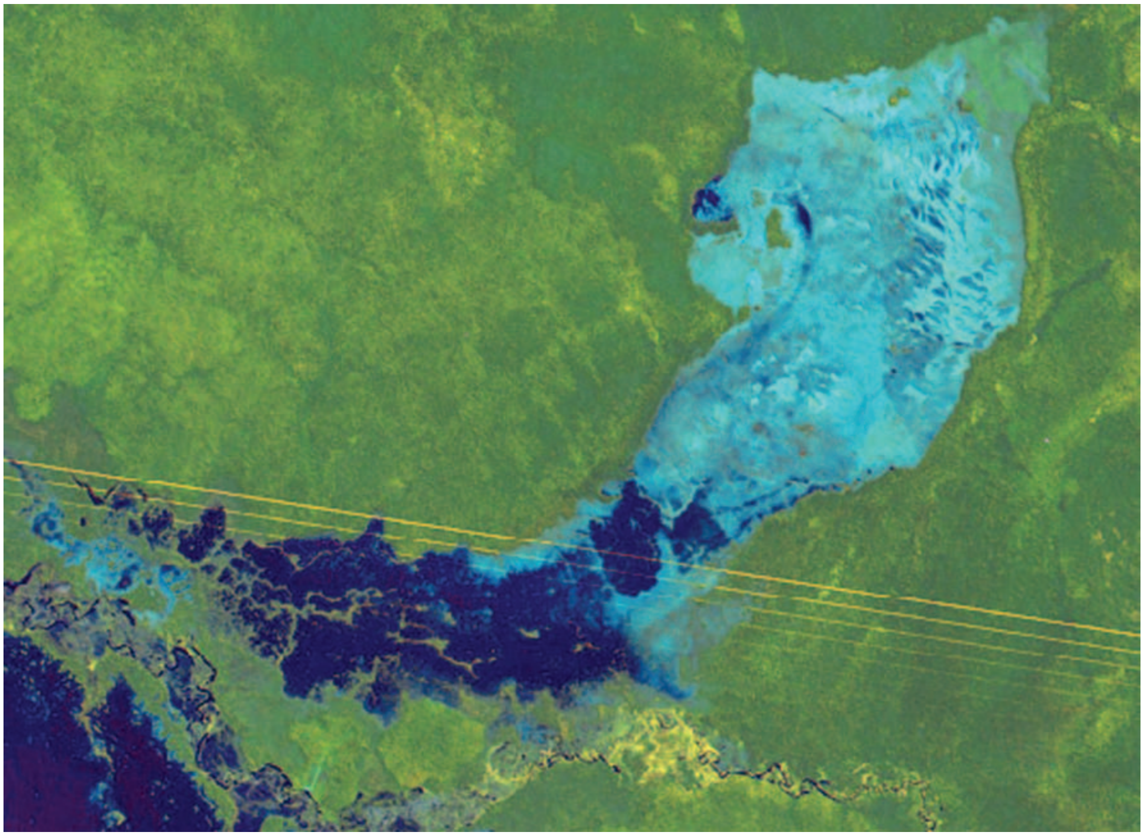

FIGURE 1.6. False color image of flooding in Los Fierros savanna 25 April 2008, during exceptionally high water levels. Darker blue indicates deepest flooding of Bajío savanna; palest blue more open, lightly flooded grasslands; olive tinge, shrubs and trees; intermediate blues, lightly flooded termite 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).

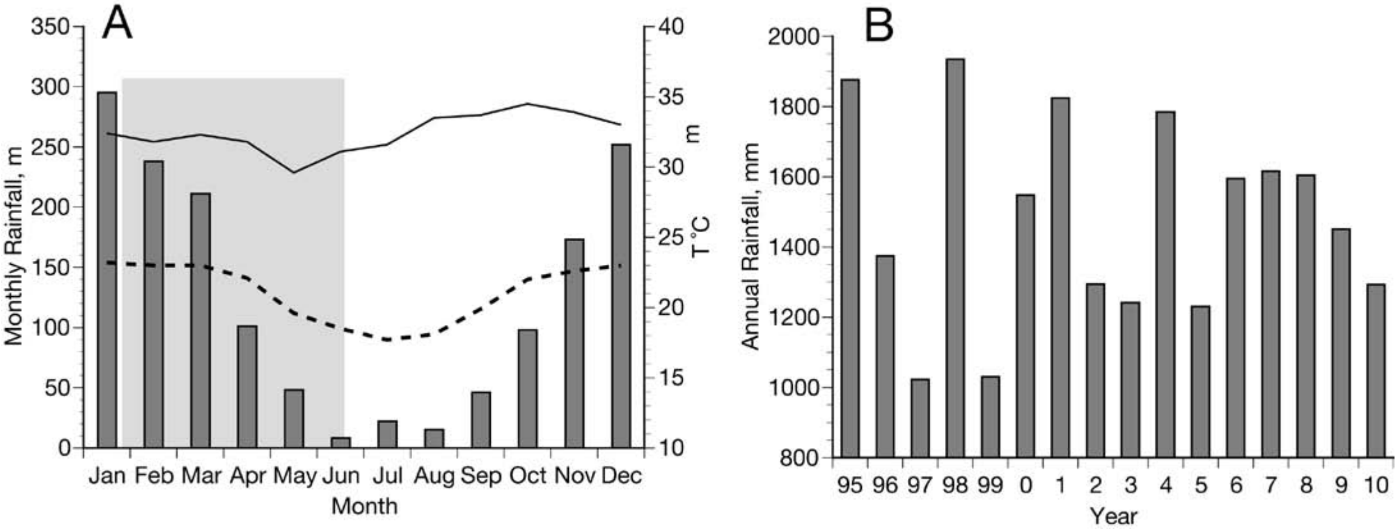

FIGURE 1.8. (A) Mean monthly rainfall (bars) and mean monthly temperature maxima and minima at El Refugio Huanchaca (lines, 2003–2010) and months when there is usually standing water on parts of the area (light shading) and (B) total annual rainfall (1995–2010).

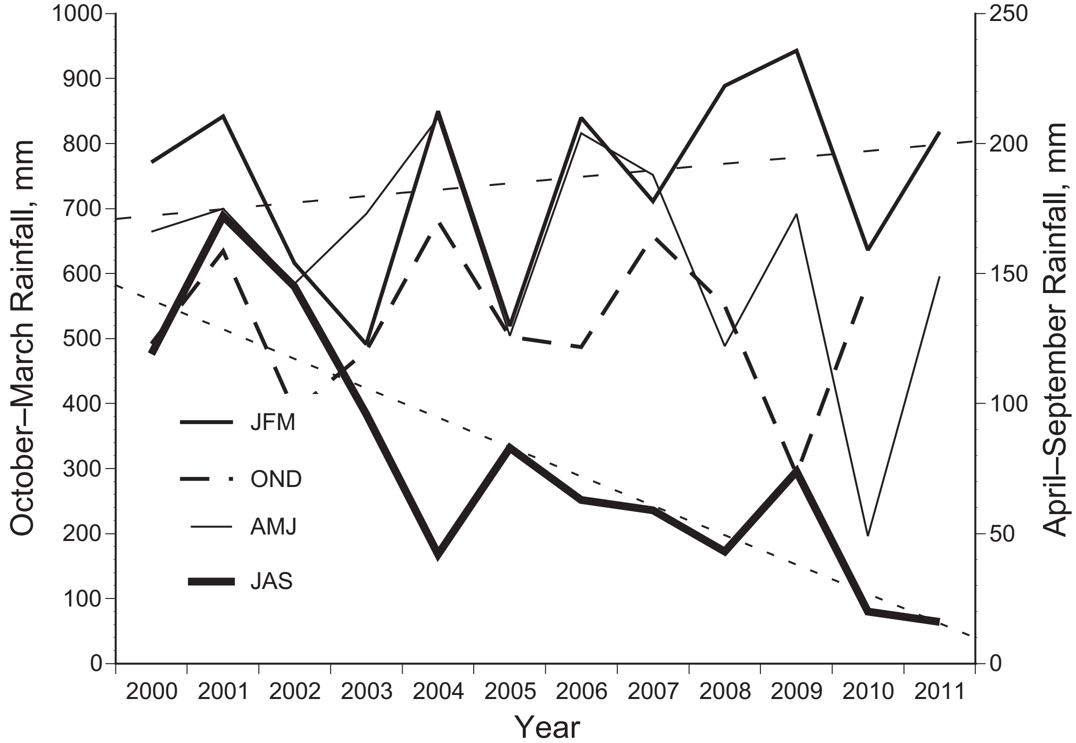

FIGURE 1.9. Rainfall trends by season during the study years, with drier seasons on the right axis. Linear regressions for the wettest (January–March) and driest (July–September) months are shown as dotted lines. Data from records kept at ERH.

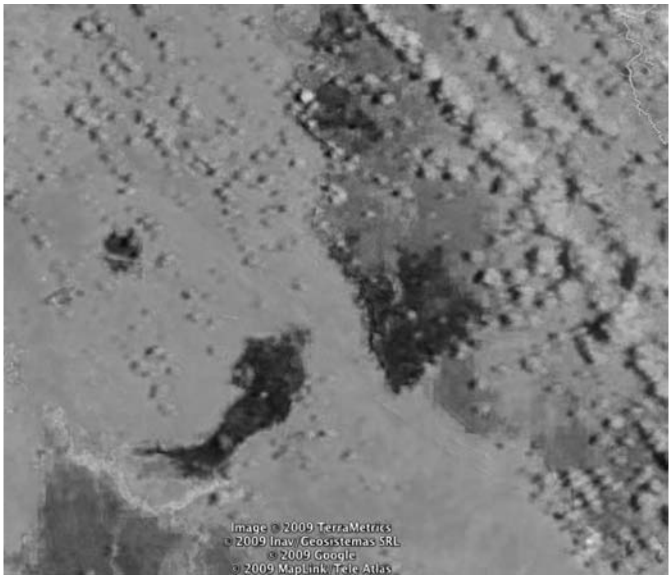

FIGURE 1.10. Fires of 2009. October 12 composite image from NASA Goddard Space Flight Center (GSFC), MODIS Rapid Response and Google Earth®. All darker areas are fire scars, except the isolated round spot on the left, which is a lake, and cloud shadows. The entire Los Fierros savanna appears carbonized (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).

2

Activity Patterns

Louise H. Emmons, Verónica Chávez, Luis Fernando Del Aguila, and Sixto Angulo

ABSTRACT. We studied the activity patterns of maned wolves (MW), *Chrysocyon brachyurus,* by VHF and GPS telemetry in Noel Kempff Mercado National Park (NKP), Bolivia, in upland and seasonally flooded savannas. Eight of 13 individuals captured on three home ranges were followed for up to six years. MW were sharply nocturnal in the dry season, but in some months of the wet season they were cathemeral. They traveled for 10 to 15 hours of each day. Total hours of activity and travel distances were longer in dry season than in wet season months. Temperature sensors on collars showed that MW became inactive as the collar temperature rose above 27°–28°C and travel rate decreased somewhat at below 21°C. The circadian activity pattern in months of drought and heat may be driven by exigencies of water balance and thermoregulation. During daytime inactivity, MW rested within hollows under tall, dense clumps of bunchgrasses. All individuals apart from females with newborns changed rest sites daily. Daytime beds were distributed over the entire home range, but there were favored zones where tall bunchgrasses were plentiful.

INTRODUCTION

In this chapter we explore the daily and seasonal activity patterns of maned wolves (MW) and discuss the environmental factors that might influence these behaviors. Activity patterns may be humdrum descriptors in behavioral ecology, but they underlie much of an organism's fundamental energetics. The time needed to acquire nutrients, with its associated energy expenditure, can determine how large an area can be traveled in daily or monthly ranging and whether females can sustain pregnancy and lactation in particular months or years. The hourly activity pattern can determine which prey species a predator is most likely to encounter. Constraints on activity may limit litter and home range sizes. Similarly, an excessive search time for particular food items could preclude their use and determine diet options.

GPS telemetry has brought an incremental leap in the depth and accuracy of movement data recordable from large species in open habitats. By

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custom-programming GPS collars to take long series of consecutive locations (fixes) at regular intervals, the movements of individuals can be plotted on landscape spatial scales and on temporal scales from minutes to years. With synchronous samples of hundreds of fixes, the behavior of different individuals can be directly compared. There is no observer bias from differences between human trackers, reflection from objects, or access to remote terrain, nor any need to use models to extrapolate ranges from small samples. We owe the data presented below to GPS technology developed in the last decade.

MATERIALS AND METHODS

Methods of capture and telemetry are detailed in Chapter 1, with descriptions of the study area, habitat, and climate. We tracked the activity of MW in Los Fierros savanna with archival GPS telemetry collars. We initially programmed collars to acquire fixes each 30 min, which limited the battery life to from three to five months. We later scheduled collars to acquire hourly fixes for three nights of each week, which yielded data sets of from 10 to 14 months. For a male (M5) and two females (F3, F11), we acquired one or more data sets for all 12 calendar months, for another male (M8) for 11 months, and for a female (F9) for 9 months. We use these long data series to examine temporal changes in activity. Three collar deployments (ATS®) returned good temperature data, recorded hourly at the time of each GPS fix. The temperature sensor was ventral to the neck and away from the body, so that it was shaded from sun and insulated from body heat by thick neck hair. We have no simultaneous hourly ambient temperature data from the study area for months when collars recorded temperature, but in July and August 2009, we took hourly savanna temperatures and other variables with a Kestrel® weather logger.

Because stationary GPS receivers record small spurious differences in location that are generated by instrument errors (registering as nonexistent "movement"), all distances of <50 m between successive fixes were treated as representing stationary, "inactive" MW and were converted to 0 m for analysis. Similarly, all interfix intervals were classed as 0 ("inactive" <50 m) or 1 ("active" ≥50 m), so as to calculate hours of activity apart from travel distance. Because the average travel rate for MW in our study was 600 to 1000 m/h, converting distances of <50 m/h to 0 has little effect on estimated daily total movement distances.

Hourly GPS telemetry fix periods are too short (55 s average) to adequately record brief events, such as drinking. Water is scarce in the study area in the late dry season, and we maintained several water holes by digging them down to the water table. To monitor the presence of MW and other taxa, we set 24 hour digital camera traps to record visits to water holes (Emmons et al., 2005), and watched behaviors from a blind. If a maned wolf was captured in several images within the same hour, only the first image is considered as a visit or event.

RESULTS

CIRCADIAN ACTIVITY

MW were largely nocturnal/crepuscular in the dry season, when they became inactive at their daytime resting sites (for brevity, "beds") by 0800–1000 hours, and resumed activity at 1600–1800 hours (Figure 2.1A). In the wet season, activity in some months showed no clear nocturnal-diurnal pattern (Figure 2.1B) except perhaps a trend for crepuscular activity. Some individuals were more likely to be active at midday in January than at 1800–2100 hours, the most active dry season hours (Figure 2.1B). The general pattern of increased diurnal activity and reduced nocturnal activity from January to March was recorded in all individuals sampled during those months. However, the degree of diurnality, and the month where diurnality was maximal, varied between years and individuals. Averaging all data sets thus dampens the truly striking behavioral differences between the most divergent months within single data sets for one individual (Figure 2.1B).

CIRCADIAN ACTIVITY AND TEMPERATURE

Three MW had collar temperature sensors operational for three to ten months. In all of the data, maned wolf activity dropped abruptly from about 90% at 27°C, to about 20% at 29°C and to nearly zero at above 30°C (Figure 2.2A). Average travel rate decreased steadily from about 600 m/h at 24°C, to about 100 m/h at 29°C (Figure 2.2A). Whereas MW were active during 100% of fixes when it was below 23°C, travel distance seemed to decline at coolest temperatures, especially below 20°C (Figure 2.2A). The circadian curve for hourly travel distance is the inverse of the curve for collar temperature (Figure 2.2B).

Hourly instrument readings within the grassland in July and August 2009 (Figure 2.3A) show daily curves with an abrupt temperature increase from the T_{min} at dawn to T_{max} at 1200–1400 hours, with a slower PM decline from T_{max} when the ground is warm. These are cool winter

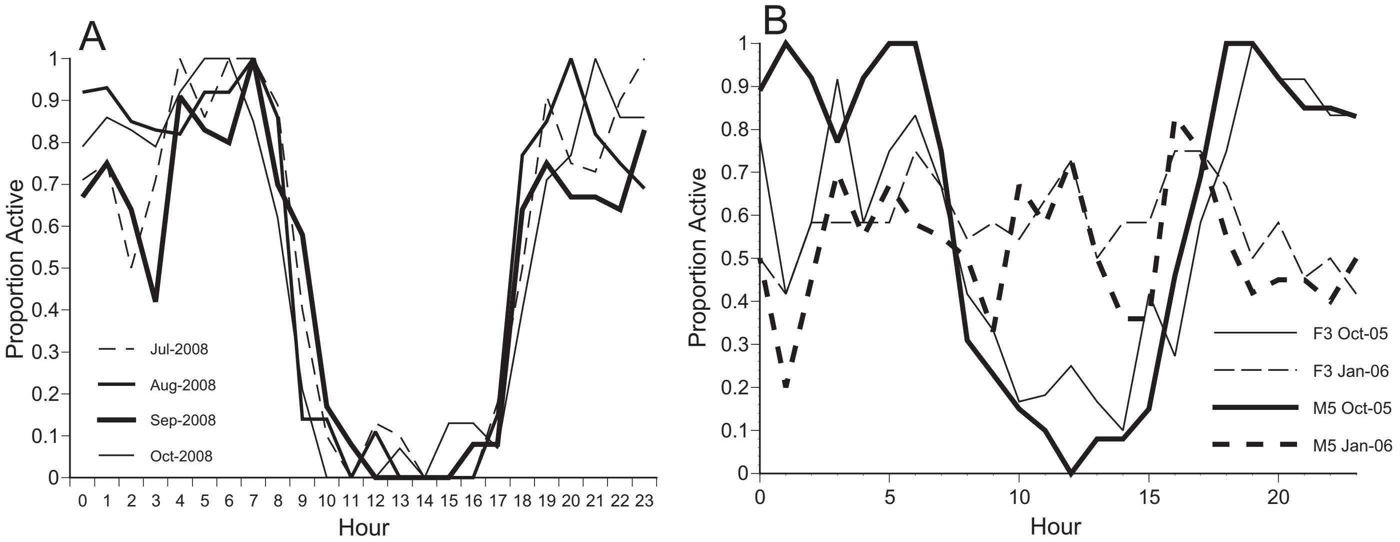

FIGURE 2.1. Average proportion of "active" intervals between hourly fixes (movement >50 m, see Materials and Methods), based on hourly GPS fixes recorded during three days of each week, with all fixes classed as either active (1) or inactive (0). (A) Monthly dry season averages for male M8, July–October 2008, from 1,080 fixes. (B) October 2005 (dry season, solid lines) and January 2006 (wet season broken lines) average hourly activity of female F3 (thin lines) and male M5 (thick lines), a pair on the same area (*N* = 269 to 304 fixes per month per maned wolf).

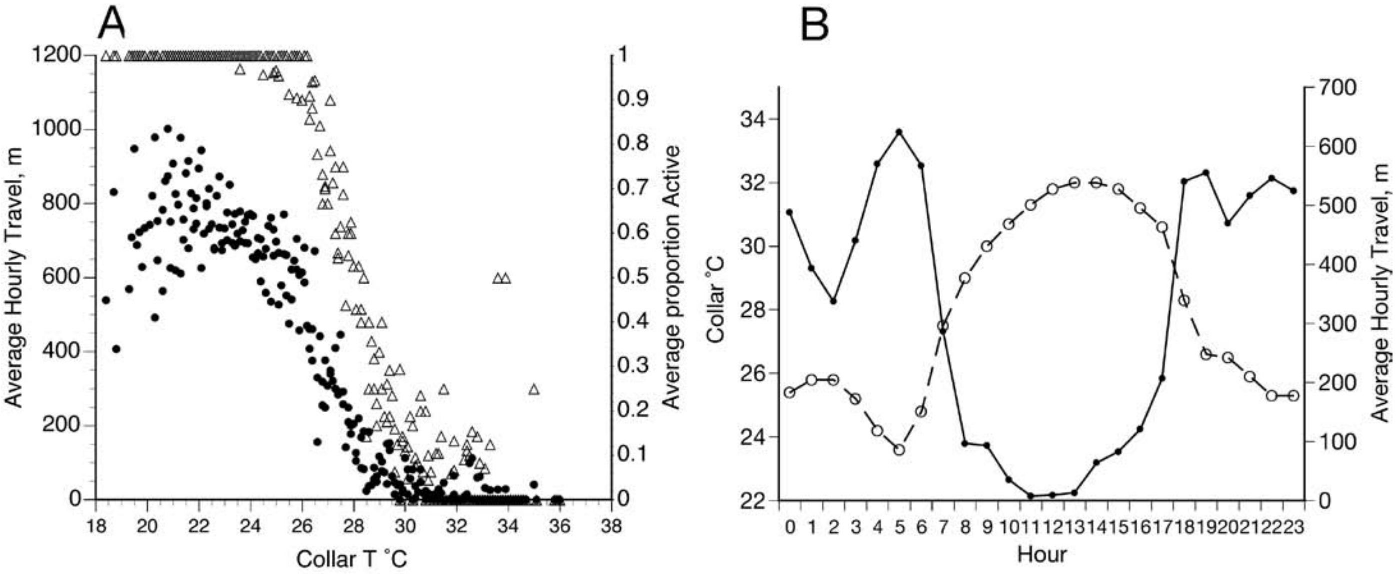

FIGURE 2.2. Activity and collar temperature for F3 October 2004–January 2005; T (°C) measured at each GPS fix by collar sensor (distance traveled is for the hour preceding the T reading; *N* = 1,847). (A) Raw data sets for distance traveled from the previous fix and temperature at that fix time (solid symbols) and proportion of fixes active at given temperatures (open triangles). (B) Average hourly travel from the same 91 day data set (solid line and symbols) and average hourly collar temperature (broken line and open symbols); 0800 to 1700 hours averaged from 84–95 fixes per hourly interval, other hours from 173–180 half-hourly fixes per interval.

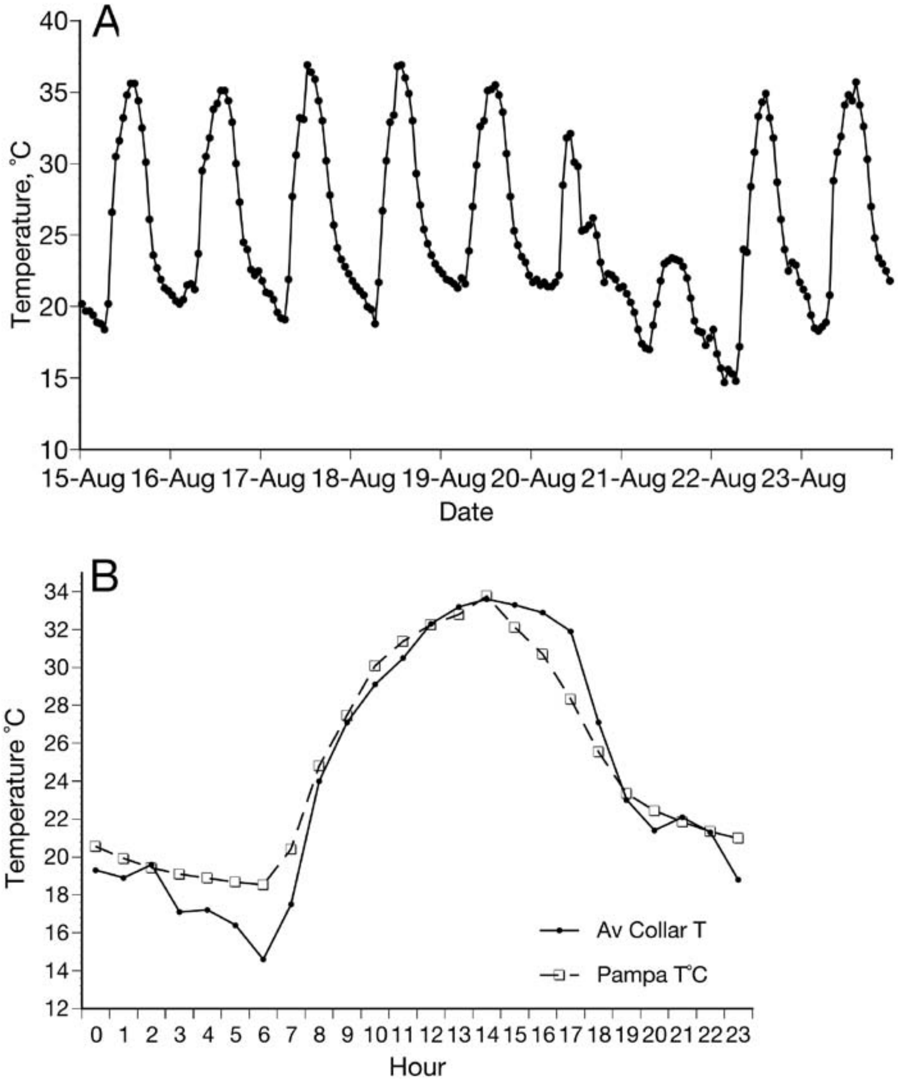

FIGURE 2.3. (A) Hourly ambient temperature 15–27 August 2009, with passage of a cold front 21–22 August (Kestrel® weather logger in open Los Fierros savanna) and (B) average hourly instrument temperature reading in savanna August 2009 during 13.5 days (N = 322 readings) (dashed line); and mean hourly collar temperature for M8 August 2007 (N = 340 fixes) (solid line). August 2007 was exceptionally cold, with mean minimum temperature of 16.2°C, compared to the 6 year mean of 18.1 for August. Collar temperatures for that month include a minimum of 10°C and maximum of 36°C. There were several strong cold fronts.

months, with frequent, overcast, cold fronts (Figures 1.8, 2.3A). We have no maned wolf collar temperatures for the same 2009 months, but a set for M8 during August 2007 (Figure 2.3B), shows a close coincidence between the diel patterns of ambient and collar temperatures. This suggests that at least in this cool month, M8 did not greatly modify his temperature exposure, compared to an instrument in the shade. The morning grass is soaked with dew in winter months; perhaps the sharp drop in collar temperature before dawn is due to evaporative cooling on a wet collar during rapid predawn travel (Figure 2.2B). The shaded weather instrument does not collect dew. However, August 2007 (mean T_{max} = 32.0°C, T_{min} = 16.2°C) was colder than August 2009 (mean T_{max} = 33.6°C, T_{min} = 20.2°C), so the predawn collar temperature drop may reflect cooler nights.

Daily temperature excursions did not seem to influence the total distance a maned wolf traveled on a given night. For a continuous 90-day data set (F3 04–05, 3,400 fixes), there is no significant correlation between the total distance traveled on a given date and the ambient T_{max} for that date as measured nearby at El Refugio Huanchaca (Spearman rank correlation, $r = -0.098$, p level 0.36; T_{max} range 22°–37°C) nor for the T_{min} ($r = 0.032$, p level 0.76; T_{min} range 15°–25°C). In contrast, for the same data set, hourly travel distance was strongly correlated with temperature for that hour as registered in the GPS collar (Spearman rank correlation $r = -0.92$, p level 0.0000). In other words, on hot days, MW traveled just as far during the cooler night hours as they did on cool days, but they hardly moved during the hottest hours.

SEASONAL ACTIVITY

Activity as categorized nominally, from whether an animal was active or inactive in a given hourly interval, gives the clearest index of presence or absence of movement, hence the circadian pattern of rest (Figure 2.4A). The ordinal measurement of distance moved between hourly fixes shows a similar pattern, but the rate of travel varies with the hour (Figure 2.4B), so the patterns are not identical. In the wettest season (January–March), MW traveled more in daylight; they were more often active at midday and would become inactive later in the morning and begin activity earlier in the afternoon (Figure 2.4). Although there was variation both between individuals in the same year and between the same individual in different years (Figure 2.5), all individuals showed the same general pattern of shortest daily movements in February–May, and longest daily movements in August–October (Figure 2.5B).

For the seasonal daily travel averages of the three longest data sets (F3, Oct 05–Jun 06; M5, Oct 05–Dec 06; F11, Feb 07–Feb 08), dry season (July–September, October–December) daily travel distances were significantly different from wet season travel (January–March, April–June) in all pairwise cases (Kolmogorov-Smirnov test, $P < 0.02$), whereas within-season trimesters were not significantly different.

RESTING BEHAVIOR

To explore resting behavior, we use data sets from the first GPS collars, which were programmed to acquire fixes at half-hourly intervals during the 15 hours of greatest daily activity. Later data sets record rests of no shorter than one hour, so are more likely to underestimate the true duration of daily resting. The average time F3 spent in daytime rest was 9.3 hours, but she usually rested for

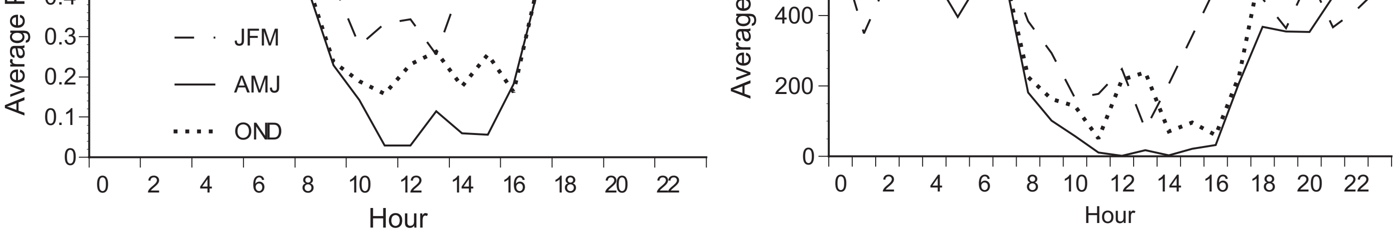

FIGURE 2.4. Hourly activity by season. (A) The average proportion of fixes for a given hour during which F3 was active (movement >50 m between fixes, nominal data active/inactive) and (B) the average distance traveled between hourly fixes from the same data set. On the basis of three-night weekly samples averaged seasonally, data continuous from October 2005 to June 2006. Dotted line, October–December (drier months); broken line, January–March (wettest months); solid line, April–June (transition months).

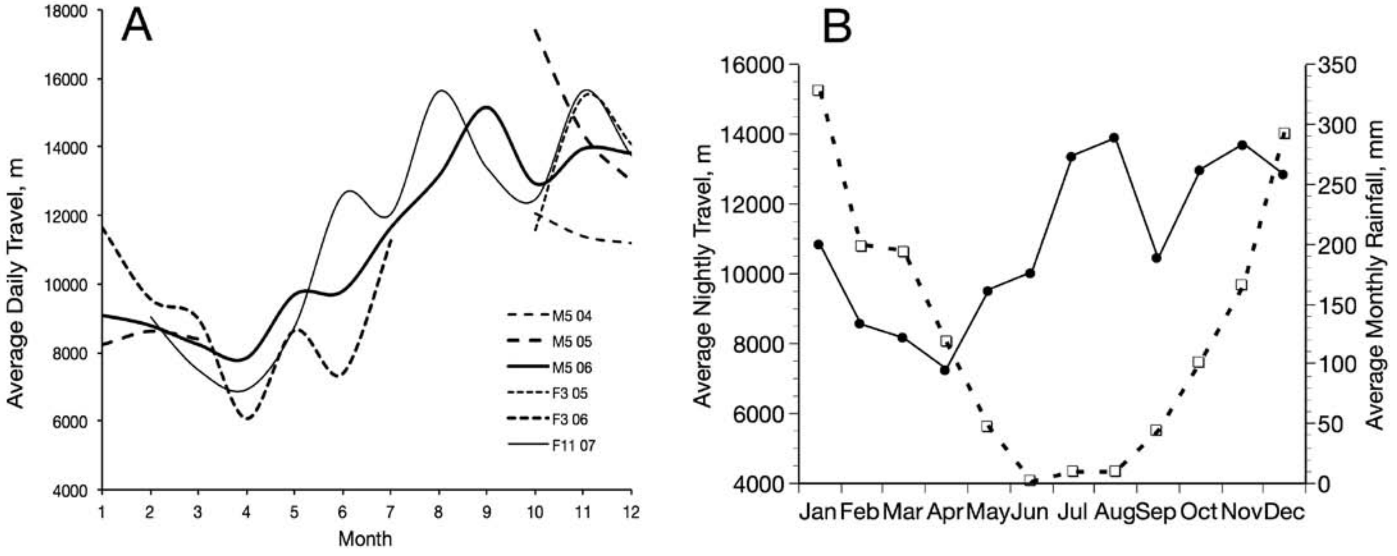

FIGURE 2.5. Average daily total travel distance (sums of average hourly travel) by month. (A) Six data sets from three individuals show the variation between individuals and months and (B) average daily travel of five adult MW combined from 40 monthly data sets 2003–2008 (solid line) and average monthly rainfall during those years (broken line).

TABLE 2.1. Resting behavior of maned wolf F3, from continuous GPS collar data for 90 sequential days 13 October 2003 to 16 January 2004, 3,403 fixes. Fixes were programmed hourly from 0800 to 1700 hours and half-hourly for all other hours. Movement during midday rest is movement >50 m between fixes, with at least one hour of rest before and after the movement.

Month	No. days	Mean hours in midday rest	Mean night rests, hours	Mean total rest per 24 hours, hours	Days moved during mid day rests	Mean rests in nighttime
Oct. 2004	22	9.0	2.5	11.48	3	2.4
Nov. 2004	30	9.6	2.1	11.60	6	1.7
Dec. 2004	31	9.7	1.9	11.51	10	1.8
Jan. 2005	7	7.1	5.3	12.42	1	3.2
Grand total	90	9.3	2.3	11.6	22	2

another hour twice during the night (Table 2.1). Although January was sampled for only 7 days, these clearly show the increased daytime activity and reduced nighttime activity seen in the other wet season data sets (Figures 2.4, 2.5). In January, the time spent resting at midday was two hours shorter than it was in October–December. This was more than compensated for by increased rest periods at night, with about a doubling of nocturnal resting time (Table 2.1). Consequently, F3 rested for a total of about an hour longer per 24 hours in January, the only month of this sample where she was inactive for more than half of the 24 hours.

On a coarser, hourly scale for the longest data sets, the mean total daily hours active (resting is the inverse), over the year and seasons, shows that the MW spent on average one or two hours more in travel and fewer in resting in the dry season than in the wet season (Table 2.2). The seasonal differences in hours active between wet season quarters (January–June) and dry season quarters (July–December) were significant for all MW (Kolmogorov-Smirnov test, *p* level 0.05), but within-season differences were not significant. The difference between highest and lowest monthly activity of individuals was approximately five hours daily, and in some months, all MW were traveling 15 to

TABLE 2.2. Mean total daily hours active, with one fix per hour, based on whether an animal moved ≥50 m since the previous GPS fix. Rests of <1 hour are not detectable, so table represents minimum resting time. Multiple data sets for a given month are averaged for a given maned wolf, N = 99 total maned wolf months of GPS data. Here n/a, not available

Month	F3	F9	F11	M5	M6	M8	Average
Jan.	13.99	12.66	11.93	12.59	10.74	10.62	12.09
Feb.	12.31	13.87	12.73	12.49	n/a	9.91	12.26
March	11.93	12.01	12.83	10.86	n/a	10.61	11.65
April	10.09	13.91	13.20	12.39	n/a	11.19	12.16
May	12.60	n/a	13.41	11.97	n/a	11.93	12.48
June	12.01	n/a	12.75	13.81	n/a	n/a	12.85
July	n/a	14.73	16.74	14.24	n/a	13.12	14.70
Aug.	n/a	14.21	14.75	15.59	n/a	13.48	14.51
Sept.	n/a	n/a	16.64	15.00	n/a	11.90	14.51
Oct.	13.67	15.26	15.16	14.96	13.76	12.54	14.22
Nov.	15.34	14.18	16.02	13.05	13.37	12.63	14.10
Dec.	13.70	13.68	15.50	13.34	12.20	11.68	13.35

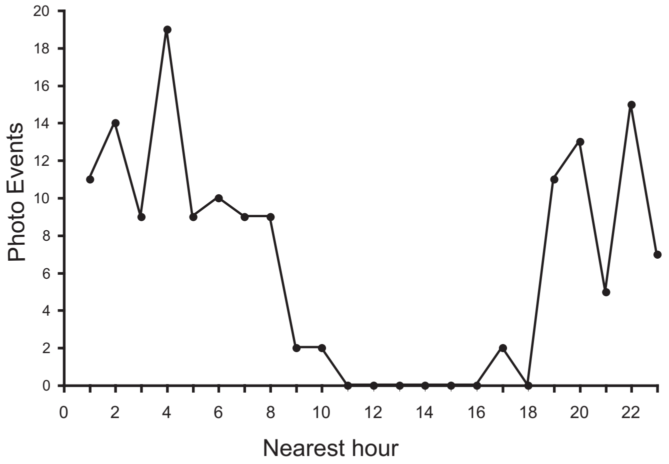

FIGURE 2.6. Circadian pattern of visiting water. Time to the nearest hour of photos of MW at water holes, including only the first photo (event) of a given individual in a given hour (N = 158 events).

16 hours of a 24 hour period (Table 2.2). Because rests shorter than one hour are not detectable in these data sets, the true hours of inactivity are likely to be underestimated and activity similarly overestimated.

TRAVEL TO WATER

Maned wolves apparently need to drink liquid water at least daily. They were not registered by camera traps at water holes when other water sources were widespread, such as after heavy rains or before the savanna dried out in about mid-August (Chapter 3). Camera trap data from 158 visits shows that MW came to water holes at any hour of the night, with peak visits from 1900–2200 hours and at 0400 hours (Figure 2.6). Cameras did not trigger well during daytime heat, but as telemetry showed MW to be generally immobile at midday in late dry season (Figure 2.1A), it is unlikely that many visits were unrecorded. We watched MW drinking from an arboreal blind. They generally drank long and intensely and could return to drink several times within a few minutes. Unlike zorros (*Cerdocyon thous*), which foraged intently around the water hole and ate items found on or dug from the boggy ground during multiple extended visits in an evening, MW usually came, drank, and departed, as also inferred from telemetry. MW tracked on foot with VHF telemetry would abruptly change pace to travel quickly, without stopping, directly to a water hole up to 4 km away.

RESTING SITES

Each maned wolf used many daytime rest sites (beds) that were scattered widely on its range (Figure 2.7). Adults without pups rarely used the same place on sequential days, but subadults sometimes did so. We visited 14 sites of five MW where telemetry showed them to have spent the day or where we encountered them by chance. Twelve of these beds were in dark, denlike hollows pushed deep under long, dense, fine grass clumps in open areas (Figure 2.8). All but two were in seasonally flooded habitats, including three that were used for litters of pups, one of which was surrounded by water when occupied. Most beds in flood-prone areas were used when the ground was dry, and many geographic information system (GIS) located beds were in uplands. There were clusters of contiguous rest sites in zones of tall dense bunchgrasses, and range mates could share these zones. A nongrass bed was in a narrow, cool, damp, dark tunnel under a dense thicket of low *Mauritiella* palms, and another was a nest in grass exposed to the sky in the shade of shrubs. Grass bed entrances were low and inconspicuous, and MW had to crawl into them through a fringe of stems. We saw M7 drop to creep on his belly into a grass bed. None had space for more than one individual. Beds were not marked by beaten pathways, but areas with many beds had networks

FIGURE 2.7. F3 rest site locations during 90 consecutive days (rest sites are at noon fixes: of 89 noon fixes, 88 were inactive from previous fix); rest sites, black dots; broken double line, outline of grassland; single black line, polygon of F3 home range during that time (60 km^2). Many locations are superimposed or apparently so owing to scale.

FIGURE 2.8. Daytime bed of M5 in a hole under long grass. The entrance was enlarged and cleared to make it visible. Photograph by L. Emmons.

of multiple trails. To us, beds had no detectable maned wolf odor, suggesting that MW may avoid urinating near their refuges (we can smell maned wolf urine marks for many weeks). MW were totally hidden in beds and either slept heavily or were reluctant to move. Three times we approached to within 5 m of resting individuals before they abruptly emerged.

DISCUSSION

ACTIVITY PATTERN AND TEMPERATURE

In our study area, MW are not obligately crepuscular/nocturnal but can vary their circadian activity to become nearly cathemeral in some months, with the flexible behavior typical of many Canidae. Quantitative records of maned wolf circadian activity from telemetry are scarce and difficult to compare to ours: Dietz (1984) divided the day into 6 hour blocks for analysis of records for seven MW in Brazil (0600–1200; 1200–1800, etc.). He found MW to be constantly active in 96% of nocturnal fixes and intermittently active in 35% of diurnal ones, but midday and early morning/evening are not distinguishable. Melo et al. (2007), with GPS collars on three MW, collected two-hourly fixes for 6 months in Minas Gerais and reported data like that in Figure 2.1A, with virtually no activity from 0700 to 1600 hours. On the basis of direct observations, Silveira (1999) described MW as bimodally active, with peaks from 0600 to 1000 and 1800–2400 hours. Seasonal differences such as we found have not been elsewhere reported. Activity patterns may differ in different habitats or latitudes, as suggested by the entirely nocturnal behavior of MW reported by Melo et al. (2007). Likewise, crab-eating zorros (*Cerdocyon thous*), the most numerous canids syntopic with MW in our study area, are noted to be strictly nocturnal in both Pará, Brazil (Macdonald and Courtenay, 1996) and in Venezuela (Brady, 1979), where Brady attributed nocturnality to thermoregulation. However, in our study area, zorros are regularly seen traveling about until 0900–1000 and after 1500–1700 hours, as also documented by Juarez and Marinho-Filho (2002).

The hourly activity of MW in relation to temperature has not been previously documented. There are two plausible explanations of the patterns in Figure 2.2: either (1) temperature itself drives maned wolf activity or (2) the observed pattern of maned wolf activity is an incidental result of a temperature-independent circadian cycle that coincides with the daily light/dark/temperature cycle. MW have a dense dorsal pelage, and when lying in the daytime shade, they pant like other canids, tongue hanging out and dripping. Thermal panting is costly in water loss: up to 50 mL/h in 25 kg dogs at 40°C (Blatt et al., 1972); but paradoxically, it is an energy-neutral behavior (Robertshaw, 2006). Dogs (25 kg) began to secrete water from the nasal glands for panting at 30°C (Blatt et al., 1972), which is exactly the temperature at which MW cease activity (Figure 2.2). MW thus seek shelter and become inactive at the threshold where panting is required for thermoregulation in dogs of the same weight. Moreover, parturition is concentrated in the cooler winter months (Rodden et al., 2004), when more diurnal foraging time below 30°C is available (Figure 1.8; Chapter 5). Under the tropical sun in the grassland, it is, of course, much hotter than shade temperatures used in meteorology.

In the late dry season our study MW could travel several kilometers to reach water, an energetically expensive activity. In captivity, MW had a water turnover rate of 2.3 L/day (Boniface, 1998; based on doubly labeled water in three MW). This is one fifth as much per kilogram as that of domestic dogs, which under intense exercise can further quintuple their water requirements (Boniface, 1998). MW thus may have some physiological adaptation for arid habitats. Nonetheless, they must drink considerable amounts, especially when panting, as supported by our observations and photos at water holes. The months with least diurnal activity (August–December) are those with both drought and highest maximum temperatures (Figures 2.4, 1.8), while those with most diurnal activity are the coolest and wettest (in terms of drinking water, January–July). The need to visit water sources (Figure 2.6) likely also contributes to longer travel distances in dry season, than in wet season, months (Chapter 3). To prevent water loss and/or hyperthermia, temperatures above 27°C may drive restriction of daytime dry season activity (Figure 2.2), but there are alternative explanations.

Diurnality of rodent prey has been invoked as the driver of diurnality in grassland Ethiopian wolves (*Canis simensis*; 96% of dietary prey occurrences; Sillero-Zubiri and Gottelli, 1995). During the early years of our study, cavies (*Cavia aperea*) were the main prey of MW, with about 80% occurrence in scats (Emmons, 2009; Chapter 4). Cavies are active in early morning and late afternoon, as are the numerically dominant mice of the savanna, *Necromys lenguarum* (Francisco et al., 1995). Cavies vanished from the study area between 2004 and 2007, with 0% occurrence in scats after 2006 and none trapped on a trapping grid after 2003 (Emmons, 2009; Chapter 4). Our observations from VHF-tracking and GPS collar results do not show that MW were more diurnal when cavies were abundant. However, because cavies do not burrow, MW perhaps could hunt them at any hour. The reverse hypothesis, that the activity of rodent prey species shifts diurnally to avoid predator activity peaks, is likewise plausible (Fenn and Macdonald, 1995).

RESTING BEHAVIOR

The daily energy balance of an individual includes trade-offs between travel, resting, and thermoregulation. Daily, monthly, and seasonal resting patterns have not previously been quantified for free-living MW. Our most noteworthy result is how little MW rested, and consequently, how long they were active (Tables 2.1, 2.2). In comparison, hypercarnivorous African wild dogs rested for 20.5 hours per day and hunted for only 3.5 hours, generally in the morning and late afternoon (Gorman et al., 1998). These two species represent the opposite extremes of resting/activity ratios among large Canidae. Coyotes (*Canis latrans*) in Yellowstone Park rested on average 66% of the day (16 hours) from December to July, when they fed on ungulate carcasses, but when they hunted rodents in October and November, resting decreased to about 27% of the day (Gese, 2004). The latter is even less rest than we documented in MW and clearly illustrates the costs of solo hunting of individual small prey. Interestingly, ocelots (*Leopardus pardalis*) in forest, which also solo-hunt rodents, traveled for daily averages of 9.4 to 11.9 hours, close to the number of hours per day used by MW, but ocelots walked slowly and traveled only about 3.2 km/night, with an estimated prey capture rate of 0.9/km; to maintain body masses one third of that of MW (Emmons, 1988). This perhaps points to a similar return per kilometer of hunting.

RESTING SITES

Few rest sites or dens of MW have been reported: Dietz (1984) described a grass den and three that were within crevices. Melo et al. (2007:34) described a den with pups as in “a maze of grass tunnels . . . [in] an open area of cerrado covered with tall grass species” similar to those that we document. The wide dispersal of daytime of beds on the home range (Figure 2.7), not previously mapped, may establish individual presence across the range, as a possible territorial reinforcement (Chapters 3, 5).

Most MW we examined lacked fleas, as also reported by Dietz (1984), while four syntopic zorros (*Cerdocyon thous*) were heavily infested. Fleas have a terrestrial larval phase, and beds and dens are the most usual foci of infestation. Daily rest-site shifts by MW should reduce flea and perhaps tick loads and any associated disease exposure (Chapter 6).

Finally, insect pests could influence maned wolf resting and activity. Los Fierros savanna is plagued with irritating insects: by day in the dry season, swarms of feral africanized honeybees (*Apis melifera*) climb over the faces of stationary MW, humans, and horses and enter their mouths, ears, and noses. Diurnal sweat bees (Halictidae) and biting flies (Tabanidae) likewise torment stationary mammals in the dry season. Before sundown, swarms of blood-sucking gnats (Simuliidae) emerge, and at night in the wet season, there are clouds of biting mosquitoes (Cuculicidae). As well as cover from the elements, the thick blanket of dense, fine, stems of grass beds (Figure 2.8) offer protection from bees and flies. Daytime wet season activity would decrease exposure to mosquitoes, and nighttime dry season activity would decrease exposure to bees and tabanids. When following VHF-tagged MW on foot, we repeatedly noted that MW moved off from their beds just as biting simuliid flies became intolerable to us in late afternoon (walking dispels gnats). Similarly, most daytime dry season moves of MW were directly from one bed to another, possibly to escape bees (or hot sun patches). Aggravating insects seem unlikely to be major drivers of maned wolf circadian patterns, but pest avoidance could push activity an hour or two in one direction or another.

In summary, MW in NKP spend 10–16 hours a day in travel that is nocturnal/crepuscular during most months of the year, but their travel shifts to increased diurnality in the months of wet season flooding. Maned wolves show an abrupt decline in activity at temperatures above 27°–30°C, coincident with rising daytime temperatures, implicating but not proving physiological issues of thermoregulation and water balance as likely drivers of circadian activity during the hottest months of drought. Long daily activity and short total resting times are probably correlates of long search times needed for hunting sufficient small prey and widely scattered fruit to nourish large body size (Chapters 4, 8). Low maned wolf reproductive rates and small litter sizes (Rodden et al., 2004; Chapters 5, 8) may be consequences of an ecology that leaves little temporal cushion to acquire extra resources.

3

Ranging Patterns

Louise H. Emmons, Verónica Chávez, Luis Fernando Del Aguila, Sixto Angulo, and Matthew J. Muir

ABSTRACT. The ranging patterns of maned wolves (MW), *Chrysocyon brachyurus*, were studied in Noel Kempff Mercado National Park (NKP), Bolivia. Adults traveled mean distances of 11 km/night based on hourly locations. When location fixes were half-hourly, nightly distance for the same data sets were 5–16% longer, or an estimated 12 km/night over all data. Nightly travel distances averaged longer during dry season (14 km/night maximum average monthly travel), than during wet season months (7 km/night, minimum average monthly travel). Ninety-nine percent kernel home ranges of adults were 40–123 km^2. MW varied their sequential nightly trajectories such that an average of 34 km^2 (minimum convex polygon) was covered during each weekly three-night data sample. Area accumulation was rapid, with a seasonal asymptote reached at 200–300 locations, or about three, three-night samples. The need to visit water holes in the late dry season may increase dry season travel distances. Reproductive MW live in monogamous pairs on territories (Dietz, 1984). Because of habitat restriction by forest, maned wolf pairs on our study area shared only one or two boundaries of their ranges with other pairs. When location data sets coincided in month, there was no range overlap between neighboring adult resident pairs, but range boundaries shifted temporally, so that out-of-phase data can show spurious overlap. Nonreproductive MW could be found temporarily within pair ranges.

INTRODUCTION

Maned wolf home range sizes have been determined by telemetry for several regions of Brazil (Coelho et al., 2008; Dietz, 1984; Jácomo et al., 2009; Melo et al., 2007; reviewed in Rodden et al., 2004; Rodrigues, 2002; Trolle et al., 2007), but little has been recorded of the nightly movements of free-ranging individuals in relation to their overall ranges, habitats, or seasons. We used GPS collars to record hourly movements of individuals, in weekly samples over many sequential months. In this chapter we report our results on ranging behavior, which comprise the first telemetry study of maned wolves (MW) in either Bolivia or seasonally flooded grasslands. Our goals for this arm of the study were to understand the land use patterns of MW in terms of their home range sizes,

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conservation needs, and general energy budget. The key topics we address include the following: (1) the relation between nightly foraging trajectories and total range size, (2) how home ranges are defined temporally, (3) how nightly trajectories vary between individuals and seasons, and (4) how individuals are spatially distributed in relation to others. Conditions for MW changed over the study years, so that year-to-year variation in use of the same area by the same or different individuals became an important ecological variable. All of these topics form a continuum with those addressed in Chapter 2 on activity patterns and in Chapter 5 on social interactions. Our study area is the only savanna in Parque Nacional Noel Kempff Mercado (NKP) with partial vehicle access. It is small, inhabited by only a few maned wolf individuals, so we focused on acquiring detailed longitudinal data on these accessible groups.

A species' daily path mirrors the distribution of all its resources and social interactions. With GPS telemetry we could follow with high accuracy the landscape-scale travels of this wide-ranging species. GPS telemetry is restricted to a finite number of locations (fixes) by the weight of the batteries that power the internal processor (about 4,000 to 8,000 fixes, depending on temporal and temperature parameters). Thus there is a trade-off between interfix interval and the total data collection time in months. We chose to program data collection in weekly, three-night samples of hourly fixes, so that entire nightly movement sequences, social interactions, and habitat use could be acquired regularly over many months. However, as each GPS fix took only about 55 seconds, the location of a maned wolf is known for at most 22 minutes of each 24 hour day. By connecting sequential locations into a route, a greater area traversed can be inferred than can be seen from individual fixes, but nightly routes neither reliably include quick visits to point resources nor generate time budgets such as can be developed with continuous observation (Coelho et al., 2007). The information acquired from GPS telemetry obviously depends on the scheduling of the GPS fixes: the closer they are in time, the more accurately the fixes map the path and the more exact spots visited are recorded (Mills et al., 2006). GPS telemetry technology has rapidly improved since we began our work, and soon, battery life may no longer be an issue (Tobler, 2009).

MATERIALS AND METHODS

Study Area

Field studies on ranging were done in the Los Fierros savanna (or pampa) in NKP from October 2001 to July 2009 (Figure 1.2). Habitats and climate are described in Chapter 1. The forest encircled, J-shaped, Los Fierros grassland is 4–10 km wide and about 26 km long and includes 219 km^2 of maned wolf habitat. It is separated by a river and gallery forest from larger savannas on cattle estancias and by 9 km of forest from a large pristine savanna on top of the Huanchaca tableland massif in NKP (Figure 1.2). Maned wolves can move between populations in adjacent grasslands. The study savanna is nearly flat and includes no permanently flowing watercourses other than at one corner that abuts the Río Tarvo/Paragua (Figure 1.2). As the ground dries from wet season flooding in June to mid-August, scattered low points retain seasonal ponds that eventually dry until there is no open water source in the savanna from late August to late October or early November. The middle and most northerly parts of the savanna include larger patches of upland Campo Cerrado habitat that never floods, and the southern end is seasonally deeply flooded "Bajío." Wet season flooding forces MW into drier areas and restricts the habitable landscape (L. Emmons and P. Cuellar, unpublished data).

Analysis of Field Data

Capture, handling, and telemetry methods are described in Chapter 1 and by Deem and Emmons (2005). In 2001–2002, MW were followed first with VHF telemetry, and after mid-2003 with GPS collar telemetry. Most GPS collars were programmed to take hourly fixes for three sequential nights of each week (samples), but some collars took few or no fixes at midday, when MW were generally inactive. The first three GPS collars deployed took continuous half-hourly fixes during maximal activity, from 1700 or 1800 to 0800 hours, and hourly fixes during the day (see Chapter 1 for collar schedules). The VHF data may be autocorrelated and biased toward maned wolf locations close to roads or trails, so we use them to generate home range boundaries and travel rates but not to analyze habitat use. Activity periods (nights) are calculated from the first radio location or GPS fix after noon on a given date to the last location before noon on the following date. Travel distances and rates are calculated only from sequential fixes within continuous data series (distances between the last fix of a three-night sample and the first fix of the next sample are excluded from all analyses). The Los Fierros savanna is small relative to maned wolf home ranges, and its irregular outline precludes use of the standard measurement of minimum convex polygon (MCP) home range areas, which would force inclusion of adjacent forest where MW never ventured, thereby overestimating range size. To estimate home range boundaries, we connected the outer points to the next nearest points (excluding forests), so that polygons may have concavities (not "convex"). Other telemetry studies show that mammalian home range edges are often concave and spiky, such that forcing convexity upon them (MCP) can create spurious home range inflation and overlaps with neighbors (Emmons, 1988, 2000), as we will see below for MW. Nonetheless, for standardized comparisons between areas estimated from subsamples of fixes (seasonal, monthly, or three-night samples), we generated MCP areas with Hawth's Tools (spatialecology.com) and R-Ade (Calenge, 2006). Each successive deployment of a new GPS collar on a given animal (generally in sequential years) is treated as a different data set if data series have gaps of longer than a month (Table 3.1).

All fixes less than 50 m from the previous fix are treated as "inactive" (or "resting") MW, and are set to 0 m apart for analysis. We assume that the animal moved if fixes were over 50 m apart, ("active"; Chapter 1). Maned wolf mean travel rates were 600 to 1,000 m/h, and we treat sequential locations as independent. None was discarded for computation of range areas (in contrast to Jácomo et al., 2009). Moreover, the large numbers of unbiased GPS locations, sampled at equal intervals, obviates the need for models to extrapolate range areas from small samples (Kenward, 1987). Relative to the kilometer scale of maned wolf movements, the random, meter-scale intrinsic GPS location errors are inconsequential to the calculation of maned wolf travel distances or rates. As the habitat is open, the success rate of GPS fix attempts was generally high (90–97% for whole data sets), with a mean time to fix of about 55 seconds. Later collars improved much in performance over the first one deployed in 2003, which had 57% fix success, perhaps from poor satellite coverage in Bolivia coupled with early technology.

Hourly fixes inadequately documented the use of water points, as MW did not linger while drinking. To explore the influence of water sources on movements, we tabulated all active locations within 150 m of all known water points. Only the first fix was tabulated for each water-proximity location event.

RESULTS

HOME RANGE SIZE

The Los Fierros savanna was divided by maned wolf home ranges into northern and southern halves (North Range, South Range). Initially (2001–2003) the northern half was itself subdivided into two areas (North Ranges 1 and 2) that subsequently merged. Home range areas from

TABLE 3.1. Data sets from which movements and range sizes were calculated. Kernel home range areas (KHR) were calculated with R-ade (Calenge, 2006), without regard to habitat edges. Long data series used for seasonal analyses shown in bold. M4 and F3 were subadults in 2002; M6 was not resident on a single range. M, males; F, females; NR, North Range; SR, South Range; n/a, not available.

					Three-night	KHR, km^2			
Animal (Site)	Collar	Data start	Data end	Fixes	samples	99%	95%	75%	50%
M2 (NR 1)	VHF	20 Oct 01	1 Jan 04	800	n/a	40.42	30.58	15.29	7.79
M4 (NR 1)	VHF	23 Oct 02	24 Feb 03	243	n/a	15.68	10.82	5.66	3.03
F3 (NR 1)	VHF	26 Sep 02	24 Feb 03	240	n/a	20.43	14.84	7.22	1.35
F3 (NR 1)	GPS	13 Oct 03	16 Jan 04	1847	n/a	52.86	39.57	19.42	8.99
F3 (NR 1)	GPS	9 Oct 04	7 Jan 05	3403	n/a	75.21	57.1	31.69	17.22
F3 (NR all)	**GPS**	**6 Oct 05**	**13 Jul 06**	**2900**	**45**	**73.88**	**56.47**	**32.63**	**16.6**
F3 (NR all)	GPS	21 Sep 07	21 Nov 07	607	9	86.07	63.51	28.54	11.72
F3 (NR all)	GPS	16 Jul 08	18 Oct 08	1008	14	77.49	60.83	29.96	12.32
M5 (NR 2)	GPS	4 Oct 04	7 Mar 05	4631	n/a	73.88	56.47	32.63	16.6
M5 (NR all)	**GPS**	**29 Sep 05**	**16 Dec 06**	**4606**	**64**	**85.29**	**67.5**	**38.61**	**21.14**
M5 (NR all)	GPS	6 Feb 07	29 Mar 07	349	6	61.44	45.99	21.47	9.42
M5 (NR all)	GPS	4 Oct 07	30 May 08	1112	16	98.2	78.08	41.87	19.63
M6 (unfixed?)	GPS	27 Sep 05	23 Feb 06	1340	21	n/a	n/a	n/a	n/a
M8 (SR)	GPS	25 Jul 07	26 Sep 07	635	10	75.5	56.11	25.85	10.14
M8 (NR)	**GPS**	**9 Jul 08**	**22 May 09**	**3329**	**46**	**108.67**	**89.29**	**48.09**	**22.55**
F9 (SR)	**GPS**	**7 Jul 08**	**16 Apr 09**	**2667**	**33**	**110.89**	**87.51**	**49.28**	**25.08**
F11 (SR)	**GPS**	**4 Feb 07**	**26 Mar 08**	**3784**	**59**	**123.19**	**92.71**	**43.86**	**18.37**

seven data sets of three resident adult males and three females (635 to 4,406 fixes per data set, including two data sets for M8 on different home ranges) averaged 89.3 km^2 99% kernel home range (KHR), 69.4 km^2 95% KHR, and 17.6 km^2 50% KHR (Table 3.1). If the VHF data set for M2 is excluded (possibly underestimated), the areas are, respectively, 96.2, 74.9, and 19.0 km^2. Females had slightly larger average 95% KHR ranges than did males (79 km^2 versus 71 km^2); but sample sizes are too small for meaningful inference. Because the home ranges are superimposed over the same 220 km^2 fragment of savanna and include pairs on the same territories, they are not independent. However, they do represent the area use and needs of different maned wolf individuals on this particular savanna. These area uses changed both interseasonally and interannually (see also Chapters 4, 5).

General Movement Patterns and Distance Traveled

Straight-line measurements between telemetry locations of resident adult MW averaged 11.1 km per 24 hours over all months of the year (Table 3.2). On-foot VHS telemetry data had gaps when signals were lost, so the data underestimate both travel distance and range area. Nonetheless, an estimate of kilometers traveled per night, from on-foot VHF telemetry, was similar to those obtained with GPS collars: mean travel of M5 for 27 October nights (850 GPS fixes) was 13.7 km/night, while that of M2 for 15 on-foot VHF-tracking nights (306 fixes) was 11.19 km/night, or within the variation seen between individual GPS telemetry data sets (Table 3.2). Subadults traveled shorter paths within smaller areas than did adults (F3 and M4 in 2002; Table 3.1).

At the scale of hourly fixes, adults typically walked in fairly straight paths that rarely zigzagged or doubled back but made large loops that extended to near an edge of the home range (Figure 3.1). On sequential nights they took different paths, so that a large part of the home range was crossed in a few nights (Figure 3.1). Adults tended not to

TABLE 3.2. Daily linear distances (km) between hourly GPS locations, averaged by month, from 92 monthly data sets of three female and two male maned wolves (MW). Standard deviations (SD), monthly means of all MW; *N*, number of monthly three-night samples.

Month (*N*)	M5 (28)	M8 (16)	F3 (25)	F11 (14)	F9 (9)	Average (92)	SD
1 (9)	8.80	10.35	12.74	11.28	11.09	10.85	1.29
2 (8)	9.00	9.85	9.43	8.85	5.74	8.57	1.46
3 (8)	7.92	10.73	8.82	6.79	6.65	8.18	1.50
4 (4)	7.68	10.06	5.87	7.81	4.99	7.28	1.76
5 (4)	9.54	10.47	8.48	9.73	n/a	9.56	0.71
6 (3)	9.65	n/a	7.24	13.26	n/a	10.05	2.47
7 (6)	11.54	15.55	11.67	13.39	14.71	13.37	1.60
8 (6)	13.07	13.13	15.89	14.38	13.03	13.90	1.12
9 (8)	10.94	11.40	8.57	10.95	n/a	10.47	1.11
10 (13)	13.74	11.44	14.47	11.61	13.70	12.99	1.23
11 (12)	12.90	14.51	15.52	13.74	13.26	13.99	0.94
12 (11)	12.41	14.61	14.90	11.69	13.87	13.50	1.25
Average	10.95	11.97	12.54	10.65	10.78	11.06	

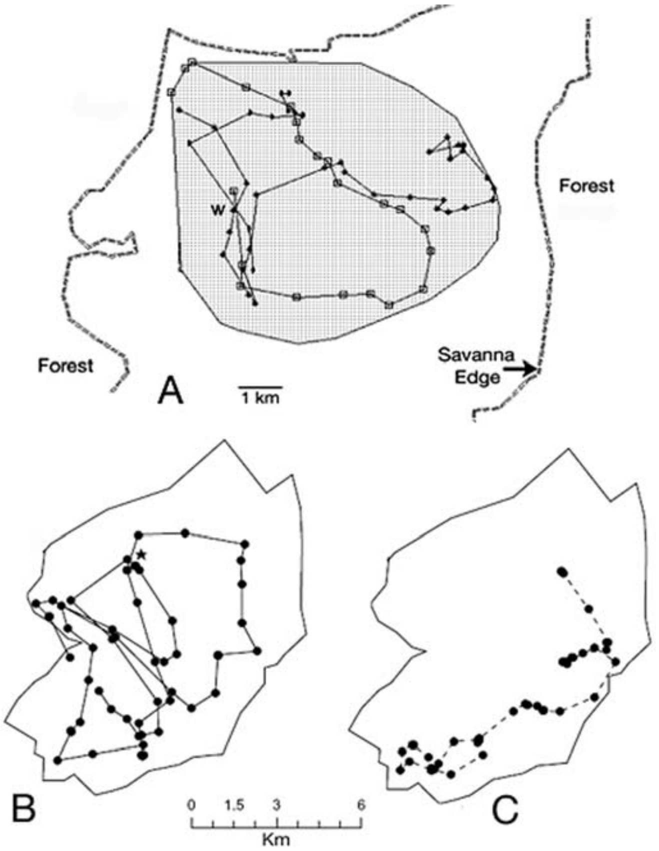

FIGURE 3.1. Pathways of single, three-night samples: (A) M2, 17–19 November 2001, each day with different symbols, double line is savanna edge, stipple, and circular outline represents the range polygon (49.1 km^2, 800 fixes), W is Pozo Matt water hole; (B) M5, dry season 6–8 October 2005 (three-night range 47.3 km^2, 59.3 km traveled); and (C) M5, wet season, 9–11 February 2006 (three-night range 24.4 km^2, 21.2 km traveled). Outline in B and C is the home range polygon from the total M5 data set October 2005–December 2006 (86 km^2). Note the travel pattern of long, straight trajectories with extensive coverage of home range. Star in B indicates Pozo Matt water hole.

TABLE 3.3. Estimation of the straightness of travel trajectories by comparison of distances traveled nightly in the same data sets when fixes were half-hourly or hourly, and the percentage of hourly to half-hourly distance. Daytime periods when all scheduled fixes were hourly are removed, so total 24 hour travel is not represented. Average nightly travel (m) for given months. Maned wolf individual and its 99% KHR home range size for the data sets (F3, 52 km^2). These MW were a pair, and from October 2004 to January 2005 the fixes were synchronous and on the same territory.

Month	Fixes half-hourly	Fixes hourly	Percent
	F3 (52 km^2)		
Oct. 2003	21,677	17,944	83.6
Nov. 2003	20,570	19,502	95.8
Dec. 2003	17,899	15,458	87.2
Jan. 2004	16,149	13,545	84.7
	F3 (75.2 km^2)		
Oct. 2004	14,481	13,528	93.4
Nov. 2004	13,765	12,762	92.7
Dec. 2004	13,967	12,781	91.5
Jan. 2005	10,868	10,836	99.7
	M5 (73.8 km^2)		
Oct. 2004	12,453	11,599	93.1
Nov. 2004	11,675	10,772	92.3
Dec. 2004	11,625	10,800	92.9
Jan. 2005	7,242	6,529	90.2
Feb. 2005	7,906	7,022	88.8
March 2005	7,518	6,884	91.6

repeat their pathways. If they had a frequently visited goal such as water or pups, a different route was taken to and from it on sequential nights of a sample (Figure 3.1A, B).

To estimate how much nightly travel might have been missed between fix times, we extracted route length from both half-hourly and hourly locations for the three data sets with fixes half-hourly, including only hours with both intervals of fixes (Table 3.3). The total daily distances between hourly fixes were on average 91% of the path length generated with half-hourly fixes. The largest trajectory differences, up to 17%, are seen in data from F3 when her home range was small (2003–2004) and likewise for M5 in January–February 2005 when his monthly ranging was shortest (Table 3.3). This likely results from simple geometry, because for a given walking rate, more turns are executed to travel in a smaller space, and it reflects a slightly more intensive use per km^2 of the landscape. Minimum actual average daily travel distance for all MW, incorporating the average difference between hourly and half-hourly data, thus should be at least 12.2 km daily, or 1.1 km longer than found by connecting hourly fixes. We note that only half of the year was sampled in this way, and possibly, some of the seasonal differences in nightly ranging might in reality be smaller if MW zigzag more in January–March than in July–September.

A result of nightly route variation is a rapid increase in range area with fix number (Figure 3.2). The area accumulation curves start to flatten at 100 to 200 fixes, and in 2005–2009 data, reach asymptote for a given data set at about 300 locations and 60 km^2. One hundred to 300

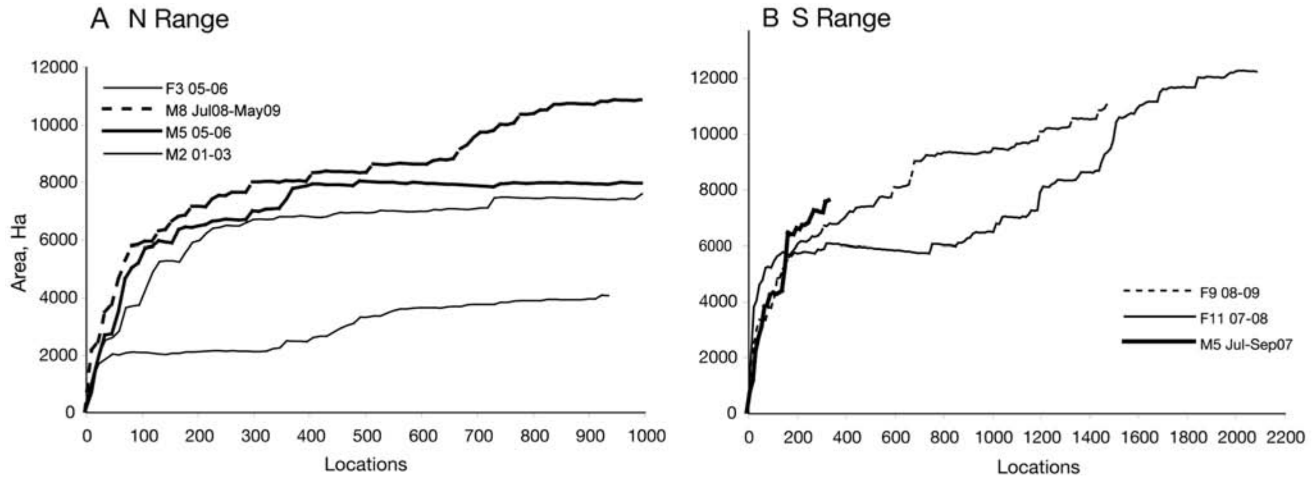

FIGURE 3.2. Area accumulation by number of hourly locations from GPS collar single data sets of adult residents, all fixes <50 m from the previous fix excluded; and one VHF data set (A, M2 lowest curve). Data are accumulated in increments of 12 fixes, to 99% KHR. (A) One female and three males on the North Range, longer sets cut off at 1000 fixes. (B) Two females and one male on South Range, the longest set cut off at 2,088 fixes.

fixes represents two to four, three-night weekly samples. The curves flatten completely at about four to six samples. Six adult residents, male and female, behaved alike. Steps in the curves represent seasonal shifts in habitat use, which were most pronounced in the more flood-prone South Range, where the slow rise above some steps represents a slow expansion into drying seasonally flooded habitat (F11, Figure 3.2B). The position of steps is a chance consequence of the collar deployment month (F11 was tagged in February and expanded her range over many months; F9 was tagged in September when her whole range was used).

Travel distances and areas encompassed during three-night samples were quite similar for all individuals, although the standard deviations are high (Table 3.4). These measures varied in parallel over wet and dry-season samples (Figure 3.3). It is curious that the areas of three-night sample polygons, in km^2, approximate the sum of kilometers traveled during given samples (Table 3.4, Figure 3.3). This results from a uniform rate of travel, similar for all MW. The geometry of travels was therefore quite constant throughout the year.

Despite the large spatial areas visited during short times, temporal use of home ranges was highly nonuniform, with about half of all locations (that is, hours when a maned wolf was at a place) in a data set falling within about 20% of the total range area (50% KHR; Table 3.1; Figure 3.5B).

TABLE 3.4. Area and distance covered in three night samples. The mean minimum convex polygon area covered (calculated in R-Ade), and mean total distance and SD of distance traveled per three night sample, for individual MW with large data sets. Data are for M8 total and segregated into samples taken in different home range areas (SR, South Range; NR, North Range). Samples for F3 with newborn pups omitted.

Maned wolf	N samples	Mean area, km^2	Mean travel, km	SD travel
F3	59	30.84	28.66	9.02
F9	30	33.51	39.79	19.70
F11	59	32.65	34.80	12.09
M5	86	33.65	33.89	9.13
M8 all	60	37.47	32.58	8.73
M8 SR	14	48.44	34.89	9.93
M8 NR	46	34.13	31.74	8.36

WATER

In the late dry season, MW seemed to travel daily to points of water (Chapter 2). There is a large dry season peak in North Range GPS events with 150 m proximity to water (Figure 3.4A). On this range, only a few natural

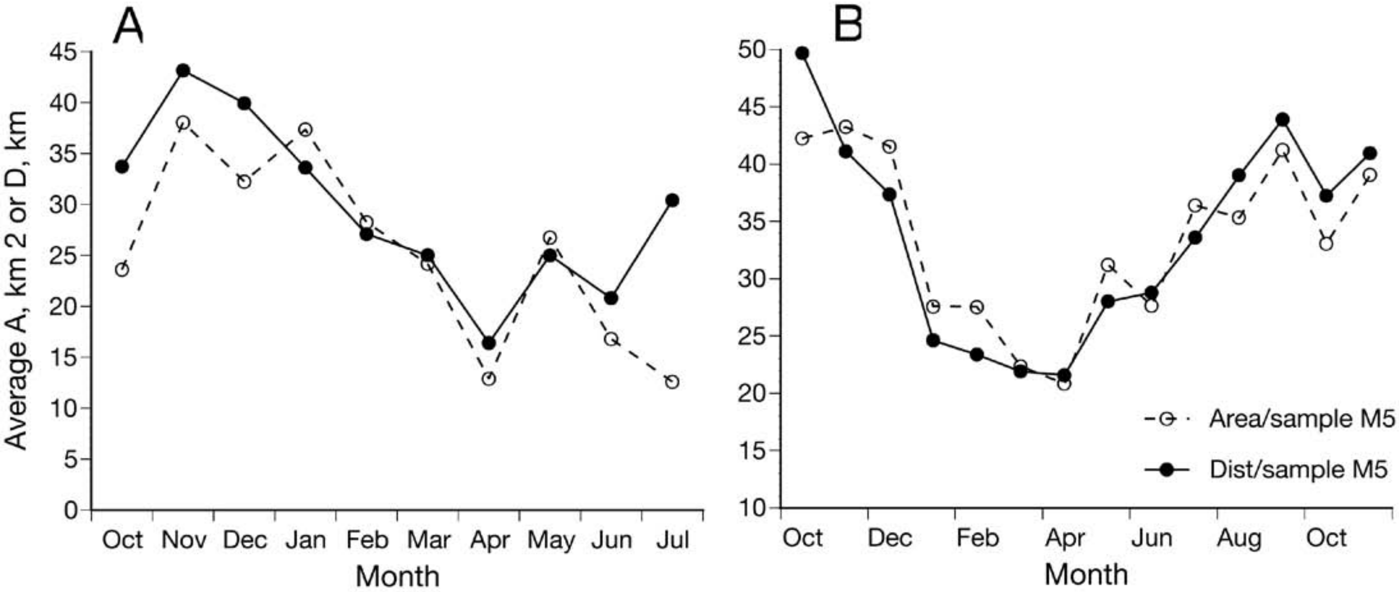

FIGURE 3.3. Average distances (broken lines) and areas (solid lines) of three-night weekly samples for the male and female of a pair, by month, in 2005–2006. (A) Female F3, 10 months of continuous data (she had new pups in July); (B) Male M5, 14 months of continuous data.

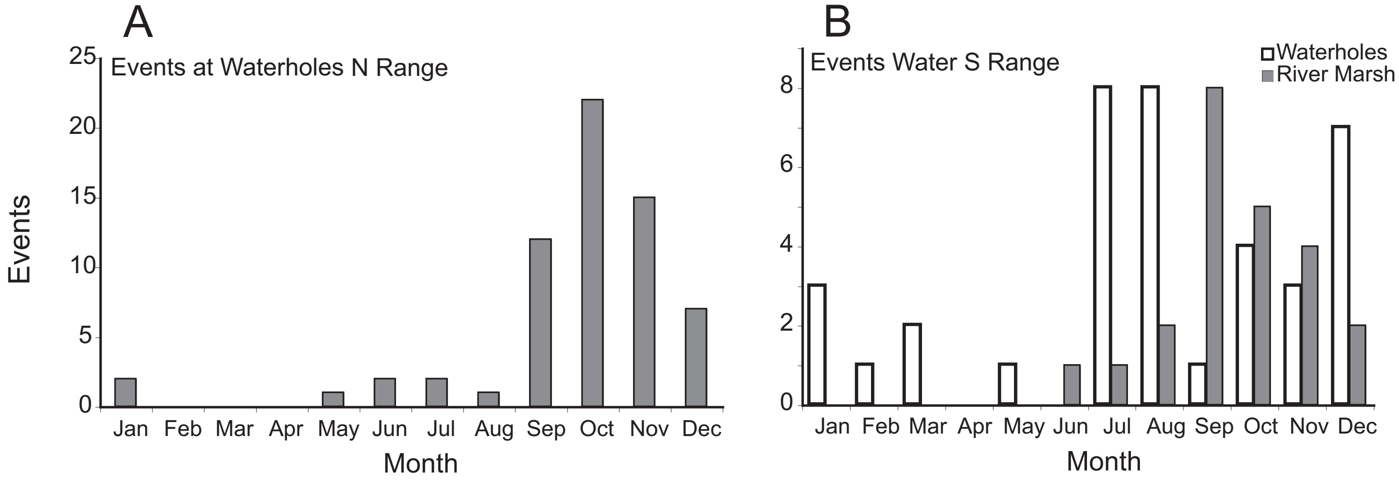

FIGURE 3.4. Proximity to water sources by month. (A) North Range, three, 11–12 month continuous data sets (35 months) from two males and a female (*N* = 64 events). (B) South Range, two, 11–12 month continuous data sets from two females (*N* = 61 events); river marsh, shaded bars. Only the first fix (event) within 150 m of a known water source was included if series were larger.

or artificial (dug by us) savanna water holes existed in the late dry season. Streams in nearby forest retained isolated pools, but we do not know if MW used these. On the South Range, MW in two data sets preferentially used savanna water holes and shifted to riverside marshes when water holes dried in September (Figure 3.4B). North Range water holes were in flood-prone terrain not generally visited when water was widespread, but South Range water holes were near often used parts of the range, where MW might go for reasons unrelated to drinking, as shown by January–May proximity when water covered much of their range.

Territoriality

We define territoriality as the exclusive use of an area by members of a class of individuals, regardless of how it is achieved. We began our study with VHF telemetry of an old adult male, M2, and two subadults/yearlings (M4, F3) that co-occupied the same home range (the presumed adult female/mother was seen and photographed, but not captured). The 2001–2004 data sets showed superposition of M2 and F3 ranges, with a sharp, common southern boundary across the savanna (Figure 3.5A). Because of difficult access, the M2 data set (from on-foot VHF tracking) likely underrecorded the SE corner of his range (Figure 3.5A). Nine months later, the first M5 data set shows a range largely south of, and abutting that of M2 and F3, and with a sharp line at its opposite, southern, border across the pampa. M5 was by then consorting with F3 on her range, so a few fixes overlap (Figure 3.5A; see Chapter 5). When we followed south-traveling M2 or F3 on foot with VHF in 2002–2003, we noted them to turn abruptly when they reached the midsavanna range boundary and then to travel along its general edge. Kernel analysis for the F3, 2003–2004 data set, shows 50% of locations concentrated in a 9 km^2 strip near the SW boundary of her 52 km^2, 99% KHR (Figure 3.5B). No obvious topographic or vegetation features coincided with any midsavanna range boundaries.

Neighboring territories met along sharp lines of locations on across-pampa range boundaries (Figures 3.5–3.8). Locations of neighbors for the same month show virtually no overlap (Figures 3.6–3.8). However, range boundaries shifted from season to season or from one year to the next (Figures 3.6, 3.8). Data that were not simultaneous, or that were summed over many months, might therefore show spurious home range overlap that did not exist in real time (Figure 3.8). The male and female of pairs tightly shared boundaries that abutted other pairs (M5 and F3 in Figure 3.8A), although they did not otherwise necessarily coincide exactly in their monthly ranges. Offspring shared the parental territories. We conclude that resident adult pairs were strictly territorial.

On the basis of range boundaries from telemetry fixes, there were three maned wolf territories on the Los Fierros savanna from 2001 to early 2004. From late 2004 through 2009, there were only two territories, the North and South

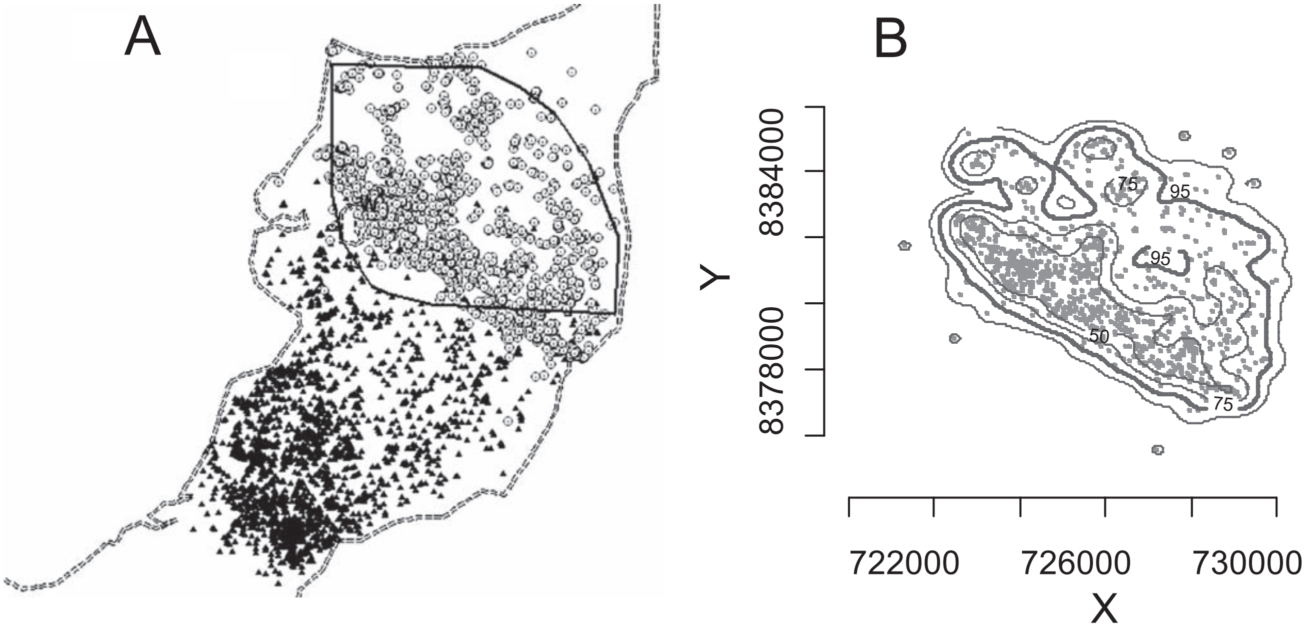

FIGURE 3.5. Positions of maned wolf ranges on the Los Fierros savanna from October 2001 to March 2005. (A) Los Fierros savanna outline with all October 2003 to January 2004 GPS locations of F3 (open circles), overlaid by M2 range polygon outline (dark pointed oval, 2001–2003 VHF locations); and M5 GPS locations from October 2004 to March 2005 (black triangles). Note sharp boundaries of southernmost range edges of F3 and M5. M2–F3 and M5 data are from different years. (B) The 50%, 75%, 90%, 95%, and 99% KHR contours for the F3 data set in A; axes are Universal Transverse Mercator (UTM) coordinates. Fixes during inactivity excluded.

FIGURE 3.6. Synchronous locations of neighboring males M5 (North) and M8 (South) during September and October 2006, home range polygons shown as thin lines. (Left) Whole ranges; (right) mutual boundary, enlarged. The cluster of locations at bottom center at left are along the river; cluster above the W on the NW side of the North Range is at Pozo Matt water hole.

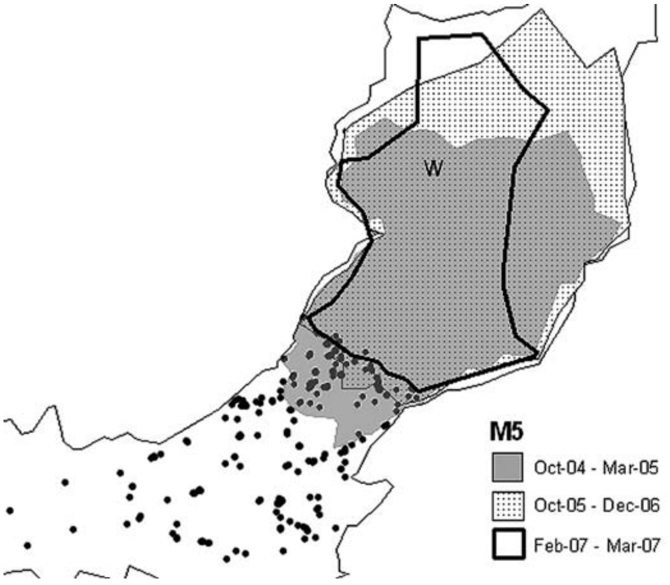

FIGURE 3.7. Home range shifts of M5, moving gradually northwestward over three years, and February 07 locations of F11 (black circles). Note that data sets are of unequal length (2 to14 months), the February–March 2007 range (heavy line) shows avoidance of a recently burned area on its NE side.

Ranges (boundaries figured in Figures 3.5 to 3.8); and by September 2010, there was only a single territory, which included all of the savanna. Range shifts are discussed further in Chapters 4 and 5.

EXCEPTIONS TO TERRITORIALITY

Even though adult pairs were territorial with respect to neighboring pairs, other individuals could be temporarily present on a territory. Most were grown young of the pairs, and some were transients recorded once in camera trap images; but there were several exceptions. In 2002–2003, other MW, likely of the neighboring group (on North Range 2), came to Pozo Matt water hole on the territory of M2 and family, then close to the territorial boundary (Figure 3.5). After 2004, when the North Range boundary was 7 km farther south, only territorial family members were photographed at this site (Chapter 5).

In September 2005 on the South Range, we caught old male M6, when M8 was present, as well as females and young pups (Chapter 5). Until December, M6 traveled in and out of the South and North Ranges, spending weeks on the territory fringes and in distant river marshes (Figure 3.9A). He crossed the river several times and traveled

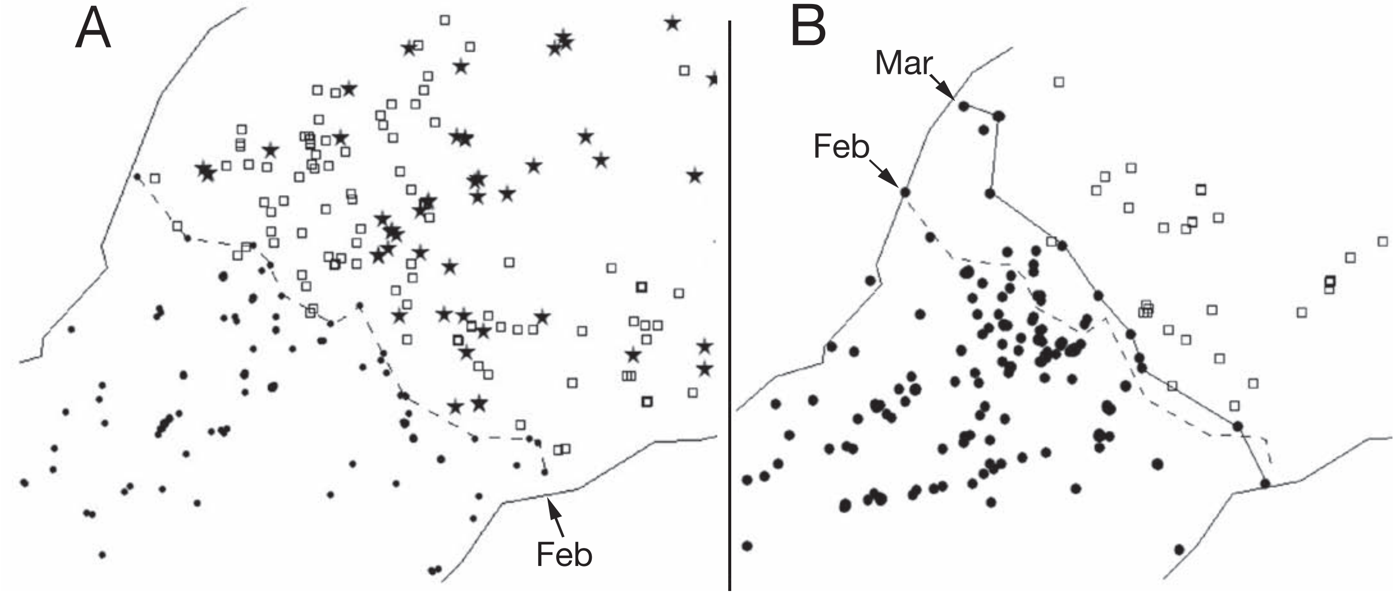

FIGURE 3.8. Fine-scale temporal boundary adjustments of adjacent pair territories. (A) February 2007 boundary (broken line) of F11 (black circles) with M5 (open squares), and F3 January 2007 locations (black stars, no F3 February 2007 locations available). The single fix of M5 that is beyond the line is 100 m from it. (B) February 2007 (broken line) and March 2007 (solid line) boundaries of F11–M5 and March 2007 locations of F11 (black circles) and M5 (open squares). Note that both maned wolf ranges shifted NE together, without incurring range overlaps, and that neighbors share locations exactly on boundaries. The savanna at the territorial boundary is 4 km wide (grassland border outlined by thin lines that bracket location points).

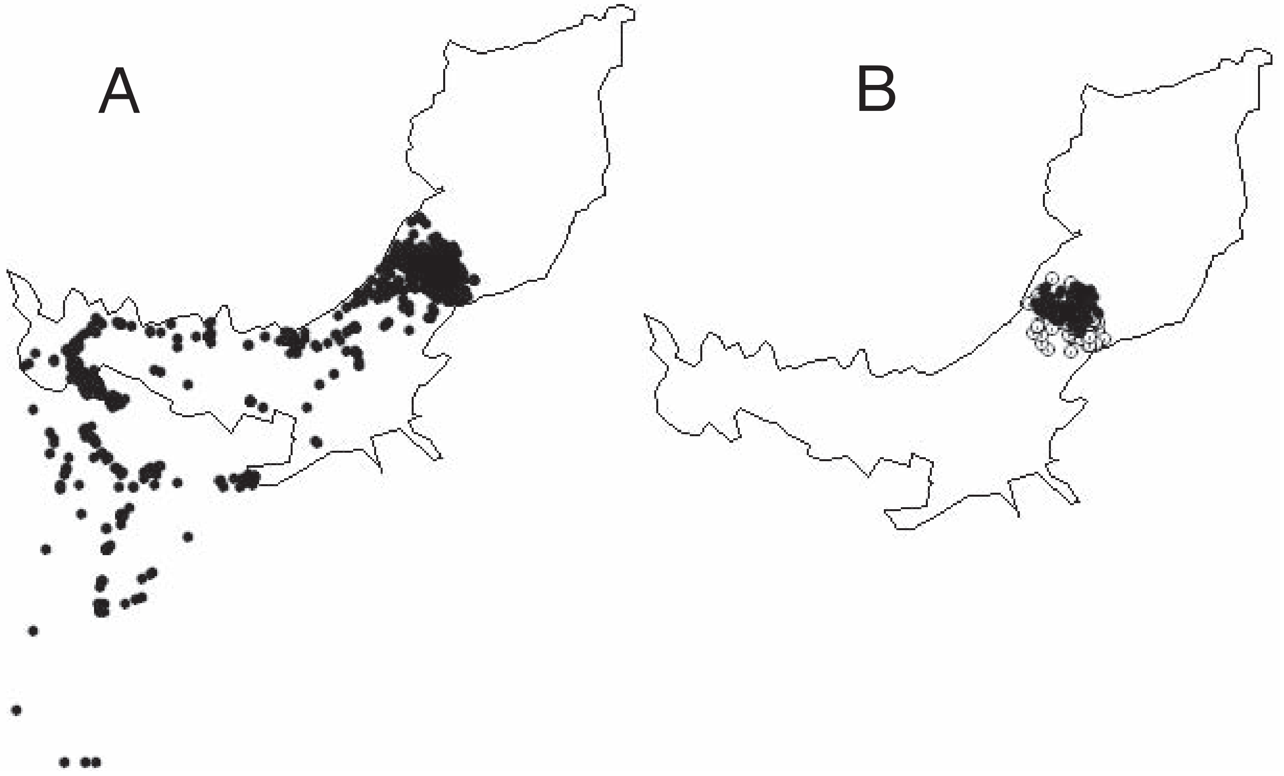

FIGURE 3.9. Movements of M6 through the territories of three or more pairs, before his death. (A) All locations September 2005 to February 2006 (concave polygon connecting points, 174.2 km^2). (B) Locations in January 2006 (open circles, area = 9.2 km^2), and 1–22 February 2006 (black circles, 4.8 km^2), when he died. Outline is the Los Fierros savanna, with river marshes and gallery forest border its southern edge; the southernmost fixes are on Caparú estancia 20 km south of the river (area image in Figure 1.2).

in October and November to a neighboring estancia in three-night samples of 51, 52, and 59 km, but otherwise he moved little (average of 18 three-night samples excluding these three longest, was 14.8 km; entire range polygon, 174.2 km^2). When rising waters flooded the marshes and savannas in December, he returned to near his capture point in the nonflooded border zone of the North and South Ranges, mostly in the North Range territory of M5, where he spent January and February with ever-decreasing movements in an area of 10 km^2 (Figure 3.9B). During synchronous samples from December to February, M5 twice briefly approached M6 to within 150 m (149 m apart 17 December 2005; 87 m apart 2 February 2006); and they certainly met for a single fix on 16 February (6 m apart at 0300 hours), after which M5 left the area and did not soon return. M6 died two days later (ceased motion).

In a case with some similarities, young male M5 made incursions into the territory of geriatric male M2 to consort with young F3 after the adult female had disappeared (see Chapter 5) and during the last 5–7 months of M2's life. With no GPS collar, the final movements of M2 were unrecorded.

DISCUSSION

HOME RANGE SIZE

Telemetry-generated maned wolf home range areas reported in the recent literature are in the same size range that we found for Los Fierros (Coelho et al., 2008; Jácomo et al., 2009; Melo et al., 2007; Rodrigues, 2002), suggesting similar ecological conditions. The largest such study, of 37 resident adult MW studied by Jácomo et al. (2009) in Emas National Park, Goiás, Brazil, had mean 95% KHR areas of 80.2 km^2 and mean 50% KHR areas of 13.8 km^2: close to our mean values of 74.9 and 19.0 km^2 for ranges from 2005–2009 (Table 3.1). In contrast, at the beginning of our study, two MW co-occupying the same range used areas of 40 km^2 (VHF, perhaps an underestimate) and 52 km^2: more like the smaller ranges of 20–40 km^2 reported by Dietz (1984) and 40–50 km^2 reported by Trolle et al. (2007) and Melo et al. (2009). In our study, increases in range sizes after 2005 corresponded to a decline in prey numbers (Emmons, 2009), which suggests an influence of resource density on range size, as we report in more detail in Chapters 4 and 5.

General Movement Patterns and Travel Distance

Maned wolf sequential nightly movements can be characterized as (1) long in path length; (2) nonrepeating in routes; (3) paths quite straight, often traveling to an edge of the range before turning; (4) likely to take divergent directions on sequential nights; (5) longer in the dry season than in the wet season (Chapter 2); and (6) generally uniform in travel rate regardless of month.

The true area seen by a body traveling 12 km, scanning a fixed-width band on each side, is the same whether it moves in a straight line or a circle, which subtend maximally different area polygons. The MCP per sample data (Table 3.4) illustrate the home range coverage patterns of MW, but they do not imply that the real area scanned for foraging is different under different configurations of the same path length. Only total path length and degree of path overlap influence the dimensions of the nightly foraging area an animal visits (Emmons, 2000b).

GPS telemetry underestimates the true path length of an animal by an amount related to the intrinsic straightness of the path and the interval between locations (Mills et al., 2006). Actual maned wolf travel distances, from the difference between hourly and half-hourly data, were on average at least 1.2 km per night longer than those estimated from hourly fixes, or 12.2 km global nightly average. For thin data sets, energy use calculated from movement distance will therefore be underestimated by telemetry (Goszczyski, 1986). May to October maned wolf travel distances reported in Minas Gerais by Melo et al. (2007) from 12 daily fixes (2-hourly) for a pair and subadult female, were much shorter than those we recorded, 9 km/day for a female and only 7 km/day for a male (not significantly different). These shorter trajectories may result from half as many locations per day, coupled with small home range sizes that produce more turns (40–50 km^2; Melo et al., 2009), additive factors that will underestimate travel distances. We note, however, that our male M2, also with a 40 km^2 range size, moved 11 km/night (N = 15 nights of VHF tracking), while F3 on a 52 km^2 range, moved a mean of 21.7 km each night in October (Table 3.2), so ranges of this size do not alone account for short trajectories.

MW at Los Fierros chose sequential nightly paths so as to rapidly visit much of the home range, as shown by steep area accumulation curves (Figure 3.2). GPS collar data from three individuals in Minas Gerais (Melo et al., 2007), showed similar rapid area accumulation, but because fixes were taken at half the rate (every two hours), asymptotes were reached at half as many fixes (i.e., within an equivalent time span). Melo et al. (2007) found no seasonal differences in daily ranging like those we document in our study animals (Figure 3.3; Tables 3.2, 3.3; Chapter 2), but their study did not include the critical months of November to March. Seasonal flooding, which is not present in Melo et al's. study area, caused seasonal ranging differences at Los Fierros. Because our study MW also shifted activity toward more diurnality and resting during the wettest months (Chapter 2), the seasonal variation in ranging was thus driven not only by the presence/absence of water but also by an undefined seasonal circadian factor such as prey type.

The nightly movement rates of MW were similar for different sexes, seasons, and territories (Tables 3.2, 3.4; Figure 3.3). The travel distances summed over three-night samples (Table 3.4) are a simple function of average rates of travel. Maned wolves of both sexes thus moved at similar average speeds, as is expected from their near monomorphy (Dietz, 1984; Jácomo et al., 2009). Similar leg and stride lengths produce similar average kilometers per hour for the same gaits. The seasonal differences in ranging (Figure 3.3) are due to changes in the number of hours that MW are active in each season, rather than to changes in travel speed. This reinforces the data in Chapter 2 that show more hours of resting in wet season than in dry season months (Table 2.2, Figure 2.5).

The parallel variation in area and distance traveled in samples from months of greater or lesser travel (Figure 3.3) shows that the shapes of travel routes remained similar when movements were compressed into to smaller areas during the wet season. Nonetheless, when the home range size of F3 was smaller, there was an increase in the relative length of trajectories of half-hourly, compared to hourly, locations: from an average of 12% difference in a home range of 52 km^2, to a 6% difference in one of 75 km^2 the following year (Table 3.3). Thus our failure to observe increased relative path lengths on smaller wet season ranges may be because hourly fixes are too widely spaced to detect increased zigzagging.

Nonrepeating and wide-ranging trajectories can establish territorial presence, uncover isolated fruit sources, and maximally spread prey encounters over time and space, so that prey have less expectation of predator encounters (wariness). However, the more frequently used 50% KHR "core" areas (Table 3.1, Figure 3.5; Jácomo et al., 2009) were often in bands adjacent to the boundaries between neighboring pairs. The influence on home range use of neighboring pairs per se is not clear, as these areas also included favored long-grass resting sites, high-ground refuges, and dense populations of a favored fruit tree, *Alibertia edulis*.

TERRITORIALITY

Among our few study animals there was sharp territoriality between neighboring adult pairs or family groups (see also Chapter 5). We did not attempt to calculate percentages of overlap between neighboring pairs, because the sole boundary that existed for most of the study (Figures 3.5–3.7) was nonoverlapping when simultaneous data sets were available. Because MW in Los Fierros savanna shared only short borders with other pairs, perhaps they devoted more effort to maintaining tight boundaries than they could have if surrounded on all sides by neighbors.

Dietz' first telemetry study of MW (1984) likewise showed strong exclusivity and stability of pair ranges, and he considered MW to be territorial, as did Rodrigues (2002). Jácomo et al. (2009), with a much larger sample of 28 MW followed in the same year, found about 20% overlap between male-male or nonpair neighbors and 8% between female-female neighbors, while presumed pairs had, by definition, >75% intrapair overlap. Their study was based on small numbers of manual VHF fixes (mean of 60 locations per animal, but as few as 10), and to prevent autocorrelation, they discarded fixes <12 hours apart (Jácomo et al., 2009). They concluded that territoriality was likely, but not definitively shown by their data. The looser-knit range structure found by Jácomo et al. (2009) might have been due to the combination of few location points coupled with data summed across a number of months. With few locations, the bordering lines of range polygons cross long stretches of terrain without points, enclosing areas that may not actually be used by the animals. All studies to date are at least consistent with the territoriality postulated by Dietz (1984), but possibly the tightness of boundaries varies.

The use of a water hole near the range boundary by adults of more than one pair, in the drought years of 2002–2003 (Figure 1.8), suggests that the need for water outweighed territorial imperatives. However, we know nothing of the family relationships or ranges of the interlopers, as we could not trap near the water hole until late 2004, when we opened a 4 km access road. All MW subsequently detected there were members of the North Range family (Chapter 5).

The movements of old male M6 in his final months show no territory, and he appears to have been seeking a place of refuge. He moved between the territories of at least three pairs. He would stay some days in a small area then move to another for up to two weeks. He returned repeatedly to his zone of capture then left quickly again for fringe areas unused by other tagged MW. A reproductive pair or two occupied the savanna across the river into which he briefly made long excursions. His final return to the territory of male M5 coincided with rising waters that flooded all of his recent haunts. Gray wolves (*Canis lupus*) commonly kill interlopers on their territories, and intergroup conflict is a major source of mortality (Vucetich and Peterson, 2004). M6 died two days after meeting M5, but he had moved little in the previous two weeks (penultimate sample, 3.4 km^2; final sample, 2.3 km^2). We cannot know whether they fought, and M5 killed him, but M6's skeleton showed severe dental and bone disease (Chapter 6) and no obvious bite marks. In the other case of overlapping adult males, M5 was on M2's territory from time to time a few months before the latter died, and both males used the water hole. As neither had GPS collars, their interactions are unknown.

This pair of events implies that adult males do not kill other males for territorial acquisition, because in both cases, younger males on the territories had months in which to kill the old males, yet they did not do so, or vice versa. Mateless old males may be able to defend small personal spaces and/or do not represent a threat worth the risk of injury to younger territorial males. Both old males died before the normal reproductive season, when extra-pair mating could become an issue (Chapter 6). We recorded no case of a reproductive female tolerating an older, unpaired female on her territory. Despite cases of range infringement by outsiders, the reproductive pair is certainly the territorial unit, as further discussed in Chapter 5. Because it is rare to observe the fates of secretive mammals at the ends of their lives, these examples give a small glimpse into what are surely complex relationships that develop over the lifetimes of the MW.

4

Variation in Diet and Resources

José Miguel Castro and Louise H. Emmons

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; "lobeira" 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 cavies (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 (MNK); from the literature; and by consultation with specialists. We generally follow the mammal taxonomy of

Wilson and Reeder (2005) and for Caviidae, of Dunnum 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.Vásquez and Ibisch. 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 × $M^{0.64}$ kJ/d, which for MW would be 1,205 kcal/d, or near the low end given by Barboza et al. (1994), of 501 kJ × $kg^{0.75}$ 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) (Goszczynski, 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 cavies 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 cavies, 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	Cavies	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.

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

(*continued*)

TABLE 4.3. *Continued*

	Wet season (15)			Dry season (93)			Percent of total biomass consumed
Food Item	*N*	FO	Percent of scats	*N*	FO	Percent of scats	
Mammals							
Euryoryzomys nitidus	2	0.031	13.3	10	0.021	10.75	1.93
Cerradomys maracajuensis	–	–	–	6	0.013	6.452	0.90
Cerradomys scotti	1	0.015	6.7	7	0.015	7.527	1.62
Akodon sp.	1	0.015	6.7	3	0.006	3.226	0.44
Didelphidae							
Gracilinanus agilis	1	0.015	6.7	4	0.009	4.301	0.27
Marmosa murina	–	–	–	1	0.002	1.075	0.09
Indet.	3	0.046	20	31	0.067	33.33	5.29
Cervidae							
Blastocerus dichotomus	–	–	–	2	0.004	2.151	17.19
Canidae							
Chrysocyon brachyurus	–	–	–	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							
Typhlops sp.	–	–	–	7	0.015	7.527	0.21
Teidae	–	–	–	8	0.017	8.602	0.39
Colubridae	–	–	–	4	0.009	4.301	0.56
Mabuya sp.	–	–	–	2	0.004	2.151	0.05
Boa constrictor	–	–	–	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
Cucurlionidae	–	–	–	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*

	Wet season (15)			Dry season (93)			
Food Item	*N*	FO	Percent of scats	*N*	FO	Percent of scats	Percent of total biomass consumed
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, *N* (65)	32	19	4	0	0	10
Percent frequency	49	29	6	0	0	15
Dry season, *N* (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 cavies 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 cavies, and most also included dermal bones of armadillos (*Dasypus* spp.). She saw many cavies and collected a voucher specimen (Emmons, 2000a). Cavies were thus a mainstay of MW for at least the decade prior to our study. Both cavies 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, cavies were not trapped after 2003. Contents of scats showed that cavies 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 cavies 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 cavies 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 cavies were recorded, in both 2001 and 2007 (Figure 4.1B); however, the rank correlations are not significant for these series.

In the absence of cavies, 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,

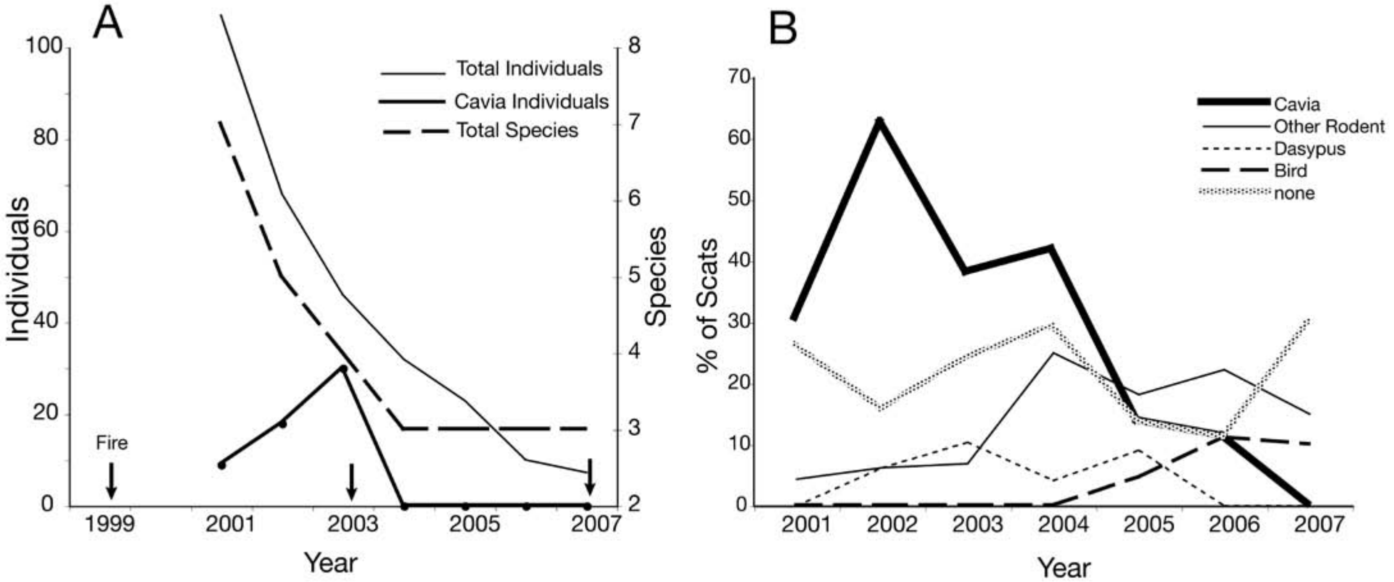

FIGURE 4.1. (A) Rodent captures over 7 years on trapping plot PA in nonflooded habitat in Los Fierros savanna, per 1000 trap nights in yearly samples. Total individuals (thin line), total species (broken line), and individuals of *Cavia aperea* (heavy line). Arrows indicate years when the plot burned. 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

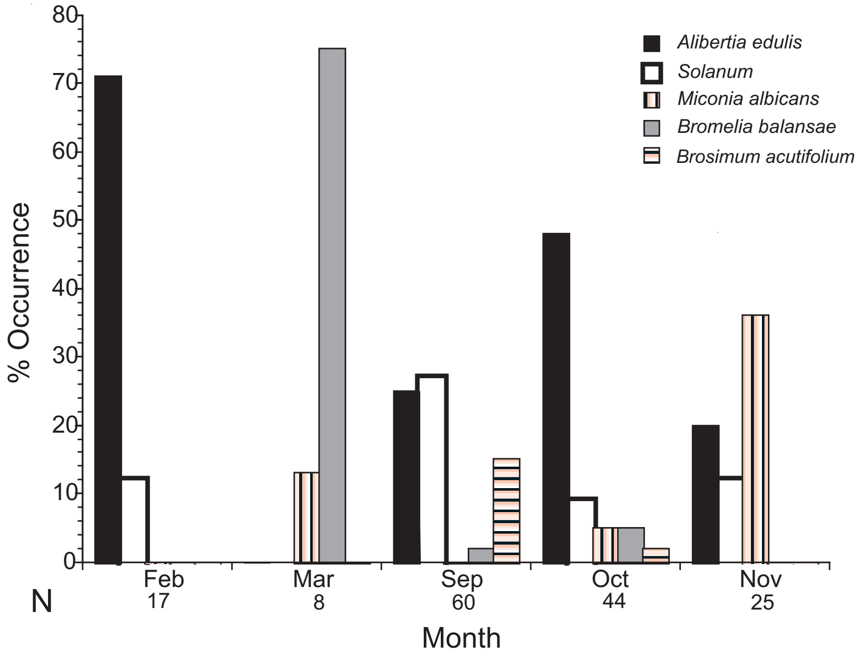

FIGURE 4.2. Percent of total scats in which the dominant six fruits occurred from 2001–2007, by month. Number below month is number of scats examined. Only seven months are represented.

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.

	Percent of scats						
Species	**2001***	**2002**	**2003**	**2004**	**2005***	**2006**	**2007**
Alibertia edulis	45	4	30	17	74	58	24
Solanum gomphodes	7	4	0	22	0	42	76
Brosimum acutifolium	0	0	0	11	32	0	24
Annonaceae all species	0	19	0	0	0	42	35
Miconia albicans	17	19	0	0	5	0	0
Cecropia sp.	0	0	20	11	0	0	0
Bromelia ignaciana	0	12	0	0	0	0	0
Discoid seed indet.	0	0	0	17	0	0	0
Emmotum nitens	0	0	0	0	0	8	6
Hancornia speciosa	0	4	0	0	5	0	0
Chrysophyllum sp.	0	0	0	0	0	8	0
Anacardium sp.	0	4	0	0	0	0	0
Astrocaryum sp	0	4	0	0	0	0	0
Dipteryx alata	0	0	0	0	0	8	0
Fabaceae	0	0	0	0	0	0	6
Ficus sp.	0	0	0	0	0	0	6
Vismia	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
N	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						
*Alibertia edulis**	30	60	18	1.31	43.89	87.78
Genipa americana	130	81.7	106.2	0.22	7.44	14.88
Solanum gomphodes†	300	41.1	124.2	0.19	6.36	12.72
Bromelia ignaciana	18.3	51	9.2	2.57	85.87	171.74
Annona coriacea	218	n/a	n/a	n/a	n/a	n/a
Hancornia speciosa	30	60	18	1.31	43.89	87.78
Annona crassiflora	650	52	532	0.04	1.48	2.97
Psidium guajava	45	64	29	0.81	27.24	54.48
Animal Prey						
Dasypus septemcinctus‡	1500	201	3015	0.008	0.26	0.52
Cavia aperea§	300	216.7	651	0.04	1.21	2.43
Proechimys longicaudatus§	250	200	500	0.05	1.58	3.16
Necromys lenguarum¶	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 × 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 × 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 km^2 (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, $p \leq 0.03$). Coincident with the decline in rodent biomass was a fire that burned half of the northern savanna in 2003. This

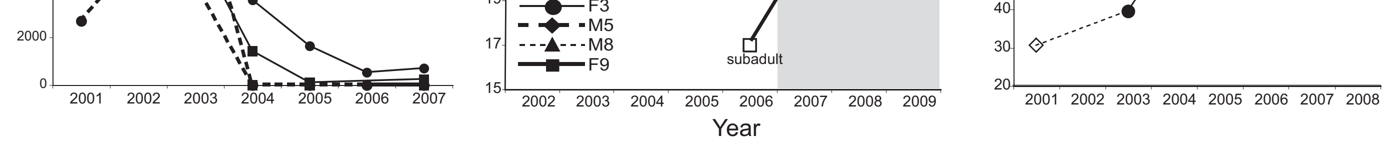

FIGURE 4.3. Rodent biomass and maned wolf weights and range sizes. (A) Biomass of rodents captured in 1000 trap nights on two trapping plots on the North Range (solid lines) and biomass of cavies (broken lines) on each plot. Plot PT (square symbols) was not trapped in 2002 or 2006. Biomass estimated 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 voucher any *Galea* presence at Los Fierros. *Galea* spp. live in burrows that could shelter them from fires (J. Dunnum, 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 *Dasypus 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 (*Blastocerus 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,

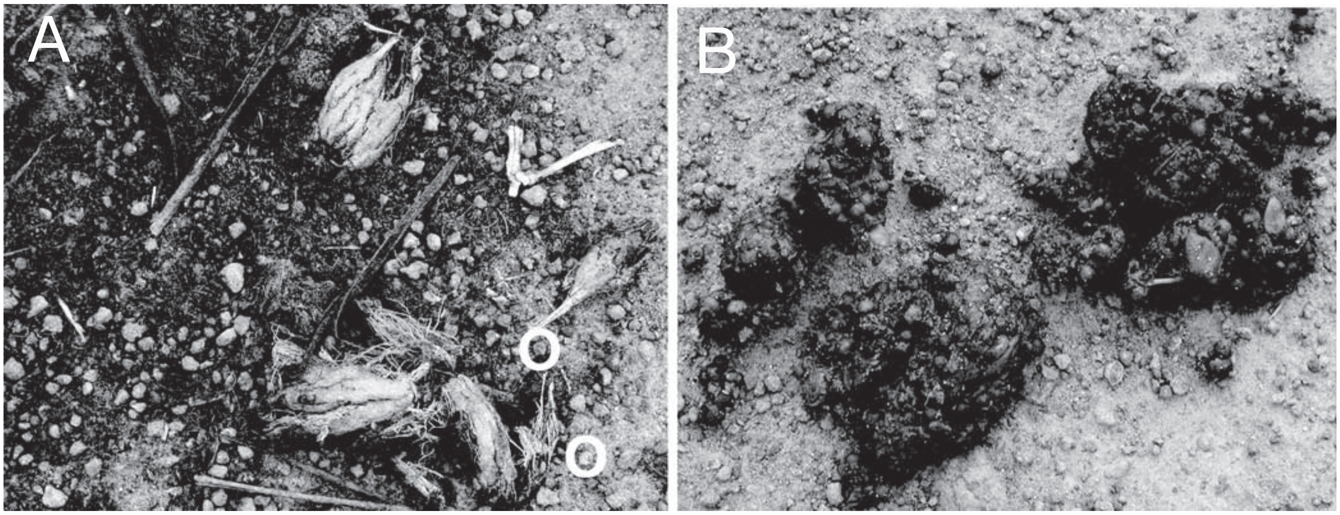

FIGURE 4.6. Fruits in maned wolf scats on road. (A) *Bromelia ignaciana*, crushed fruits, and rodent foot in old, rain-washed scat; two bromeliad seeds are circled. (B) *Miconia albicans* (nearly whole berries) and *Duguetia* sp. (leaf-shaped sheaths and isolated seed on right below mass).

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 *Dasypus 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 km^2 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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5

Social Interactions and Reproduction

Louise H. Emmons, Verónica Chávez, Luis Fernando Del Aguila, Sixto Angulo, and Matthew J. Muir

ABSTRACT. Social interactions of a small population of maned wolves in Parque Nacional Noel Kempff Mercado, Bolivia, were studied by radio telemetry for over eight years. Reproductive pairs co-occupied exclusive territories. Outside of reproductive periods, members of adult pairs on a territory rarely traveled together or met for long enough to be recorded by hourly GPS fixes. An exception was a young pair that met on 55% of all days during three months, traveling together for an average of 7.6 hours when they met. Members of family groups with young often met or interacted vocally. Two young females remained on the natal territory with the parents as presumed "helpers" and inherited the territory upon the death of their mothers. Another female helper was replaced by a younger one, and we recorded only single female helpers. Young males and other females seemed to emigrate when over a year old. Females were the holders of territories into which males moved to form pairs and possibly females are the dominant sex.

INTRODUCTION

The first important account of maned wolf social behavior was by Dietz (1984), who combined radio telemetry of free-living animals in Brazil with observations of captive animals in large enclosures at the National Zoological Park (Smithsonian). He described maned wolves (MW) as monogamous canids in which reproductive pairs share territories but seldom meet during their activities (Dietz, 1984). In the next two decades, Dietz' conclusions were generally confirmed by VHF telemetry studies, but without additional insights on maned wolf social organization (Jácomo et al., 2009; Juarez and Marinho-Filho, 2002; Rodrigues, 2002). More recently, a GPS telemetry study contributed the first data on *in situ* interindividual interactions (Melo et al., 2007). For six months, Melo et al. followed a single pair and a young female that shared the same home range while the pair raised a litter (Melo et al., 2007). Subsequently, they observed care of young *in situ* (Melo et al., 2009).

We studied the behavioral ecology of MW for nine years on a small savanna in undisturbed, flood-prone habitat in Noel Kempff Mercado National Park

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(NKP), Bolivia. Our goals were to learn how free-living MW interact with each other at different stages of their lives and to fit their social organization into the vista of their ecology and conservation. We began by following MW on foot with VHS telemetry but later switched to GPS telemetry, which allowed us to follow pairs simultaneously throughout nearly all months of the year, and to follow a few individuals for most of their lives.

GPS telemetry produces accurate and objective arrays of location points (fixes) on a geographic information system (GIS) map. When we followed a focal maned wolf on foot, triangulating with VHF telemetry, our location data were imprecise, but we took coordinates all night and knew from their signals the proximities of other collared individuals. By physically following them across the landscape in real time, hearing their calls, and once in a while glimpsing them, we gained different insights into their behaviors and interactions than those that can be extrapolated from GPS locations mapped months after the events.

Materials and Methods

Study Site and Field Methods

We followed MW by radio telemetry from October 2001 to October 2011, in the small Los Fierros savanna of NKP. The climate and habitats of the study area, and trapping and handling methods for MW, are described in Chapter 1. The key feature of the habitat is that much of the savanna is flood prone from late January to May. The northern part (“termite” savanna) floods with shallow water, and the southern part (“bajío”) fills with water too deep for MW to occupy at that season (Chapter 1) and takes longer to dry. In a seasonal reverse, no surface water may be available on the northern savanna from mid-August to October, when water becomes a strong attractor for MW (Chapters 2, 3). The vegetation is dense, and we rarely saw the animals. To monitor marked and unmarked individuals, we set camera traps at water holes and along roads. For field and photo recognition, telemetry collars and ear tags were marked with colored reflective tape (Frontispiece).

All adults and subadults over 20 kg in mass were fitted with radio collars, for a total of 28 collar deployments on 10 individuals (Chapter 1, Table 1.3). In 2001–2002, three MW carried VHF collars, but from 2003–2009, all but two subadults and one adult carried archival GPS collars. From 2001 to 2004 we trapped MW on the northern part of the pampa, and from 2005–2010 we trapped in all territories. Our on-foot VHF following was limited to October 2001 through September 2003, when we followed adult resident M2 and subadults M4 and F3, and to six nights in October–November 2005, when we followed M8 (Mx, males; Fx, females). We used VHF signals to locate MW throughout the study: on foot, from vehicle roof, or by climbing trees; and we chartered light aircraft to search for missing signals. When we followed MW on foot, we kept silent, well out of sight, and behind them, so as to avoid influencing their behavior. If one was near, we turned off our light and sat still until it moved away. We attempted to follow VHF-tagged animals for complete nights, with three bearings taken for a fix each 20 min, as close in time as we were able to (sit for 10 min, take bearings 10 min, etc.), but when they traveled, we walked continuously to keep up, taking bearings each 100 or 200 m. Meetings between VHF-collared animals were defined as distances of <100 m between locations (as with GPS data), but we could also identify them in real time, when we noted bearings of collar frequencies converge until the bearings coincided, with equal signal amplitude.

We quantified calling behavior as we followed MW on foot, by noting the numbers of calls, the bearings of calls and answering calls; and the identities of callers from VHF collar frequencies. Calls of young were recognizable by their higher pitch, and to us, several MW had clearly distinguishable voices, although we did not use this for identification without confirmation from associated radio frequencies.

The GPS collars were programmed to take synchronous locations for all collared individuals. To explore movements in detail, the first three GPS deployments took fixes half-hourly, except around midday (2003–2004). After 2005, all collars were scheduled to take hourly fixes, in three-night weekly samples. Early collars were shut off around midday to save battery life, but recent improved technology has permitted complete, 72 hour (72 fix) weekly samples. Functioning collars with the latter schedules took from 10 to 14 months of data. Repeated GPS collar failures prevented the success of many attempts to get complete reproductive behavior of pairs. Study animals were recaptured approximately yearly and the collars exchanged, and each discontinuous collar deployment is treated as one data set. Collar deployments and schedules are listed in Chapter 1 (Table 1.3).

We captured six immature animals, all in September and October. It was difficult to estimate the exact ages of these “subadults,” which were characterized by lack of tooth wear, small size, and nonreproductive state, as well as by subjective traits (high pitch of barks, lack of odor, slender build, and timid behavior). With a growth curve generated from captive bred animals (Smithsonian Conservation Biology Institute; M. Rodden, pers. comm.), we interpolated the weights of the six youngsters, and backdated them to estimated birth months. At 17–24 kg, with full dentition (achieved at 7–8 months; Maned Wolf Species Survival Plan, 2007), these young corresponded in weight to 7–10 months-old *ex situ* youngsters. Other evidence, including dates of sightings of pups (3–4 months old), condition of the presumed mother, and slightly more tooth wear, suggested that the two heaviest youngsters were older than predicted by body weight alone (thinner than same-age captives), likely 14–18 months.

Data Analysis

With simultaneous GPS locations, we measured the proximity between pairs of animals at each fix time. We classify an interanimal distance of <100 m as an encounter (meeting), so as to capture a time window when animals were moving together or apart. From the average maned wolf movement rate between hourly fixes (Chapter 2), 100 m represents only 6.3 min (Table 5.1) or 3.2 min from a contact between two MW to a separation of 100 m if they go in opposite directions. Only encounters of longer than the interfix interval (30 or 60 min) were certain to be recorded. Because the duration of an encounter could be measured only in increments longer than an interfix interval, averages of time spent together were by definition averages of the minimum time animals were in proximity (if animals were together 1.8 hours, hourly fixes would show them as together for one hour).

To compare the proximity of maned wolf pairs to that expected from a random distribution of points for each data set of a male-female pair tracked synchronously, the temporal order of the actual locations of each animal was randomized, by randomizing the sequence number of each fix (fix ids), pasting it into the data set, and resorting it into numerical order. The distances between the two location sets were measured in the order that they were in after randomization (distance from fix 1 to fix 1, 2 to 2, . . . , *N* in each set). Using the same locations inserts a possible bias into the data, because animals might preferentially use particular areas of the home range because the other animal was likely to be present. For comparison, we also generated two shapefiles of random points within the home range polygon of each data set, each with the same number of points as there were synchronous acquired fixes for the pair. We then measured the distances between the two sets of random points. Because use of the home range is highly nonuniform (50% of fixes are in 20% of the area; Table 3.1, Chapter 3), the degree of "random" proximity is much less by this method (because the fixes are distributed on the whole home range, rather than concentrated as the animals actually used it). The first method is the most likely to overestimate random encounters and therefore is a more stringent comparison, and we use it below.

RESULTS

PAIR FORMATION AND TERRITORY ACQUISITION

We followed one or both members of five resident adult pair combinations by GPS telemetry, but we acquired

TABLE 5.1. Adult resident pairs for which synchronous GPS data sets were acquired, with dates, number of acquired synchronous fixes for the pair, schedules of collars, the average distance that females moved between successive fixes while active in those data sets, and the size of the home range during those data sets. Collars of F11 and M8 were not well synchronized, that of F11 took fixes only from 1600 to 1000 hours on the following date for part of the set. Here n/a, not applicable.

Pair	Data start	Data end	Fixes	Days	GPS schedule		Distance between successive fixes, m	Home range, km^2
F3/M5	9 Oct 04	7 Jan 05	2712	91	Half hourly	Continuous	620	74.1
F3/M5*	Same	Same	1596	91	Hourly	Same	985	Same
F3/M5	6 Oct 05	13 Jul 06	2707	274	Hourly	3 days/week	797	75.2
F3/M5	4 Oct 07	22 Nov 07	472	27	Hourly	3 days/week	908	76.6
F11/M8	25 Jul 07	26 Sep 07	456	64	Hourly	3 days/week	977	65.5
F3/M8	16 Jul 08	18 Oct 08	728	94	Hourly	3 days/week	1022	66.5

*The same as the previous data set but including only hourly fixes for comparability with other data. The short distance between successive fixes in the first data set is because there were twice as many fixes per hour.

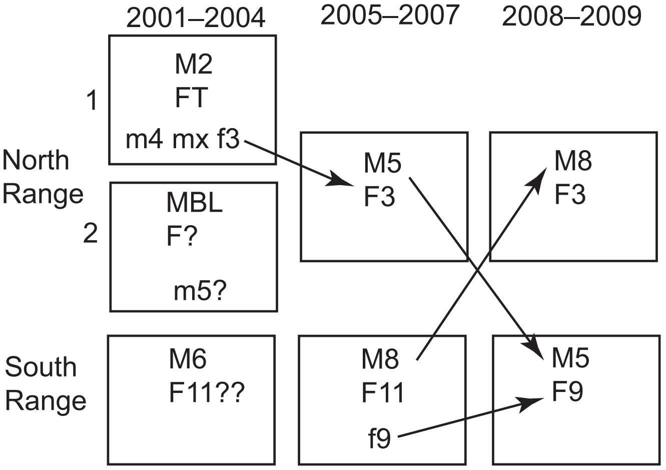

FIGURE 5.1. Schematic outline of maned wolf pairs followed and their locations in the study area. The two territories on the North Range merged in late 2004/early 2005 (Chapters 3, 4). Lowercase letters (f3) indicate subadults. FT was seen, but not captured.

synchronous fixes for only two males (M5, M8) and three females (F3, F9, F11), in five data sets. Three male-female combinations were followed for a total of 95 weeks (Table 5.1). Other pair members were not captured the same year or yielded no useful telemetry data. A male of a reproductive pair, M2, was followed only by VHF, along with two youngsters of his family (F3, M4). From 2001 to 2004, there were three territories on the Los Fierros savanna, which became reduced to two after 2004 (Chapters 3, 4) and then to one in 2010–2011. Adult pairs on our study area occupied exclusive territories with sharp interpair boundaries (Chapter 3). The individuals and spatial arrangements of resident adults changed several times (Figure 5.1).

We recorded three cases of new pair formation. Female F3 was a nulliparous subadult–young adult on North Range 1 in 2002, when it was occupied by adult pair M2–FT (FT was not captured, but we saw and photographed this grizzled maned wolf for over a year). F3 had many interactions with M2, her presumed father. She was of full body length and had almost no tooth wear. She at first used a small area (13 km^2) within North Range1 that over a year expanded to 50 km^2 (Figure 5.2A). A litter born

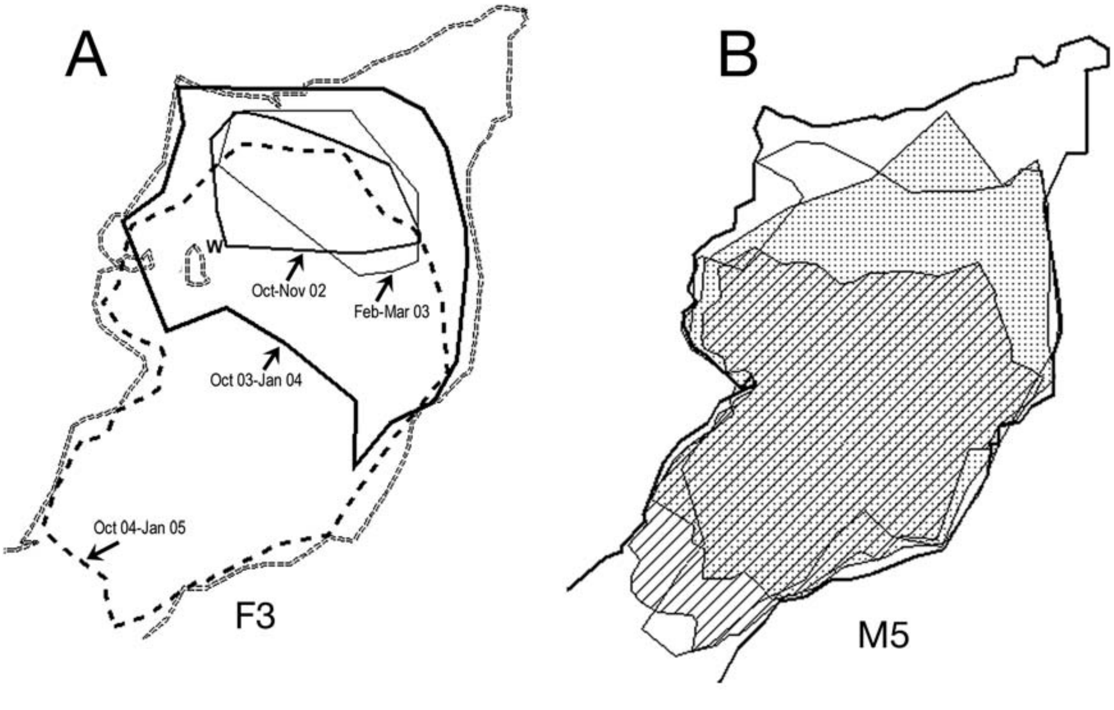

FIGURE 5.2. (A) Range expansion of F3 from subadult in 2002 (20.4 km^2 99% kernel home range [KHR]) to "helper" using full parental range (North Range 1) in October 2003 (52.3 km^2 99% KHR) and to breeding territorial adult using combined North Ranges in October 2004 (75.2 km^2). Double broken line is the LF savanna outline, W is PM water hole. (B) Range shifts of M5 to coincide with F3; 2004–2005, diagonal lines; 2005–2006, stipple; 2007–2008, no shading.

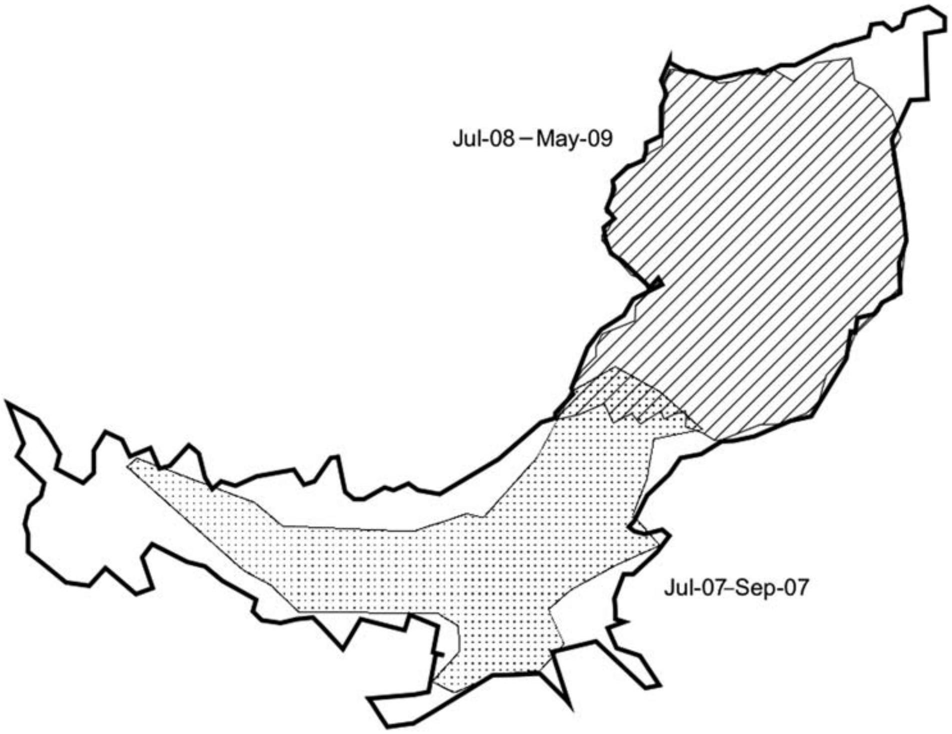

FIGURE 5.3. Switch of M8 from South Range (with F11) to North Range (with F3), note that boundary remained nearly the same.

on North Range 1 in about March 2003 was seen in May (three pups) and July (two pups), but mother and young had disappeared by October and were presumed dead. Adult male M2 was geriatric and also died in about January 2004. F3 was nulliparous in October 2003, when M5 was seen and photographed with her in North Range 1 (when M2 was alive there), although he chiefly occupied North Range 2 (Figure 3.5A). By October 2004, F3 and M5 had established as the adult resident pair on a single, larger, combined North Range territory (Figure 5.2B).

Subadult female F9 occupied the South Range territory with adult pair F11–M8. At first capture in September 2006, F9 was below adult size and too small for a telemetry collar (17 kg). In 2007 she was fitted with a VHF collar, followed in 2008 by a GPS collar. Females F9 and F11 were closely associated in 2007: they shared the same home range, rested near each other by day, and once were trapped side by side on the same night. The adult pair F11–M8 remained together with nulliparous F9 on the South Range until the death of F11 on 26 March 2008, but there was no evidence that any litter was born after 2006. By June 2008, M5, from the neighboring territory (with F3), had moved into the South Range with F9. Owing to GPS collar failures, the movements of M8 and F9 were not recorded until July 2008. By then males M5 and M8 had entirely switched territories, while the females remained where they had been, so that the North Range was now occupied by F3–M8 and the South Range by F9–M5 (Figures 5.1, 5.3). The new range boundaries of M8 were similar to the previous ones of M5 (Figures 5.1, 5.3). Thus, in one case on each range, one female young stayed on the natal territory until adulthood, as a nonbreeder, and when the adult female on that range died, she became the territorial resident, paired with a male from outside the range. Males moved into the territories where females were established on three occasions, but in the first case, the female also eventually expanded her own territory to encompass his former range as well as her own (Figure 5.2A; Chapter 4).

INTERACTIONS BETWEEN ADULT PAIRS: GPS TELEMETRY

In 2004–2005, the number of encounters between newly formed pair F3–M5 vastly exceeded that recorded in later years, both between this pair, and between all other male-female pairs (Tables 5.2, 5.3). In this 91 day data set,

TABLE 5.2. Numbers of fixes at different proximities of adult M-F pairs for complete data sets of synchronous fixes. The numbers of actual fixes within different distance categories, compared to those of the same set of points assorted randomly in time. Table 5.1 lists home range sizes during the data series. Number of synchronous fixes (*N*) is given in the column head.

F/M Proximity	Actual	Percent actual	Same fixes random	Percent random
A. F3/M5 Oct 2004–Jan 2005 (2712)				
0–50	326	12.02	2	0.1
50–100	160	5.90	7	0.3
100–300	129	4.76	21	0.8
300–1,000	162	5.97	169	6.2
B. F3/M5 Oct 2005–Jul 2006 (2707)				
0–50	158	5.8	0	0.0
50–100	9	0.3	3	0.1
100–300	40	1.5	14	0.5
300–1,000	163	6.0	83	3.1
C. F3/M5 Oct–Nov 2007 (472)				
0–50	0	0.0	0	0.0
50–100	0	0.0	1	0.2
100–300	8	1.7	6	1.3
300–1,000	37	7.8	23	4.9
D. F11/M8 July–Sept 2007 (456)				
0–50	0	0.0	1	0.2
50–100	1	0.2	0	0.0
100–300	1	0.2	4	0.9
300–1,000	22	4.8	20	4.4
E. F3/M8 July–Sept 2008 (728)				
0–50	1	0.1	0	0.0
50–100	14	1.9	1	0.1
100–300	25	3.4	7	1.0
300–1,000	90	12.4	27	3.7

F3 and M5 met on 55% of all nights, when they traveled together for long distances, for an average minimum of 7.6 hours spent together when they met (Table 5.2A, Figures 5.4, 5.5). The nights when they met were distributed across the three month sample. Their relative movement patterns showed that either F3 or M5 could deviate from a previous course to join that of the other. Before meeting, one would occasionally follow the other's exact path with a 30 min delay (the time between fixes), consistent with tracking by scent trail. The most common pattern of encounters (23 nights) was for the pair to meet late in the night and travel tightly together for some hours until after dawn, when they separated each to its own rest site (bed) at 0700–0800 hours (Figure 5.6). Thrice they spent 22–24 hours together, and on 9 days they bedded together ≤25 m apart (within the error of the GPS fixes). On seven other days they rested <100 m apart, but on most days (80 others), beds were far apart (2.46 km overall average).

TABLE 5.3. Frequency and duration of encounters of pair F3-M5, and the mean minimum time they were together if they met. In 2007, no fixes were <100 m apart, so <300 m is used as the criterion for meeting (weak/no evidence of association). For data set B we use calendar days instead of nights, because samples started and ended at 0000 hours because of a factory programming error (two whole and two half nights).

Data set	Percent fixes meet	Percent nights meet	Mean time together, hours
A. 2004–2005 (*N* < 100 m = 486)	17	55	7.6
B. 2005–2006 (*N* <100 m = 50)	6.2	16.5	13.9
C. 2007 (*N* < 300 m = 8)	1.7	18.5	0.6

After 2005, F3–M5 rarely were recorded meeting or traveling together outside of the period of estrus and pregnancy (Figure 5.4B). Likewise, pairs F3–M8 and F11–M8 scarcely met and never traveled together during the months when they were followed (Table 5.2D, E). Of the six meetings of F3–M5 in 2007, three were for single fixes and three for two fixes, or over an hour, and the two encounters (at <300 m) of F11–M8 were for single fixes of probability no greater than random (Table 5.2). In a different pattern, F3–M8 registered no fixes <100 m apart during late pregnancy and lactation (16 July 2008 to 18 September 2008), although they were often <300 m apart (Table 5.2D,E). After loss of their litter, they met on 5 days: on two of these, they bedded <100 m apart, and on one, they traveled near each other for about 3 hours.

We watched, from a blind at a water hole, F3 meet M5 for 10 minutes, and we saw F3 there three times that night. However, GPS fixes registered the closest pair proximity as 321 m, and no fix was at the water hole. The 100 m, proximity/time window that we define as encounters (see methods), strongly biases our recognition of proximity in favor of long meetings, but longer distances between maned wolf locations, of 100–300 m and 300–1000 m, occur at the

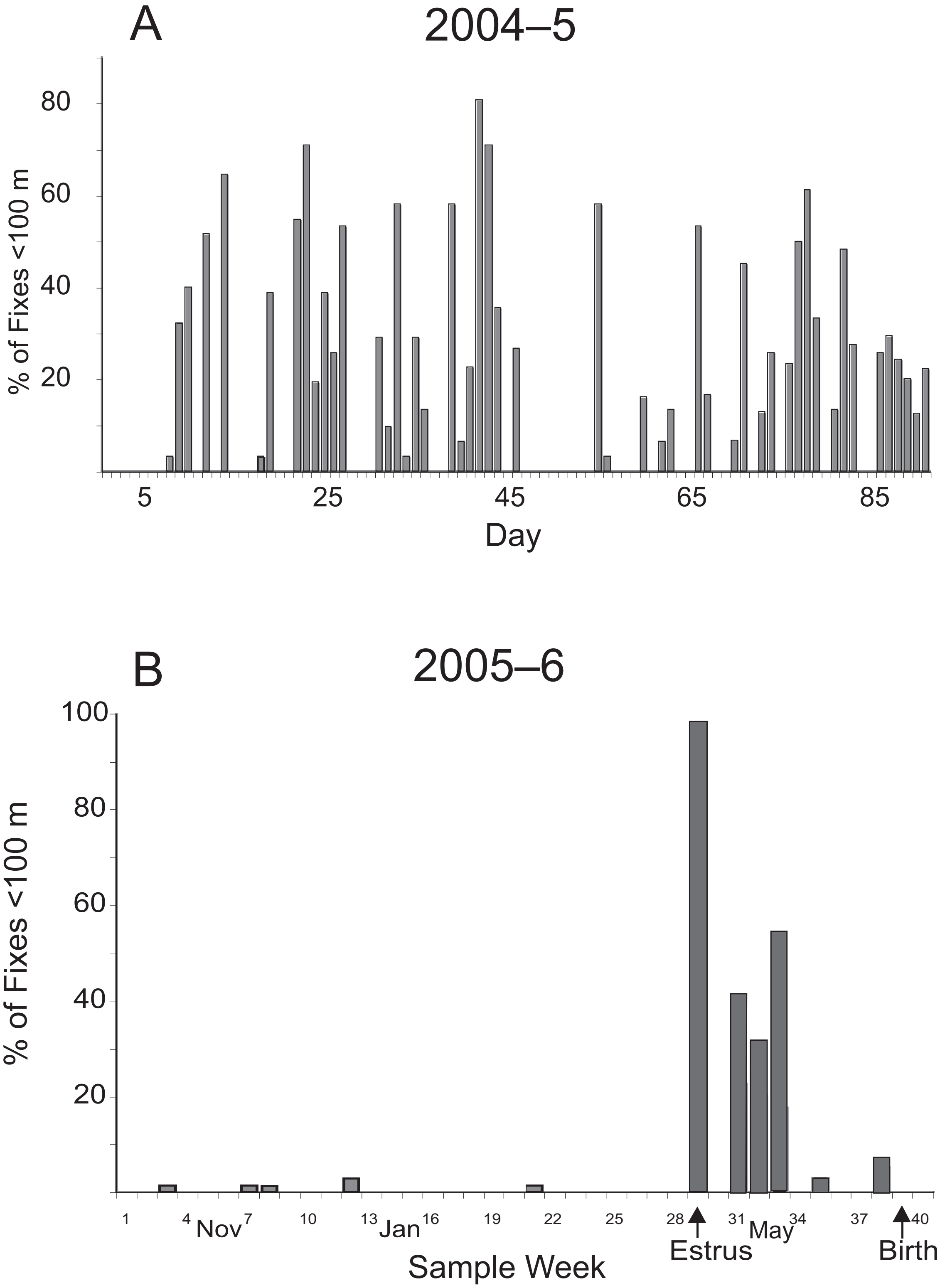

FIGURE 5.4. Percentage of total fixes during which F3 and M5 were <100 m apart. (A) During 91 days of continuous, half-hourly locations, 9 October 2004 to 7 January 2005 (2947 fixes). (B) During 3 day weekly samples of hourly fixes, over 10 months in 2005–2006. Note that the scales are different.

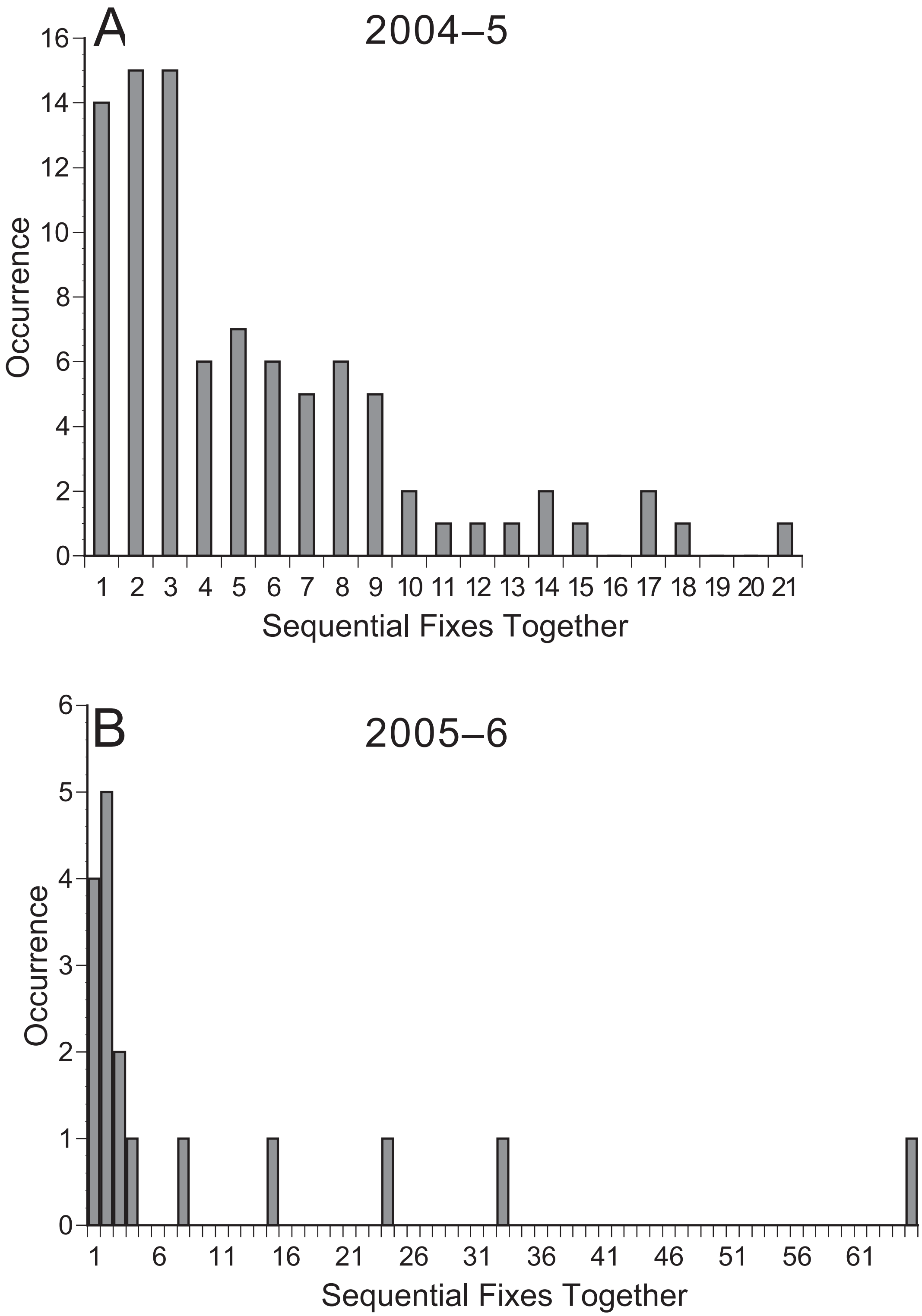

FIGURE 5.5. Distribution of minimum lengths of time (number of sequential fixes <100 m apart) that pair F3 and M5 were together. (A) Nights of a continuous 91 day series of half-hourly fixes, 9 October 2004 to 7 January 2005 (2947 fixes). (B) During the 15 meetings in the 2005–2006 data set. From the same meetings shown in Figure 5.4.

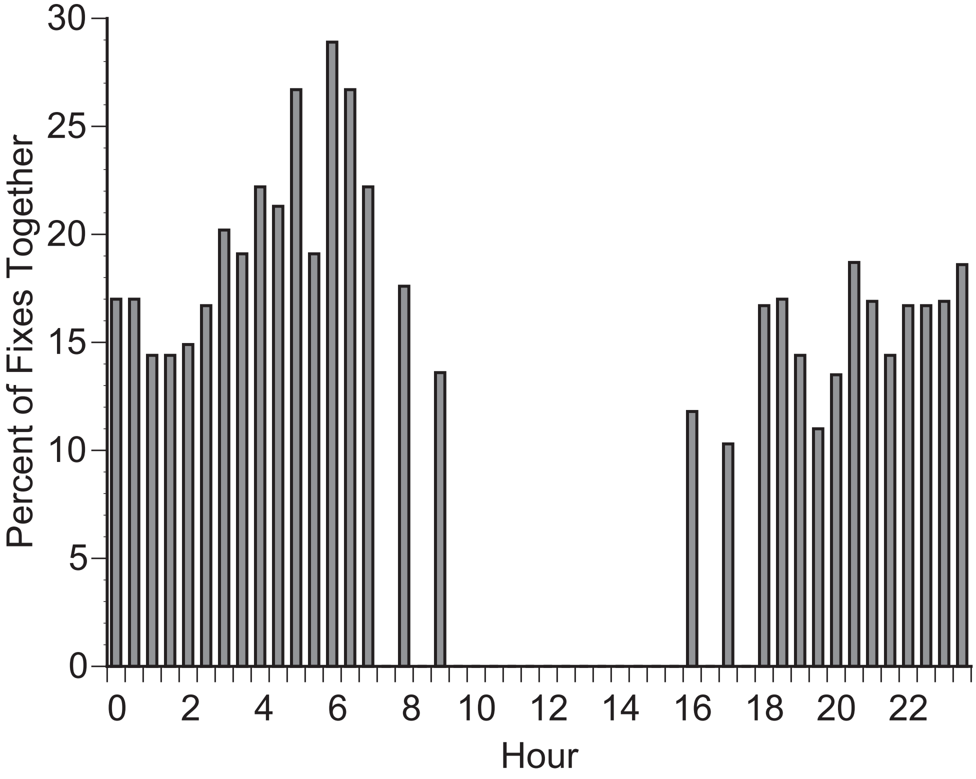

FIGURE 5.6. Hourly distribution of 326 synchronous locations of F3–M5 <50 m apart, during 91 days in 2004–2005, as a percentage of all locations at that distance. There were no data from 1100 to 1600 hours, but in this data set the animals usually were stationary during those hours (same location at 1000 and 1600 hours).

same frequencies in both actual and some random data sets (Table 5.2C, D), so we cannot justify expanding our definition to classify larger separations as "meetings."

Family-Group Social Interactions

Because we followed VHF-tagged animals nearly continuously, we were able to identify short meetings between MW with greater success than with hourly GPS fixes. Most of our on-foot VHF following was of members of a single family group, adult male M2 and subadults F3 and M4 of the North Range. At that time this group also included an unmarked adult female and a male littermate of M4. These MW met often, and each encountered all others (Table 5.4). We were never aware of agonistic interactions, heard no growling, nor noted MW chasing each other. There were more encounters between subadults F3 ($N = 13$) and M4 ($N = 12$) and others than between adult M2 and others ($N = 9$), but as F3 and M4 shared a smaller home range, they were more likely to meet. As the subadults aged, recorded meetings decreased (Table 5.4).

We saw a meeting of adults F3–M5 (from a blind), then paired for two years. Male M5 approached to 15 m behind F3 when she was at the water hole. She turned and walked toward M5, and as she approached, he lay down flat to the ground on his sternum, head down. As she reached him, M5 rolled onto his back, belly-up, while F3 stood straddling him, with her tail up, for several minutes. In this position, the pair played briefly by sparring with their mouths, calling with high-pitched whines. The posture of M5 was the classic canid "passive submission" display, linked with the classic "dominance" stance of F3 (Ewer, 1973).

Roar-Bark Vocalizations

MW communicate with explosive, deep-throated "roar-barks" (Kleiman, 1972) audible to us for hundreds

TABLE 5.4. Percent of nights (N) that maned wolves (MW) were recorded meeting during all-night on-foot VHF tracking of the North Range 1 family group, including adult male M2 and subadults M4 and F3. Monitoring was not always continuous, so records represent minimum numbers of encounters between MW.

		Percent of nights met		
Field dates	Nights followed	M4 and F3	M4 and M2	F3 and M2
Oct.–Dec. 2002	9	67 (6)	33 (3)	33 (3)
Jan.–Feb. 2003	24	8.3 (2)	4.2 (1)	8.3 (2)

TABLE 5.5. Summary of roar-bark calls heard during on-foot VHF radio tracking of the MW group on North Range 1. Some roar-barks were at our hearing limits, so answering calls are likely to be underestimated.

Dates	Total bouts	Total answered	Percent answered	Answered by 2–3 MW
Oct. 2001–March 2002	28	19	68	5
Sept. 2002–Feb. 2003	82	16	19	11
Total	110	35	31	16

TABLE 5.6. Roar-barks ascribed to individuals, September 2002–February 2003, when three of at least five MW present on North Range 1 were radio tagged. Number of bouts, and mean number of barks in each bout are provided. Initiators and answerers were identified by radio signals of appropriate frequency and strength from the azimuth of calls. One unmarked adult female, and one unmarked littermate of M4 were part of the family group. Here n/a, not applicable.

Initiator			Answerer			
	Mean no. barks	No. bouts	M2	F3	M4	Unknown
M2	8.1	13	–	2	0	0
F3	8.5	23	1	–	1	7
M4	11.4	13	0	3	–	2
Unknown	n/a	33	1	3	1	–

of meters but to MW perhaps across a home range. Most roar-barks occurred at night, when MW are most active (Chapter 2) and sound travels best in humid air, but once in a while, we heard barks by day (not quantified). Barks are given singly or in irregularly spaced series of up to 30, spaced 2–8 s or more apart (Dietz, 1984; Kleiman, 1972). Wide spacing of calls permits listening for replies, and our subjective impression was that callers often waited for a reply before calling again, thus alternating calls (Table 5.5). From October 2001 to February 2003, when two or three adults and two or three young were present, other MW answered in 31% of 110 calling bouts. Often, more than one answered, such that roar-barking was a group activity. Countercalling MW sometimes approached each other.

When three of at least five MW on North Range 1 were identifiable by telemetry (M2, M4, F3), 21% of 82 calling bouts were answered (Table 5.6). Subadult F3 both initiated and answered more calling bouts than did other known individuals. If M4 and his unmarked littermate brother initiated/answered equal numbers of calling bouts (13/2), then the unmarked reproductive female may have initiated the remaining 20 bouts, equivalent to F3. This hypothesis is supported by the scarcity of replies from unknown MW, if an unknown maned wolf initiated calling (we knew of only one unmarked male juvenile who could have answered). In September–October 2003, when there were no young on North Range 1, and the former reproductive female had disappeared, we noted no roar-barks during 6 nights of on-foot telemetry of F3 and M2. When we observed most of the tabulated calling behavior, the family group was far from a territorial boundary with other MW (3.5 km), and answering calls did not come from outside the territory. We never heard with certainty any countercalling between neighboring territories, but we cannot exclude it, as we could not localize far-distant calls.

There was a calling-fest of 37 roar-bark bouts on 4 November 2005, as we followed M8 all night on foot (South Range). A minimum of 6 MW were known to be on South Range at that time (M8, subadult F7, geriatric M6, at least two young pups, and presumably, their mother). Sixteen bouts were answered with countercalls from within the South Range: at least six were initiated by M8, three of these answered by a (high-voiced) pup; at least three were initiated by a pup, two of which were answered by M8; four bouts included at least three MW. M8 once approached a caller, another caller once approached M8 (countercalling until they were at the same bearing), and after hearing many roar-barks from a maned wolf that was following M8, we saw a three- to four-months-old pup trailing 100 m behind him. Barking was so frequent that it was hard to define discrete bouts or to decide which MW had initiated them. Barking was almost as frequent on the following two nights.

Reproductive Behavior and Seasonality

We followed female F3 throughout her reproductive life (Tables 5.7, 5.8). She was presumed born in July or August 2001 on the North Range 1, the daughter of M2–FT. After the death/disappearance of both FT (about August 2003) and M2 (January–February 2004), when she was about three years old, she became the resident adult, paired with male M5. She was still nulliparous in October 2004 and may have given birth to her first litter in February 2005 (no GPS record), for by October 2005, her mammae showed use (pigmented and elongated), but she was past lactation. M10 was a likely offspring of this litter, as his birth date, backdated from tooth wear and weight at capture, both suggested that birth month. Her first well-documented litter was born on 1 July 2006, when she was five years old (Table 5.8), and she had two to three more litters by 2008.

TABLE 5.7. Outline of known and presumed events of reproduction and presence of immature MW on the study area by year and territory. Nonparous females were first captured at 7–18 months old, as subadults, M10 was a young adult recorded in two territories. MX, unidentified male; FX, unidentified female; UX, unknown sex. Here n/a, not applicable or unknown. In 2010–2011 both ranges were occupied by a single pair.

Territory	Adult male	Adult female	Nonparous female	Immature male	Births
			North Range		
2001	M2	FT	"White tail"?	n/a	July
2002	M2	FT	F3	M4, MX	Feb.–March
2003	M2	n/a	F3	n/a	Feb.–March
2004 (Sept.)	M5	F3	none	none	none
2005	M5	F3	none	none	Feb.–March
2006	M5	F3	none	M10?	1 July
2007	M5	F3	F12, FX	MX	March?
2008	M8	F3	none?	none	30 July
2009	M8	F3	none	none	n/a?
			South Range		
2004	n/a	n/a	n/a	n/a	Feb.–March?
2005	M6, M8	F11	F7	none	July
2006	M8	F11	F9	M10	none?
2007	M8	F11	F9	none	June?*
2008	M5	F9	none	none	none
2009	none	F13	none	none	none
2010	UX	F13	none	none	October?†
2011	M14	F13	none	none	n/a

*F11 appeared to be postlactation (mammae with thin watery milk, 18 July), but continuous, February–July GPS trajectories indicate no point-focused behavior consistent with lactation, so she either lost a litter near birth or lactation resulted from pseudopregnancy.

†F13 was pregnant at capture 16 September, but GPS records do not indicate lactation, so she lost her litter or was pseudopregnant.

GPS telemetry recorded an estrous period. In three weekly samples from 7 to 23 April 2006, F3 and M5 registered no proximity <300 m. In the next sample, on 27–29 April, 65 of 66 sequential fixes of the pair were so tightly together that most were superimposed, with 63 locations <50 m apart while they traveled together for 16.4 km. In the following weekly sample (5–7 May) the pair did not meet (Figure 5.4). Calculated back from her 1 July parturition, 27–29 April corresponds to a 65 day gestation (Rodden et al., 2004). During this estrus, F3–M5 had slow and reduced movements, averaging only 145 m/h for the 72 hour sample, compared to an average of 432 m/h for F3 over all 41 weekly samples of the same data set. During estrus, the pair stayed near the South Range border, where there was another adult male.

On days 12–28 of pregnancy (11–27 May), F3–M5 traveled together continuously during large parts of three samples (Figure 5.4), logging bouts of 12, 4, 15, 2, 19, 5, and 33 sequential hours together; for 42% of the total sampling time (including three samples truncated by GPS shutoff). This chummy behavior abruptly ceased in June, when the pair was recorded together only thrice, but interestingly, two of these were in the 48 hours prior to parturition, when they met for bouts of three and two hours. They registered no other proximity through 13 July, at GPS failure for F3.

The prior year, 2004–2005, when the pair often traveled together during three months (Figure 5.4A), F3 was initially nulliparous. On the basis of the behavior in 2006, she may have been in estrus from 19 to 22 November (Figure 5.4; nights 42–44), when the pair were <100 m apart for 75% of 85 fixes and <300 m apart for 100% of simultaneous locations. Shortly after this, there was a gap of a week when they did not meet, but four weeks later, there was another period of extended meetings (Figure 5.4A). This partially mirrors the pattern during estrus and pregnancy in the following year, when there was a week of extended proximity two to four weeks after estrus (Figure 5.4B).

TABLE 5.8. Reproductive life of F3. Litter dates are backestimated from size of young (see Materials and Methods) and from records of their presence, reproductive state of F3 at capture, and preliminary genetic evidence of kinship. Two litters were born on known dates, and two were estimated from estimated ages of young captured as subadults. "Successful" indicates that at least one young lived to weaning. F3 ceased behavior consistent with lactation of the fourth litter about 18 days after parturition. Her fate was not known after 2008 as her collar was not recovered. NR, North Range; SR, South Range; n/a, not applicable or unknown.

F3 reproductive life	Date	Age	Birth interval	Fate of litter
Born on NR1 to M2-FT	July 2001*	0	n/a	n/a
First capture	Sept. 2002	1.2	n/a	n/a
First seen with M5	Sept. 2003	2.2	n/a	n/a
Territory with M5, NR	March–Sept. 2004	3	n/a	n/a
Birth first litter (young M10?)	Feb. 2005*	3.6	n/a	Successful?
Birth second litter with M5	1 July 2006	5	17 mo	Successful
Birth third litter (3 young weaned)	March 2007*	5.6	7 mo	Successful
Change male to M8	May 2008?	6.6	n/a	n/a
Birth of fourth litter with M8	30 July 2008	7	17 mo	Failed at 18 days
Last record, photos only	20 July 2009	8	n/a	n/a

*Date estimated. Possibly born in February 02. See discussion.

MATERNAL BEHAVIOR

Two parturitions of F3 were recorded by GPS telemetry, in July 2006 and July 2008. The first was signaled by a striking change to a den-centered behavior on the last day of a weekly 72 hour sample. On 1 July, F3 traveled 2.87 km to the pup den between 0500 and 0700 hours, after a normal night of travel (9.9 km) that included a rest at 0200–0300 hours (Figure 5.7). She then was present at the den at all hourly fixes for 15 hours, until GPS sampling ended at 2300 hours (Figure 5.7A). For 2 days prior to parturition she had no locations near that den site. During the following sample (6–8 July, pups 5–7 days old), her movements were characterized by 11 to 12 hour absences from the den, followed by abrupt return after long movements; then uninterrupted 10 to 14 hour stays at the den (Figure 5.7B). Only once, at 2200 hours on 7 July, did she return for a short visit to the den during her night's activity. The second parturition was quite similar: there was no evidence of a birth 23–26 July, but birth had evidently occurred by 1300 hours on 30 July, when the next GPS sample began. She may have given birth on that day, as she stayed in the den until after 2100 hours. As before, F3 spent the day at the den and left it at night, but in contrast to 2006, she returned to the pups once or twice during the night on six nights (Figure 5.8).

We have no data on litter sizes at birth, and none on maternal behavior beyond 16 days postpartum, but F3 was still abundantly lactating on 4 September 2006, two months after parturition. We saw pups of only three months old or older, with a maximum number of three.

PATERNAL BEHAVIOR

The male M5 registered no approach to either the pup den or to F3 during the three samples from birth of the young, to 15 days postpartum, when the GPS collar on F3 failed and we could no longer be certain of their location (Figure 5.9). However, at 4–6 weeks postpartum (August–September), M5 showed repeated, daily returns to a focal point near to the pupping den. If, as we think, M5 was then visiting the pups daily, they had moved about 150 m.

In contrast to the behavior of M5 after parturition, M8, newly resident with F3 in 2008, often visited the area of the pups in the days following birth (about 30 July). On each of 30 and 31 July, he came to the pup den at 2200 hours and on the next night at 0500 hours. F3 was absent at the first visit and present at the following two. In the next sample (6–9 August), he spent the whole day of 8 August 360 m from the pup den, and at 1700 hours approached to 160 m, where he stayed two hours. During

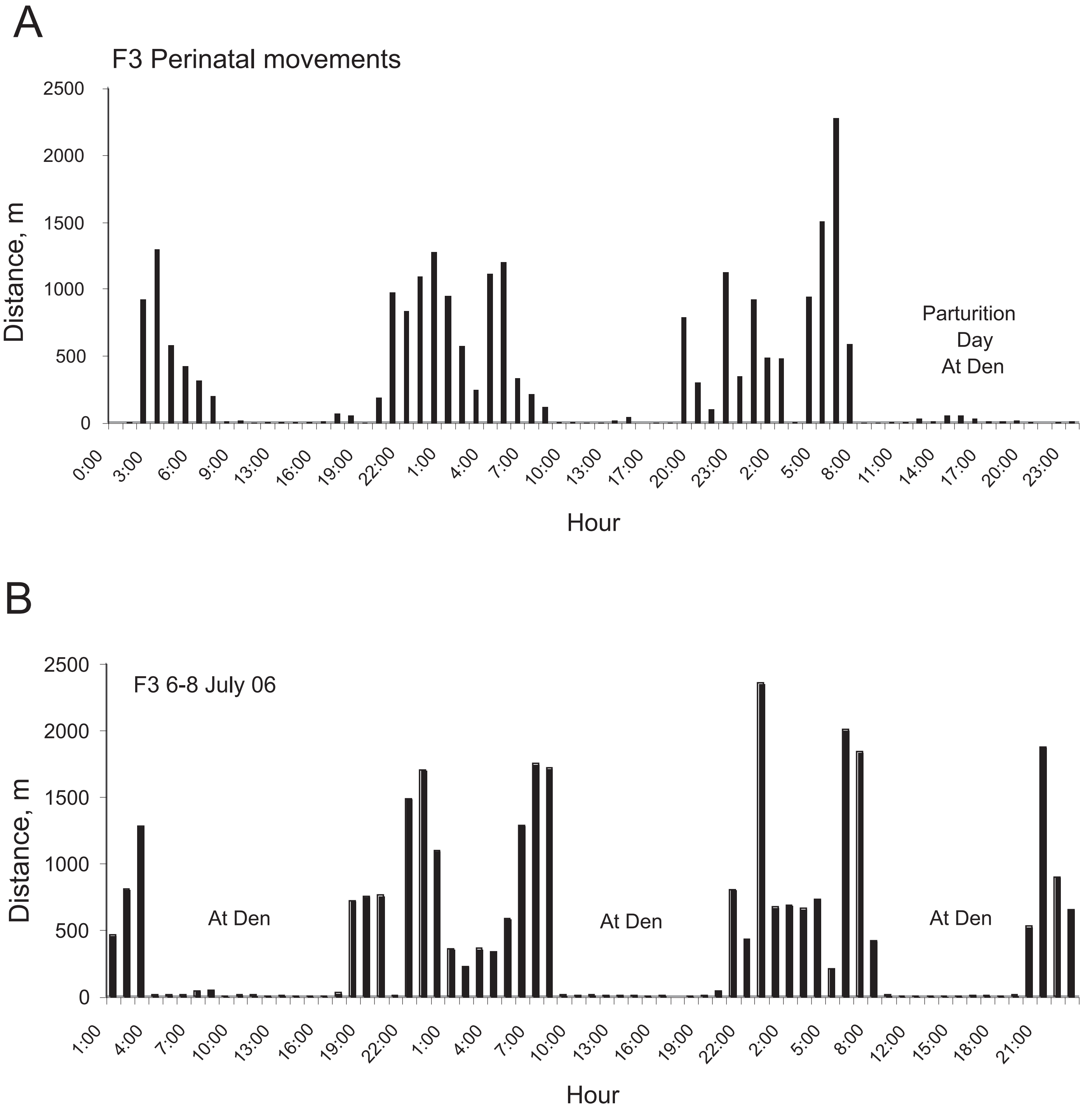

FIGURE 5.7. (A) Distance traveled between hourly fixes of F3 on the 2 days prior to and on the day of parturition (1 July 2006). (B) Movement pattern in the following sample (6–8 July) when she is at the pup den whenever inactive, including at 2200 hours on the second night.

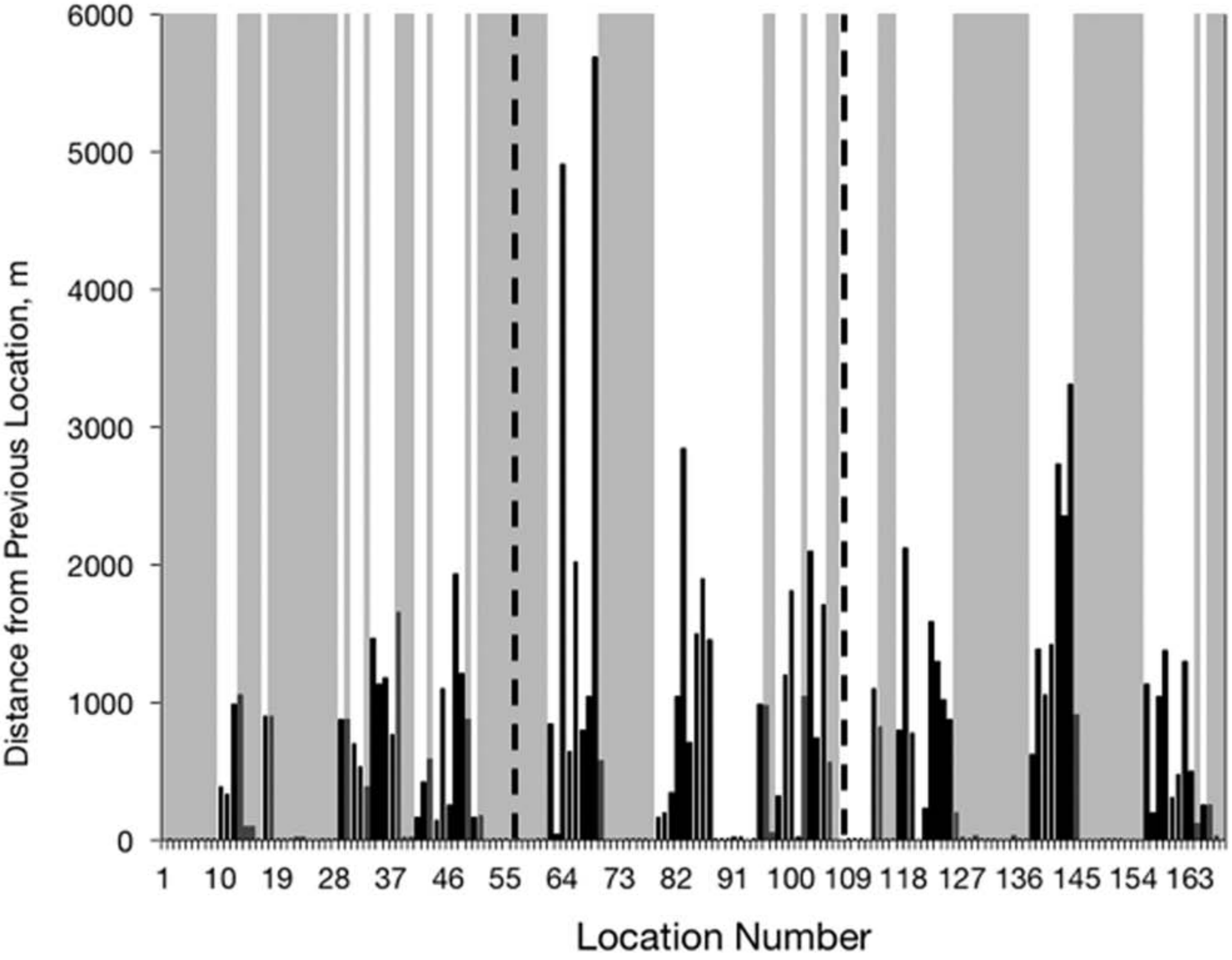

FIGURE 5.8. Entire recorded location record during lactation for F3 in July–August 2008. Gray bars are times in the pup den; black bars indicate the distance moved from the previous location. Broken lines indicate breaks between weekly samples: 30 July–2 August, 6–9 August, and 13–16 August. By the following sample on 20 August, all behavior indicating lactation had ceased.

the final sample (13–16 August), M8 rested 1 day at 760 m from the pups but was recorded no closer.

When we followed M2 by on-foot VHF tracking in March 2002, he showed strongly point-centered activity, a radical change of movement pattern that we ascribed to attendance on pups. He made long, direct travels to return repeatedly to the same site and spent the day there. He had frequent vocal interactions with an unmarked maned wolf in his territory. When one of us (LHE) went in to find M2 by day, she heard a low growl before the signal moved away. Nothing was visible in the dense, chest-high grass, and LHE left so as not to disturb pups. This was the only time a free maned wolf growled at our approach. The same month, tracks of small pups were seen with those of an adult.

Dispersal of Young

Of the six young captured in the study area, we know the lifetime fates of just two: females F3 and F9, who remained on their parental territories and inherited them at the deaths of their mothers. They stayed on those territories for their whole lives. In September 05, subadult female F7 occupied South Range along with adults and a litter of 3–4 month old pups. She disappeared by March–April 2006, at 12–18 months old. By September 2006, a new subadult, F9, now occupied the South Range, along with adults F11 and M8. Female F12 (North Range, too small to collar at capture October 2007), was not recorded the following year. Male M4 (VHF collar October 2002) and

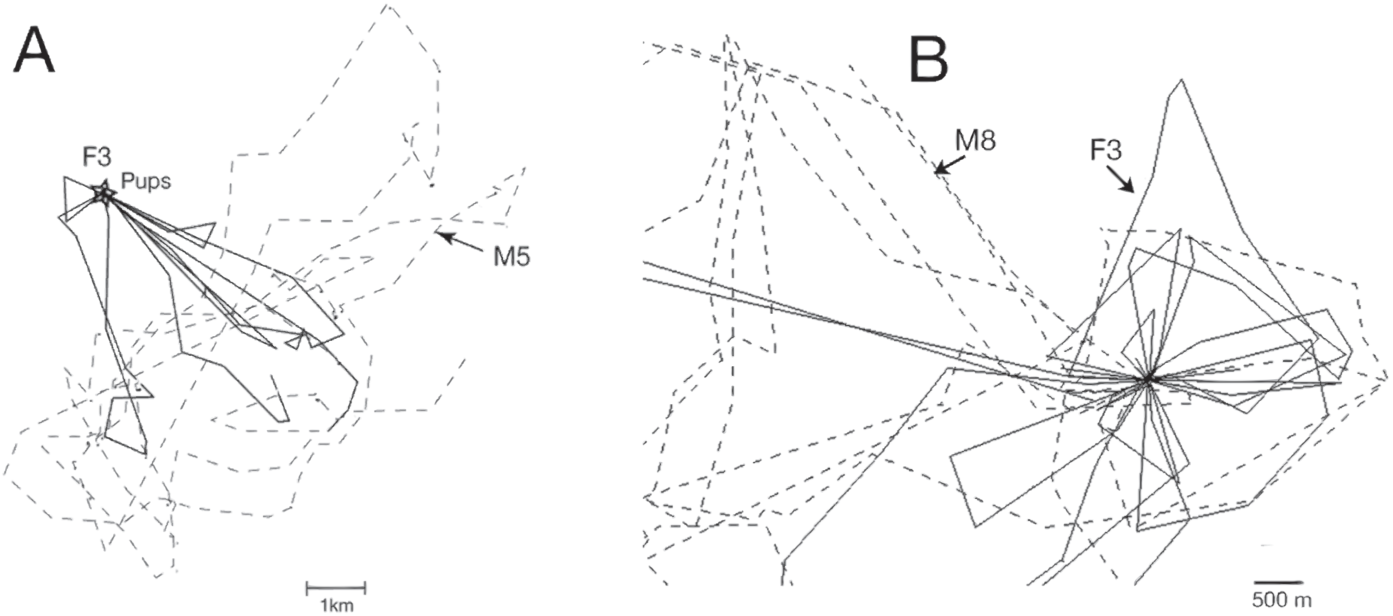

FIGURE 5.9. Movements of males M5 and M8, and female F3, following parturition. (A) Parturition 1 July 2006, movements 1 July to13 July. M5 did not approach the pups. Although the trajectories interdigitate, no simultaneous locations of F3–M5 were less than 300 m apart, and only four were within 1000 m, all distant from the den, and 8 days after birth; (B) Parturition about 30 July 2008, movements 30 July to 16 August. In this case, M8 visited the pups. Broken lines, trajectories of males; solid lines, trajectories of F3 radiating from pup den. Note that adults take different routes each night and that none are exactly repeated. Birth of young can immediately be identified by point-focused movements of the mother. Such focus never occurred otherwise (e.g., Chapter 3, Figure 3.1). Note the difference in scale.

his littermate brother disappeared from the natal territory between February and May 2003, at 12–18 months old. Another litter was born on that territory in about March, and the brothers had gone by June, presumably emigrating. Male M10, presumed from the first litter of F3–M5 (VHF collar, October 2006), was captured 2.5 km outside the parental territory at about 18 months old. He returned to the North Range, where he was located in December 2006 near the PM water hole. Aircraft search failed to locate him in February 2007, so he had apparently emigrated at 20–22 months old. No young males were recorded again after they had left the area, but one 2.5-year-old female (F13) may have returned from a neighboring estancia after death of a resident female (see Postscript).

DISCUSSION

Social Organization

As reported by other authors, MW at Los Fierros are socially monogamous, with pairs co-occupying territories in long-term relationships (Dietz, 1984; Rodden et al., 2004). However, pairs were not always lifelong, as we recorded males switching to pair with other females, in one case after the pair had been together for four years and produced multiple litters. We found variable amounts of association between maned wolf pairs and group members. Some appeared "solitary" as earlier reported (Dietz, 1984; Melo et al., 2007; Rodden et al., 2004): "The maned wolves of the Serra da Canastra led predominantly solitary existences. Wolves were never observed resting together, and they rarely traveled or hunted together" (Dietz, 1984:16). In contrast, we sometimes recorded more cohesive behavior, as reported by Melo et al. (2006) with a GPS-collared pair and subadult female: "During the night . . . the three individuals avoided contact with each other. However, during the day, the adult pair usually slept together and their juvenile slept within a few hundred meters of their location." (Melo et al., 2007:1). Unlike either Dietz (1984) or Melo et al. (2007), we recorded frequent nocturnal meetings between maned wolf family members when juveniles were present and when we followed them on foot with VHF. One GPS-collared pair without young also initially showed strongly cohesive behavior (F3–M5), but they greatly decreased their encounter rates between their first year together and the following years. We believe that many brief meetings are unrecorded when GPS locations are at hourly or greater intervals, thus leading to underestimation of intrapair sociality. The two-hourly interfix intervals used by Melo et al. (2007) may have failed to capture some nocturnal encounters between active MW.

During pregnancy, F3–M5 had episodes of prolonged proximity (Figure 5.4B). These may correspond to the large progesterone peaks recorded at about 5–7 days and 35–40 days postestrus, or to the sharp peak of estrogen at 20–30 days (Velloso et al., 1998). High female hormone levels perhaps trigger attraction between the pair. Unlike the pair followed by Melo et al. (2007), it was exceedingly rare for F3–M5, or any other pairs, to rest together by day (except during estrus), but exceptionally, during midpregnancy, the pair rested together on a third of days. Melo et al. (2007) began their study during a female's pregnancy, which perhaps contributed to their finding that a pair "slept together."

If the close association of F3–M5 when first paired (Figure 5.4A) was partly due to proestrus, estrus, and pregnancy, three months seems, nonetheless, far too long for reproduction to explain the whole duration of cohesiveness (Figure 5.4). As a new pair with a nulliparous female, perhaps close proximity was a male strategy to advance estrus though hormonal stimulation (DeMatteo et al., 2006). However, between 2004 and subsequent years, there was also a dramatic change in the prey resources and diet of MW in the study area (Chapter 4).

Another hypothesis for the unusual level of close cohesiveness in 2003–2004 is that this pair hunted cavies (*Cavia aperea*) cooperatively. White-toothed cavies do not burrow but shelter in tunnels under dense bunch grasses. Maned wolves could flush them or drive them toward each other, a tactic also perhaps possible with armadillos, which are large enough prey to share. Cavies sharply declined after 2004, then disappeared to zero in the diet after 2006, while armadillos did not appear after 2005 (Chapter 4; Emmons, 2009). Any cooperative hunting for these prey thus would have ceased. That either male or female could initiate contact (change its trajectory to join the other) may support this hypothesis, but unfortunately, we never saw the pair when they traveled together. The hypotheses are not mutually exclusive. Pair cohesiveness thus varied between pairs, years, and reproductive condition.

Parental Behavior

Maned wolf pairs cooperate to provision young (Bestelmeyer et al., 1996; Melo et al., 2009; Rasmussen and Tilson, 1984). Our brief data sets indicated that in one case the male did not interact at all with the newborn litter or their mother, but when the young were about a month old, he showed repeated, regular return to a focal area near the birth den, consistent with provisioning. In captivity, provisioning by regurgitation begins as nursing bouts decline at four weeks of age (Rodden et al., 2004), which matches our interpretation that M5 began to visit pups several weeks postpartum. In contrast, M8 (who had previously raised young successfully) started short visits in the week of parturition, and the second week twice rested by day near the pup den. After both births, the female spent most of each night away from the pups and all day with them. Melo et al. (2009) directly observed a pair attending a den with one pup. The male attended the mother and pup and provisioned the female, but he rarely visited when she was absent (Melo et al., 2009). Their observations (1700–0600 hours) showed both the female and male to spend a great many more nighttime hours at the den than we recorded (71% and 31%, respectively). These MW were fed daily with meat at a hotel, and the authors note that this might have both reduced the need to forage and accounted for the pattern of visits (return to pups immediately following feeding; Melo et al., 2009).

On the basis of the mother's behavior, the 2008 litter died at about 18 days of age. The male M8 had been with F3 on the territory for less than three months (M5 was there earlier). The possibility that the young were not fathered by M8 and that he killed them seems unlikely. He visited the pup den when the female was absent on the first day we recorded lactation, and he did not kill them then but continued to visit. Moreover, his visits declined the week before they died.

Vocal Communication

The only quantitative report of maned wolf calling behavior *in situ* is that of Dietz (1984), who heard maned wolf roar-barking 46 times during his two year study, with maximal calls (eight bouts) in August and zero to one bouts in March–May. Dietz' study wolves did not successfully raise young, but one litter was lost. We noted much higher levels of vocal interaction between group members than did Dietz (1984). Our data on roar-barking highlights calling as an intragroup activity that is most frequent when young are present and probably serves for within-group communication across the great distances of the home range. Countercallers sometimes converged, as if calls were used for finding group members. The rarity of calling when no young were on the territory, as noted both by ourselves and by Dietz (1984), suggests that calling is not primarily a between-group spacing signal associated with territorial behavior (Brady, 1981), although we do not rule out a territorial function. The most intense calling that we noted, involving three- to four-month-old pups and two or three adults may have been triggered by anxious, newly weaned pups beginning to forage alone, countercalling with their parents, sibs, and the female helper.

Dispersal of Young

We recorded only females to be philopatric, and we documented three cases of a single female young present beyond the birth of the next litter. In one, the young female (F7) was replaced the following year by another young female (F9); and in the other two (F3, F9), she acquired the maternal territory on the death/disappearance of her mother over a year later. There was a probable fourth case (2001), when an "extra" unmarked animal was seen and photographed several times near pups, but was gone and "replaced" by F3 the following year. Melo et al. (2007) likewise documented with GPS telemetry the presence of a young female with an adult pair and their litter. Their data suggest that the young female was a "helper" that guarded and/or provisioned the pups (Melo et al., 2007). It now seems certain that, as in all other large Canidae and many small ones (Macdonald et al., 2004a), young of MW can stay in the parental group beyond the birth of the next litter and likely assist in the care of younger siblings. Three male young dispersed from the study area at the estimated ages of 15–22 months old, but there is much ambiguity in birth dates. Another, present at 6 months, was likewise gone by 18 months.

The rare data so far point to helpers being female, being restricted to one, being common, but not obligatory, and sometimes remaining for only about two years. With small litter sizes (one to three), yearling female helpers may not always be available, and perhaps females stay on the natal range only until replaced by another yearling female. If so, it would be interesting to know the mechanism by which this occurs (does a mother drive out her older daughter when she has another? Does a daughter evaluate the chances of her mother's survival, and stay, or leave?). A helper may directly benefit a reproductive pair and her own inclusive fitness by increasing pup survivorship, and a mother could favor the survival of her matriline by allowing one daughter to remain, who if she dies, immediately acquires a full territory and optimal potential for reproduction.

The little available data suggest that MW are not long-lived, with a mean survival rate for all age groups of about 0.64 per year (Sollmann et al., 2009), but highly variable by year from 0.97 to 0.28 (Sollmann et al., 2010). In our study area, tooth wear, tooth loss, and tooth infections start to affect most individuals by the time they are about five (Chapter 6). All known mortality on our study area was "natural," and most occurred in the late wet season (January–April). Because the yearly probability of death is quite high, it could benefit a youngster to remain on the natal territory at least past the season of most likely liberation of territories by deaths of parents or neighbors.

The inheritance of territories by females, with males switching territories while females remained, and females apparently the helper sex, suggest that female MW are the socially dominant sex and the primary "owners" of territories. This was supported by our observation of F3 displaying dominance over a prone, belly-up, M5. Likewise, as a yearling, F3 was strong smelling and aggressive when trapped and initiated many calling bouts. As a youngster with a small home range, she marched prominently up and down the road depositing scats, as if participating in territorial behaviors. In contrast, young male M4 was odorless (to us) and whined like a pup when trapped, initiated half as many calling bouts, and kept more hidden from sight in the grass. Maned wolf males are only slightly larger than females (Dietz, 1984; Jácomo et al., 2009), with inconspicuous genitalia. The sexes were to us generally indistinguishable by sight or in lateral photographs (Frontispiece, Figure 8.1). The visual similarity between male and female MW may be a correlate of female dominance (or absence of male dominance), as it is in some other mammals (e.g., hyenas: Mills, 1989).

We lack a telemetry record of the intriguing switch of males after the death of F11, when neighboring M5 moved into the South Range territory to pair with F9, and M8 joined F3 on North Range (Figure 5.1). This double move obviously prevented incest between F9 and M8, but there are unanswered questions: Did nulliparous F9 drive out M8 and seduce M5 into her territory? Or did M8 leave voluntarily and displace M5? Or did M5 seek a younger female, abandon F3, and force out M8? The missing details are key to understanding the social dynamics of the species. When F9 in turn died, M5 disappeared, but we do not know if he died or emigrated or (his collar had expired).

Dietz (1984:15) observed a parallel case: two months after death of the female of a pair, a new young female moved into her territory, and a month later, the male of the previous pair, who had not associated with the new female, moved outside of it and disappeared, just as a new young male took over the territory with the new female. This sequence closely matches behaviors we observed: (1) after the death of a female, the male left the territory and did not pair with the replacement female; (2) a new male joined the replacement female after she had established as resident on a territory. As we recorded three (possibly four) times, a male moved in to join a female on her territory, not the reverse.

Reproductive Season

The two known birth dates of litters on our study area were in July, as were two others based on estimated ages of observed pups (Table 5.7). Our data present an enigma regarding other birth dates. In September and October we caught immature females of 17–18 kg, with body measurements below adult size. At least one of these youngsters had grown in length by the following year. Captive bred MW reach full weight (26 kg) at 10.5 months (M. Rodden, pers. comm.). Backdating their birth dates from their weights at capture (see Materials and Methods) yields births in about February, as it does for some other youngsters of 21 kg. This presents two possibilities: (1) young really were born in January–March or (2) they were born the previous year and were not fully grown at 12–14 months old. In one case (young F12), the mother (F3) was known to have given birth the previous 1 July, and she was still lactating in September. If F12 was of that July litter, she would have weighed only 18 kg at 15.5 months old and been incomplete in body measurements. Otherwise, the mother gave birth twice in the same year, once on 1 July, and again in the following February–March. There is some evidence that F3 also gave birth to her first litter in around January–February 2005 (estrus in November, presence of M10 of the right age; see above) and that the final litter of M2 was born February–March, as tracks were seen in March and pups were seen in May. In Emas Park in Brazil, gestation is reported from April to August, and births from June to August (Vynne, 2010), consistent with some of our results. Dietz (1984) reported the birth months of 21 litters, from local interviews in Serra da Canastra. Maximum births also occurred from July to September (three to five litters each), but two were reported in February, one each in March and May, and two in April. Vynne (2010) shows a small uptick in December maned wolf fecal progestin levels in Emas Park, which could signal early estrus in a few females.

MW are believed to enter estrus just once per year (Asa, 1997, Rodden et al., 2004; Velloso et al., 1998), but two South American Canidae, including bush dogs (*Speothos venaticus*; the nearest living relative of MW) and crab-eating foxes (*Cerdocyon thous*), are polyestrous or can even have two litters a year (*C. thous*; DeMatteo et al., 2006). We lack data to prove that a February–March birth can follow a July birth by less than 8 months, but some evidence implies it to be so, and long-term *in situ* data are needed.

After inheriting a territory and acquiring a mate, F9 died at three years old, (12.5 months after her mother), without indication of ever giving birth. The riskiness of maned wolf life could foster seasonally early breeding to result in February–March litters in nulliparous females or if an earlier litter is lost. Velloso et al. (1998) suggested that estrus in MW is triggered by photoperiod, because Northern Hemisphere *ex situ* MW breed in autumn, six months displaced from the autumn reproduction of Southern Hemisphere females. This idea merits another look as young were born at Los Fierros over at least half the year.

Does July parturition benefit MW? Both forest and savanna rodents and marsupials in NKP have fairly synchronized reproductive peaks in the first week in September, before which few juveniles can be trapped. Reproduction subsequently continues for several generations, so that high small mammal numbers coincide with the early rainy season (November–December; L. Emmons, unpublished). The dominant fruit in the diet, *Alibertia edulis,* is found in scats from July to February (Chapter 4, Figure 4.2). Pups can start to accompany parents to hunt at seven weeks but are provisioned by regurgitation for up to seven months (event timing reviewed in Rodden et al. [2004]). July births thus result in maximal resource availability at weaning (three months old) and maximal yearly abundance of prey and fruit when postweaning pups begin foraging. Pregnancy and lactation occur when food resources may be more limited, with possible prejudice to maternal body condition. Maned wolves have short lives and few young. With adult survivorship that can be as low as 0.28 per year (Sollmann et al., 2010), a female should favor survival of her current young over that of her possible future young: that is, the birth month favors survivorship of the young somewhat more than that of the mother. An influential factor might be that as February–July are months of lowest yearly maximum temperatures (Figure 1.8), in these months increased hours below 30°C (the temperature limit of maned wolf activity, Chapter 2) are available for foraging to compensate for low resource levels, but we do not know if this occurs. Likewise, water is abundant throughout the Cerrado during these months (Chapters 2 and 3), so little energy is expended to acquire it.

To conclude, we have raised more questions than were answered in this chapter. Every aspect of maned wolf social interaction and reproductive biology that we describe needs confirmation with a great many more *in situ* studies, especially the kind of longitudinal research that has provided understanding of the socioecology of gray wolves, African wild dogs, Ethiopian wolves, coyotes, and jackals (MacDonald and Sillero-Zubiri, 2004). Even when Canidae can be directly observed and followed throughout their activities, it has taken decades to chronicle sufficient life histories to understand the sociobiology of a species. It will be a daunting task to acquire such knowledge for MW.

POSTSCRIPT

After writing this chapter we continued our work Los Fierros. F9 had died in April 2009, and her mate M5 had disappeared by July, when F3 and M8 were still the pair of the North Range territory. On 19 August 2009 we photographed a new young female (F13) in F9's old territory, but we could not trap her. The largest fire in over 25 years burned nearly all of the savanna in October 2009. When J. M. Castro returned briefly in November 2009, he could find no tracks or signs of MW nor any signal from M8 who had carried the only functioning collar. We recorded no further trace of F3, M8, or M5. We captured F13, now primaparous (pregnant) in September 2010 during the most severe drought of recent memory. She then occupied both North and South Ranges, and there was evidence of but one other maned wolf on the savanna. In September 2011, an even more severe drought year, we captured F13 and recovered 52 weeks of GPS data, and we captured and collared her mate, M14. These were the only individuals in the study area, and they used the whole savanna. At least eight MW, including pups, had been present in 2008. Because nulliparous F13 had replaced F9 by August 2009 (with no evidence of a mate), and she became primaparous only in September 2010, this represents a fourth case on our study area of a female first acquiring a territory, subsequently to be joined by a male. Photographs suggest that F13 was sibling to F12 and one of a litter of three weaned by F3-M5 in 2007. If so, three generations of a matriline have sequentially inherited the Los Fierros savanna, but no males of the family persist there. Genetic support for these relationships is pending.

6

Morbidity and Mortality

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ABSTRACT. The health status of a population of maned wolves (MW), *Chrysocyon brachyurus*, in Noel Kempff Mercado National Park (NKP), Bolivia, was studied from 2000 to 2009 by direct observations, GPS and VHF telemetry, and biomaterial collection. A total of 12 MW were anesthetized for 33 events. Causes of morbidity included severe dental disease, skin lesions, lameness, endoparasites (among them, *Dioctophyme renale* and *Dirofilaria immitis*), ectoparasites, urinary cystine calculi, traumatic injuries, and exposure to infectious disease agents. During this decade, five of the 12 (42%) MW died. Age at time of death varied from 1.5 to >10 years. Pathologic findings identified postmortem included vertebral pathology (n = 2) and severe dental disease (n = 2). The remaining seven MW either emigrated with fate unknown or were alive in 2009 and ranged in age from 8 months to 7 years. Maned wolves in NKP are geriatric by age 8 or 9. We estimated that a total of seven litters were born to three resident adults. Of these seven litters, five included at least one pup raised to 6–8 months subadults and two litters were lost, one at 16 days and the other at 5 months (Chapter 5). Our data support the observation that dental and skeletal diseases are limiting factors for the longevity of both captive and free-living MW.

INTRODUCTION

One of the main goals of conservation is to evaluate and, if possible, optimize the factors that are most important for maintaining population fitness of a species. Knowing the causes of mortality and morbidity of a free-ranging species is essential to knowing how best to protect it from hazards that pose present or future threats to species survival. During our studies of the ecology of the maned wolves (MW) (*Chrysocyon brachyurus*) in Noel Kempff Mercado National Park (NKP), we took advantage of the trapping and immobilization required to deploy telemetry collars for collecting as much health information as we could under primitive field conditions. This part of our research was a major collaborative effort that over the years involved not only our field crew and four veterinarians but also the specialist knowledge of diagnostic laboratories,

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parasitologists, medical entomologists, laboratory technicians, and a dentist.

Few studies have been conducted on the health of free-living MW, however, available reports include baseline hematology and chemistry profiles (Dietz, 1984; May-Júnior et al., 2009) cystinuria and cysteine calculi (Carvalho and Vasconcellos, 1995; Deem and Emmons, 2005; Dietz, 1984), descriptions of endo- and ectoparasites (Beldomenico et al., 2002; Bevilaqua et al., 1993; Carvalho and Vasconcellos, 1995; Deem and Emmons, 2005; Robbins and Deem, 2002), dental trauma (Furtado et al., 2007), and evidence of exposure to a number of infectious agents (Deem and Emmons, 2005; Deem et al., 2008). All diseases reported in free-living MW (except gunshot wounds and trauma caused by vehicle contact) are also commonly reported in captive MW, including some not yet identified in free-living individuals, such as dermatitis, proliferative gingivitis, neoplasia, and spondyloarthropathy (Fletcher et al., 1979; Hammond, 2012; Maia and Gouveia, 2002; Norton, 1990; Reid et al., 2005; Maned Wolf Husbandry Manual, 2007; Rothschild et al., 2001).

Causes of mortality of MW in captivity are similar to those reported above for morbidity. However, euthanasia (commonly elected due to pain and immobility resulting from skeletal problems) and perinatal losses account for many *ex situ* deaths (National Zoological Park, unpublished data). The majority of captive MW die by 15 years with the longest lived captive-born MW in the North American population recorded at 16 years 7 months for males and 17 years 10 months for females (M. Rodden, pers. comm.). Causes of mortality in the wild, except by vehicle road kill and shooting, are largely unknown, as is age at death. A recent study by Sollmann et al. (2009) in Emas National Park, Brazil, found survival rates of approximately 64% annually for both genders and for subadults and adults alike.

We describe what we learned of the causes of morbidity and mortality in a population of free-living MW in NKP, as an integral part of a study of their ecology. We compare our findings to causes of morbidity and mortality in captive MW at the Smithsonian Conservation Biology Institute.

Materials and Methods

Field Site

Noel Kempff Mercado National Park lies between 13°31′–15°05′S and 60°14′–61°49′W at the interface of Amazonian forest with diverse savanna ecosystems, and it includes broadleaf semi-evergreen forest, dry forest, inundated forest, dry savannas, and flood-prone savannas. The habitats and climate are described and illustrated in Chapter 1. The complex habitat mosaic of NKP results in a rich fauna of 604 bird species (B. Hennessy, Armonia, pers. comm.) and 172 mammal species, including 20 Carnivora (Emmons et al., 2006a, 2006b); all with potential to interact with MW: as prey, predators, and vectors or hosts of pathogens and parasites. The territories of the MW in our study population in Los Fierros savanna are isolated from direct contact with human settlements, pets, or livestock, except horses that travel briefly on one road a few times a year (without staying overnight or grazing). However, at least one GPS-collared maned wolf (M6) traveled 30 km to a neighboring estancia that has dogs, cats, poultry, and hoofstock and then returned into Los Fierros savanna (Chapter 3), so isolation is incomplete. There is little vehicle traffic on the single, potholed, dirt road that crosses the savanna, and we found only one maned wolf road kill, in about 1995, when there were logging trucks still speeding on that road.

Sample and Data Collection in the Field

Maned wolves were captured within NKP in wooden box traps or hardware-cloth cage-traps baited at first with live chicks, but later with sardines and fatty dried beef (see Chapter 1 for more detail). From February 2000 to July 2009, 12 MW were captured for a total of 33 anesthetic events. Immobilization was with tiletamine plus zolazepam (Telazol®, Fort Dodge Laboratories, Fort Dodge, Iowa 50501, USA; 3.5–4.5 mg/kg, intramuscular [i.m.]) or a ketamine (Ketaset®, Fort Dodge; 6–8 mg/kg, i.m.)/xylazine (Xylazine: TranquiVed, Vedco, Inc., St. Joseph, Missouri 64507; 1.1 mg/kg, i.m.) combination delivered through Telinject® plastic darts (Telinject USA Inc., Agua Dulce, California 91390, USA) using a Telinject® pistol (Bronson et al., in preparation). If needed, anesthesia was supplemented with ketamine (Ketaset®, Fort Dodge; 25–50 mg increments, intravenous or i.m.). For the ketamine/xylazine combination, the xylazine was reversed with yohimbine (Wildlife Pharmaceuticals, Inc., Fort Collins, Colorado 80522, USA; 0.125 mg/kg, i.m.).

A physical examination was performed on each maned wolf at the time of anesthesia and included temperature, pulse, respiration, detailed oral examination, detection of skin lesions, and abdominal palpation. Ages were estimated by physical characteristics (e.g., dentition, coat appearance, mammae appearance, and body measurements) according to the criteria of Dietz (1984) and in comparison to known-aged individuals of our study. We documented with photographs the whole body, dentition, and lesions, and various samples were collected from each maned wolf. Blood was collected by venipuncture of the jugular, cephalic, or the lateral saphenous vein and was immediately placed in ethylenediaminetetraacetic acid (EDTA) anticoagulant tubes (Becton Dickinson, Franklin Lakes, New Jersey 07417, USA) and serum separator tubes (Corvac Sherwood Medical, St. Louis, Missouri 63103, USA). The sample tubes were placed in the shade until clot formation, at which point sera were separated by centrifugation (Mobilespin, Vulcan Technologies, Grandview, Missouri 64040, USA) at 3,000 g for 15 min and stored in a freezer. Alternatively, blood was allowed to clot at ambient temperature, and the serum was then decanted and kept in a cool place for 48 hours before storage in a freezer.

Blood in EDTA was used to prepare thin blood smears fixed with 99% methanol. Packed cell volumes (PCV) were determined using a portable 12 V centrifuge, and plasma total solids (TS) were measured with a handheld refractometer (Schulco, Toledo, Ohio 43608, USA) calibrated at the site. White blood cell (WBC) counts were determined manually with a prepackaged dilution system (Unopette Test 5877, Becton-Dickinson Vacutainer Systems, Rutherford, New Jersey 07070, USA). Samples were transported on dry or wet ice to the Department of Animal Health, Smithsonian National Zoological Park, USA, for storage at –70°C and laboratory testing.

Fecal samples were collected manually from the rectum and preserved in 10% formalin. Ectoparasites were collected, stored, and shipped in 70% isopropanol or ethanol. Urine was collected by cystocentesis using a 0.7mm × 25.4 mm needle, and 12 mL syringe, but not all individuals could be sampled. Urine samples were divided into aliquots and frozen in cryotubes as well as fixed in formalin. The remaining urine was evaluated using a refractometer calibrated at the site, and with Multistix-Reagent Strips for Urinalysis (Bayer Corporation, Elkhart, Indiana 46515 USA), followed by immediate centrifugation at 3,000 g for 5 min. Urine sedimentation was examined directly by microscope in the field. Preservative solutions were removed before air travel and supplemented upon arrival in the USA. All appropriate export and import permits accompanied the samples during transport and the studies were approved by the IACUC of Smithsonian National Zoological Park and Smithsonian National Museum of Natural History.

With the exception of subadults weighing <20 kg, GPS or VHF telemetry collars were placed on each maned wolf at the initial anesthetic event (see Chapter 1). On the basis of signal immobility, MW assumed dead were retrieved and any teeth or bones were collected for later evaluation. Salvaged skeletons were deposited in the Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia.

Laboratory Diagnostics

Thin blood smears were stained with a modified Wright-Giemsa stain (Hematology Three-Step Stain, Accra Lab, Bridgeport, New Jersey 08014, USA) or a Diff-Quick stain (DipQuick Stain, JorVet, Jorgensen Laboratories, Loveland, Colorado 80538, USA) and examined for blood parasites, blood cell morphology and WBC differentials. Serum biochemistries were processed on a COBAS MIRA Plus chemistry system (Roche Diagnostic Systems, Inc., Branchburg, New Jersey, 08876).

Serologic testing for antibodies was conducted at the New York State Veterinary Diagnostic Laboratory (Cornell University, Ithaca, New York) using serum neutralization for canine adenovirus (CAV-II), canine coronavirus (CCV), canine distemper virus (CDV), and canine herpesvirus (CHV); using hemagglutination inhibition for canine parvovirus (CPV); using slide agglutination/agar gel immunodiffusion for *Brucella canis*; using indirect hemagglutination assay for *Toxoplasma gondii*; and by microagglutination for *Leptospira interrogans* serovars. The same laboratory was used for detecting *Dirofilaria immitis* antigens using an occult antigen test. The five *L. interrogans* serovars tested included *L. pomona*, *L. hardjo*, *L. icterohaemorrhagicae*, *L. grippophytosa*, and *L. canicula*. Serologic testing for rabies virus was performed at Kansas State Veterinary Diagnostic Laboratory (Kansas State University, Manhattan, Kansas) using the rapid fluorescent focus inhibition test. Antibodies to *Ehrlichia canis*, *Borrelia burgdorferi*, and *Rickettsia rickettsii* were tested at the Texas Veterinary Medical Diagnostic Laboratory using an immunofluorescence assay. These serologic diagnostic tests are targeted at canine pathogens known from North America, leaving unexplored the world of native sylvatic pathogens.

Fecal samples were examined by direct microscopic examination, sodium nitrate flotation, and sedimentation methods at the New York State Veterinary Diagnostic Laboratory. One adult worm was collected perirectal and submitted to Dr. Michael Kinsella for identification. Adult ticks were identified on the basis of external morphology, using the keys of Kohls (1956) and Jones et al. (1972). Urine was assayed semiquantitatively for increased cystine concentrations using the cyanide-nitroprusside method (Shih, 1973).

Data Analyses

Results were analyzed using a commercial statistical software package (NCSS, Kaysville, Utah; SPSS, version 13.0, Chicago, Illinois). Numerical data were inspected for normality and t-tests were performed on normal data and Mann-Whitney U-tests were used where normality was rejected (Petrie and Watson, 2006). Statistical significance was determined as $p < 0.05$.

RESULTS

Among the 12 MW, seven were immobilized once, three were anesthetized two, four, and eight times, respectively, and two others were each immobilized six times. Maned wolves were generally immobilized and sampled once yearly, but a few were immobilized twice within a year at intervals of over three months. Six were male and six were female.

PHYSICAL FINDINGS

Body weights were recorded for six females (16 measures) with a mean of 23.2 kg ± 3.6, range 17–29 kg and for six males (13 measures) as 26.2 kg ± 2.4, range 21–29 kg. Males were significantly heavier than females (t-test; *P* = 0.0076) when both age groups (i.e., subadult and adult) were combined. Body weight of adult females, based on 10 measures from three animals, was 25 kg ± 2.9, range 22.9–27.1 kg. Body weight of adult males, based on 11 measures from four animals, was 26.96 kg ± 1.64; range 23–29 kg. Adult female body weights were significantly lower than adult male body weights (t-test; *P*= 0.03).

The most striking lesions on physical examination were the dental lesions, such as abnormal conformation, wear and attrition, fractures, missing teeth, gingivitis, and caries (Table 6.1 and Figures 6.1, 6.2). Male M5 had class II brachygnathia (underbite) and several other oral lesions (Table 6.1). Other specific findings included the following: M2 was blind in the left eye due to a shrunken globe at time of anesthesia, female F3 had signs of old ear pinna trauma (probably from myiasis around an ear tag), M6 was thin with mild crepitus in multiple metatarsal joints on palpation, M8 had moderate conjunctivitis and a grade IV/VI heart murmur and was limping on release following anesthesia, F12 had a laceration on the caudal footpad, and two animals (F3, M4) had bald areas on the lateral thigh regions. Uncaptured individuals photographed by camera traps had similar ear lesions (one) and large bald areas on the thigh (one).

HEMATOLOGY

Males had higher packed blood cell volumes (PCV) (37% ± 3.8) than did females (32% ± 5.3) and lower total

TABLE 6.1. Clinical and pathological dental findings for free-living maned wolves (MW) (*C. brachyurus*) in Noel Kempff Mercado National Park (NKP). Ages are estimates. Here n/a, not present; X, present.

ID	Age, Years	Abnormal conformation	Wear	Fractures	Missing teeth	Gingivitis	Gingival hyperplasia	Caries	Osteomyelitis
F1*	0.7	n/a	X	n/a	n/a	n/a	n/a	n/a	n/a
M2*	10+	n/a	X	X	X	X	n/a	n/a	X
F3	1.5–8	n/a	X	n/a	X	X	X	X	n/a
M4	0.8	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
M5	3–7	X	X	X	X	n/a	X	X	n/a
M6*	10	n/a	X	X	X	n/a	n/a	X	X
F7	1	X	X	n/a	n/a	n/a	n/a	n/a	n/a
M8	3–7	n/a	X	n/a	X	n/a	n/a	X	n/a
F9*	0.6–3	n/a	X	n/a	X	n/a	n/a	X	X
M10	1	n/a	X	n/a	n/a	n/a	n/a	n/a	n/a
F11*	8–10	X	X	X	X	n/a	n/a	X	n/a
F12	0.6	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

*Animal died during course of study. Skull was recovered for evaluation.

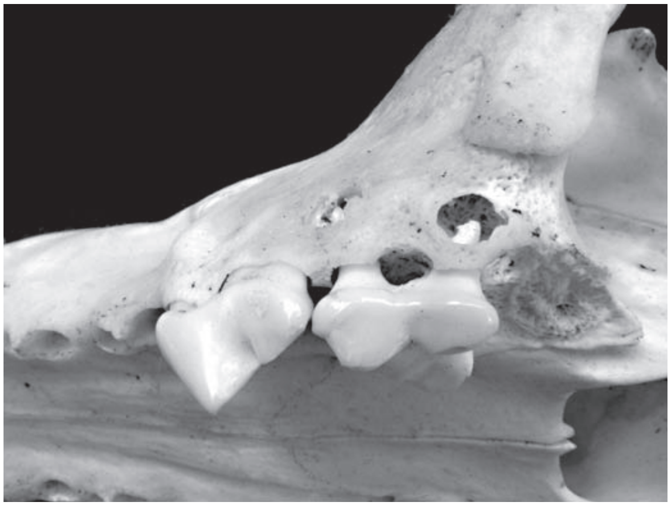

FIGURE 6.1. Upper left teeth P4 and M1 of maned wolf F9, 3 years old at death. Note that M2 was lost before death and the alveolus healed (closed), that the labial cusps of M1 are already worn flat, and that P4 shows almost no wear. P2 and P3 were lost postmortem. Osteomyelitis has eroded the bone at the root of M2. The right M2 was likewise missing. Photograph, L.H. Emmons.

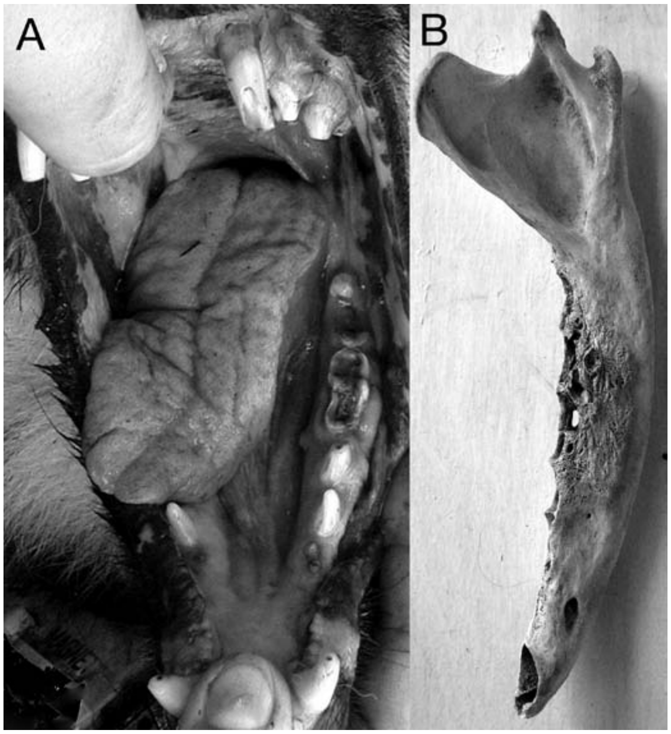

FIGURE 6.2. Teeth of geriatric male M6 with multiple dental lesions. (A) Teeth at capture including slab fracture of upper canine, other canines and premolars worn to root canals or broken off to roots, missing first lower premolars and outer upper incisors, and the broken, worn, and infected lower molars and third premolars. (B) Recovered mandible of M6, who died about 5 months after the photo in A, showing the severe bone infection underlying the cheek teeth shown in A. Photograph, L.H. Emmons.

solids (7.1 mg/dL ± 0.5) than females (7.9 mg/dL ± 0.6) (t-test; $p < 0.05$). One female (F3) had a PCV of 22% in 2007 and 2008 but had values in the normal range in other years (38% in 2005, 35% in 2006, and 31% in 2008). When we removed the two lowest PCV values (22% and both from F3), there was still a significant difference between males and females (34% ± 3.3) (t-test; $p < 0.05$). All other hematological values were not significantly different between the sexes (Table 6.2).

SERUM CHEMISTRY

Among all the parameters we measured, only the serum creatinine kinase (CK) activities differed (Mann-Whitney U-test; $p < 0.05$) between genders, with a median of 353 U/L ($n = 10$) for males and of 147 U/L ($n = 12$) for females. This may be due to the high value in one male (M5 1,310 U/L), and that both of the highest CK values were males (Table 6.3).

SEROLOGIC TESTING

All 11 of the MW had antibodies to CAV-II at every sampling date ($n = 30$) with titers ranging from 512 to 4096 (Table 6.4); 85% of samples were heartworm (*D. immitis*) antigen positive and 56% tested positive for toxoplasma (*T. gondii*) antibodies. A low prevalence of antibodies to CDV, CPV, *Ehrlichia canis*, and the five serovars of Leptospira (*L. interrogens*) was found (Tables 6.4, 6.5).

ENDOPARASITES AND ECTOPARASITES

Eggs of endoparasites were found in all of the 14 fecal samples from the 7 MW evaluated. One adult worm, found perianally on F9, was identified as a dog roundworm (*Toxocara canis)*. Eggs of pinworms, mites, and mite eggs from the family Listrophoridae were detected in 4 samples from 3 MWs (F3, M8, and F9). All ticks identified were from the pantropical genus *Amblyomma*. Few

TABLE 6.2. Hematology for free-living MW (*C. brachyurus*) in NKP. Here n/a, not applicable.

		Male	
Measure	*N*	Mean (SD) or median	Range or 10%–90% quartiles
PCV (%)*	11	37 (3.8)	31–42
TS (mg/dL)*	11	7.1 (0.5)	6.4–8.2
WBC ($X10^3$/μL)	9	13,036 (6,130)	4,840–21,780
Neutrophils (%)	12	79.5	51.4–91
Bands (%)	12	0	0–2.4
Lymphocytes (%)	12	10	5–33.9
Monocytes (%)	12	2.5	0.3–12.8
Eosinophils (%)	12	1	0–8.7
Basophils (%)	12	0	0–0

		Female	
Measure	*N*	Mean (SD) or median	Range or 10%–90% quartiles
PCV (%)*	13	32 (5.3)	22–41
TS (mg/dL)*	12	7.9 (0.6)	6.9–8.8
WBC ($X10^3$/μL)	9	10,872 (5,937)	5,500–23,015
Neutrophils (%)	11	87	53.2–91
Bands (%)	11	0	0–2.6
Lymphocytes (%)	11	8	0–28
Monocytes (%)	11	3	0.2–10.8
Eosinophils (%)	11	1	0–22.6
Basophils (%)	11	0	0–0.8

			Both sexes	
Measure	*P* value	*N*	Mean (SD) or median	Range or 10%–90% quartiles
PCV (%)*	0.01*	n/a	n/a	n/a
TS (mg/dL)*	0.04*	n/a	n/a	n/a
WBC ($X10^3$/μL)	0.46	18	11,954 (5,959)	4,840–23,015
Neutrophils (%)	0.54	23	81	56.4–91
Bands (%)	0.93	23	0	0–2.2
Lymphocytes (%)	0.19	23	10	2–26.4
Monocytes (%)	0.58	23	3	0.4–10.6
Eosinophils (%)	0.25	23	1	0–12.4
Basophils (%)	0.3	23	0	0–0

*t-test; statistical significance.

individuals had fleas and they were rare on those that did carry them (Table 6.6).

URINARY FINDINGS

Nitroprusside test results were strongly positive for urine from two of four males and for both females tested, indicating that these MW carried the inherited disease cystinuria. Three of five urine sediments that we evaluated microscopically revealed cystine crystals. Curiously, cystine crystals were found in the urine sediment of M6, who tested negative by cyanide-nitroprusside testing. Perhaps dissolved cystine had precipitated, and only the supernatant was examined by nitroprusside testing. In contrast, urine from F3 was negative for cystine crystals by microscopy but positive by nitroprusside testing. Furthermore, ova of the giant kidney worm, *Dioctophyme renale,* were detected in three of five maned wolf samples examined by microscopic evaluation in the field (Table 6.7).

MORTALITY

Up to September 2009, five of the 12 MW studied died, with four deaths occurring between February and April, and three of these five were over 7 years of age (Table 6.8). Following a major fire that swept the entire area in October 2009 (Figure 1.10), two other adults disappeared (F3, M8) and were presumed dead (Chapter 5, Postscript). Examination of five retrieved skeletons revealed severe vertebral pathologies (Figure 6.3), and tooth loss and osteomyelitis of the skull in two geriatric individuals (Figures 6.1, 6.3). An exception was for elderly F11, who had molar teeth worn down to the gums, but no skeletal and only minor dental lesions: a lost premolar and a small slab fracture of a canine tooth. One female (F9), 3 years old at time of death, had an infected tooth and was positive for *D. renale* and *D. immitis* antemortem and died when the study area was experiencing unusually strong flooding. The other young female that died (F1) was believed to have succumbed to an infectious agent as the fox (*Cerdocyon thous*) population in the same section of NKP was decimated at this time.

We estimated that at least seven litters were born to three females (Chapter 5; Table 5.7). Of these, five included at least one pup raised to ≥6–8 month subadults, and two litters were lost, at 16 days (F3 in 2008) and at 5 months (unmarked mate of M2 in 2003), respectively.

TABLE 6.3. Chemistry profiles for free-living MW (*C. brachyurus*) in NKP. Here n/a, not applicable.

	Male			Female				Both sexes		
Measure	*N*	Mean (SD) or median	Range or 10%–90% quartiles	*N*	Mean (SD) or median,	Range or 10%–90% quartiles	*P* value	*N*	Mean (SD) or median	Range or 10%–90% quartiles
Glucose (mg/dL)	10	70.1 (12.8)	51–88	11	67.1 (16,7)	44–88	0.65	21	68.5 (14.7)	44–98
AST (U/L)	10	57.5	22.7–125.3	12	33.5	18.3–135.3	0.08	22	39.5	19.9–123.9
ALT(U/L)	10	85.5	25.3–350.4	12	58.5	17.9–191	0.21	22	67	24.9–214.4
ALP(U/L)	10	6	1.92–41.7	11	9	1.84	0.20	21	8	1.84–22
TP (g/dL)	10	7.26 (0.8)	5.7–8.2	12	7.66 (0.7)	6.7–8.7	0.21	22	7.5 (0.74)	5.7–8.7
Albumin (g/dL)	10	2.5 (0.5)	1.5–3.5	12	2.3 (0.4)	1.9–2.9	0.32	22	2.4 (0.5)	1.5–3.5
Globulin (g/dL)	10	4.74 (0.5)	3.9–5.5	12	5.35 (1.0)	4.2–7.0	0.96	22	5.07 (0.8)	3.9–7
BUN (mg/dL)	10	29 (14.4)	15–55	12	30.8 (10.2)	16–46	0.84	22	29.6 (12.0)	15–55
Creatinine (mg/dL)	10	1.25 (0.2)	1–1.7	11	1.2 (0.3)	0.9–1.7	0.83	21	1.2 (0.2)	0.9–1.7
Phosphorus (mg/dL)	10	4.2	3.6–6.6	11	4.3	3.3–7.6	0.92	22	4.25	3.53–6.67
Calcium (mg/dL)	10	8.51 (0.97)	6.7–10.2	11	8.54 (0.45)	7.9–9.3	0.94	22	8.5(0.7)	6.7–10.2
Sodium (mmol/L)	10	147.5	127.9–156.8	12	146	140.3–154.4	0.43	22	146.5	140.3–155
Potassium (mmol/L)	11	4.4	4.12–7.12	11	4.3	3.94–4.76	0.13	21	4.4	4.1–4.88
Chloride (mmol/L)	10	121.5	101.4–124.9	12	117	106.9–125.2	0.16	22	118	106.9–124.7
Bilirubin (mg/dL)	10	0.3	0.2–0.49	12	0.3	0.2–0.4	0.68	22	0.3	0.2–0.4
CK (U/L)*	10	352.5	136.6–1310.2	12	146.5	50.9–520.3	0.01*	n/a	n/a	n/a

*Mann-Whitney U-test; statistical significance.

DISCUSSION

Physical Condition

The 12 MW we evaluated in NKP over a 10-year study period included equal numbers of males and females and ranged in age from 0.6 to over 10 years. The sex and age structure suggest juvenile recruitment into the population, although three of seven observed litters had no successful pups reared. Body weights for the MW in our study were less than those for MW in a recent study in Brazil (May-Júnior et al., 2009). The difference in body weight could be related to food availability as individuals lost weight coincident with a decline in rodents (Emmons, 2009; Chapter 4; Figure 4.3).

The most significant physical findings in live-captured MW were associated with dental disease (Figures 6.1, 6.2). Many individuals had lesions consistent with caries, which could be caused by the high quantities of sugars and acids from fruits in the diet (Chapter 4; Bestelmeyer, 2000; Dietz, 1984; Motta-Junior et al., 1996). Many MW had evidence of traumatic injuries to their teeth (slab fractures). This is consistent with findings from free-living MW in Brazil (Furtado et al., 2007) and captive MW (Hammond, 2012). Although we did not see the degree of gingival hyperplasia commonly seen in captive MW in the 1980s and 1990s in North America (Norton, 1990), three MW had some evidence of gingival hyperplasia.

Other clinical findings included probable traumatic injuries (e.g., blind left eye and split lower lip and eyelid in M2 and paw lesion in F12) and possibly infectious agents (e.g., conjunctivitis in M8). Additionally, the IV/VI heart murmur in this individual (M8) may have been associated with heartworm infestation as he consistently tested high positive to *D. immitis* antigen. M8 also demonstrated persistent weight-bearing lameness over 3 years and a slow recovery after one anesthetic event. A diagnosis for the cause of the alopecia in the hindquarters of three youngsters, seen only in 2002–2003, was not determined but most likely was due to parasitic or traumatic events.

One blood sample was removed from the data set for hematology and chemistry analyses as values from this sample were not consistent with life, and thus improper sample handling was suspected. Only PCV and TS differed

TABLE 6.4. Test results for selected parasitic and pathogenic agents of free-living MW (*C. brachyurus*) in NKP. CAV-II, canine adenovirus; CCV, canine coronavirus; CDV, canine distemper virus; CHV, canine herpesvirus; CPV, canine parvovirus; ND, no data.

ID	Date	*Leptospira ictero*	*L. grippophytosa*	CAV-II	CCV	CDV	CHV	CPV	*Dirofilaria immitis*	*Toxoplasma gondii*	Rabies	*Ehrlichia canis*	*Rickettsia rickettsii*	*Borrelia burgdorferi*
F1	15 Feb 00	0	0	512	0	0	0	10	Positive	0	0	ND	ND	ND
M2	20 Oct 01	0	0	512	0	12	0	10	0	0	0	ND	ND	ND
F3	7 Oct 03	0	0	512	0	12	0	10	0	0	0	ND	ND	ND
F3	9 Oct 04	0	0	1536	0	12	0	40	0	256	16	ND	ND	ND
F3	2 Oct 05	0	100	1024	8	16	0	0	0	512	0	80	Positive	0
F3	4 Sep 06	0	0	256	0	0	0	0	Positive	256	0	0	64	0
F3	21 Sep 07	0	0	2048	8	0	0	0	0	ND	0	0	256	ND
F3	15 Jul 08	0	0	4096	0	0	0	0	Suspicious	ND	0	320	0	ND
F3	19 Oct 08	0	0	768	0	0	0	0	Low	180	0	80	64	0
M5	4 Oct 04	0	0	1024	0	24	0	20	High	128	13	ND	ND	ND
M5	28 Sep 05	0	0	512	0	0	8	0	High	128	0	80	Positive	0
M5	29 Jan 07	0	0	384	0	0	0	0	High	256	0	0	0	0
M5	26 Jul 07	200	0	4096	0	0	0	0	High	ND	0	80	0	ND
M5	16 Jul 08	200	0	768	0	0	0	80	0	ND	0	0	0	ND
M6	27 Sep 05	0	0	1024	0	8	0	0	Positive	512	0	80	Positive	0
F7	21 Oct 05	0	0	1024	0	8	0	0	0	128	0	80	Positive	0
M8	25 Oct 05	0	0	512	0	0	0	0	High	128	0	80	Positive	0
M8	5 Sep 06	0	0	512	0	0	0	0	High	128	0	0	64	184
M8	25 Jul 07	0	0	1024	0	0	0	0	High	ND	0	80	0	ND
M8	8 Jul 08	0	0	2048	0	0	0	0	High	ND	0	0	0	ND
M8	22 Oct 08	0	0	768	0	0	0	0	High	180	0	320	64	0
M8	7 Jul 09	0	0	3072	0	0	0	0	High	180	ND	80	64	0
F9	4 Sep 06	ND	ND	512	0	0	0	0	Low	128	ND	0	256	242
F9	18 Jul 07	0	0	4096	0	0	0	0	Positive	ND	0	0	256	ND
F9	7 Jul 08	0	0	768	0	0	0	0	0	ND	0	80	256	ND
F9	12 Oct 08	0	0	2048	0	0	0	0	High	60	ND	80	ND	120
M10	16 Sep 06	ND	ND	512	0	0	0	0	0	64	ND	0	256	25
F11	4 Feb 07	ND	ND	192	0	0	0	0	High	256	ND	80	0	161
F11	18 Jul 07	0	0	1024	0	0	0	0	High	ND	0	0	0	ND
F12	16 Oct 07	0	0	2048	0	0	0	0	0	ND	0	0	256	ND
Total		1/11	1/11	11/11	1/11	5/11	1/11	4/11	7/11	8/10	2/10	7/9	8/9	4/8
Animals		(9%)	(9%)	(100%)	(9%)	(45%)	(9%)	(36%)	(64%)	(80%)	(20%)	(78%)	(89%)	(50%)
Total		2/27	1/27	30/30	2/30	7/30	1/30	6/30	20/30	17/20	2/25	14/25	16/24	5/15
Samples		(7%)	(4%)	(100%)	(7%)	(23%)	(3%)	(2%)	(67%)	(85%)	(8%)	(67%)	(67%)	(33%)

TABLE 6.5. Comparison of seroprevalence of selected parasitic and pathogenic agents of free-living MW (*C. brachyurus*) in the NKP and domestic dogs on the perimeter.

Animal	*Dirofilaria immitis*	*T. gondii*	Rabies	CAV-II	CHV	CDV	CPV	CCV	*Leptospira*	*E. canis*	*R. rickettsii*	*B. burgdorferi*
MW	7/11	8/10	2/10	11/11	1/11	5/11	4/11	1/11	2/11	8/9	8/9	4/8
(*n* = 11)	(64%)	(80%)	(20%)	(100%)	(9%)	(45%)	(36%)	(9%)	(18%)	(89%)	(89%)	(50%)
Dog*	13/40	32/40	22/39	7/40	28/40	37/40	34/40	3/40	8/40	19/22	19/22	0/22
(n = 40)	(33%)	(80%)	(56%)	(18%)	(70%)	(93%)	(85%)	(8%)	(20%)	(86%)	(86%)	(0%)
P value	NS	NS	0.04	<0.001	<0.001	<0.001	0.003	NS	NS	NS	NS	0.003

*Data from Bronson et al. (2008). Here NS, not significant.

TABLE 6.6. Ecto- and endoparasites of free-living MW (*C. brachyurus*) in the NKP.

Parasites	Males	Females
Endoparasites (eggs)		
Ancylostoma caninum	1	1
Ancylostoma sp.	3	2
Ascarid-like egg (avian)	0	1
Capillaria aerophilia	3	3
Capillaria sp.	4	2
Coccidia	0	1
Diphyllobothrium sp.	2	1
Fluke-like eggs	1	0
Gnathostoma sp.	0	1
Isospora sp.	1	0
Mite and mite eggs (Family Listrophoridae)	3	2
Physaloptera sp.	2	0
Pinworm eggs	3	2
Strongyle-like egg (avian)	0	2
Trichuris sp.	3	1
Toxocara canis	0	1 adult
Ectoparasites		
Amblyomma sp.	14	6
Amblyomma ovale	4	0
Amblyomma cajennense	6	2
Amblyomma pecarium	0	1
Amblyomma tigrinum	6	5
Amblyomma triste	4	3
Mallophaga (chewing lice)	1	0
Rhopalopsyllus australis spp. (flea)	0	1

TABLE 6.7. Results from urinary testing in free-living MW (*C. brachyurus*) in NKP. Here n/a, not available.

Identification (no. of samples)	Laboratory	Microscope
F1 (1)	n/a	No crystals; *Dioctophyme renale* ova
F3 (1)	Positive	No crystals; *D. renale* ova
M5 (3)	Positive	Crystals (3/3); *D. renale* ova (2/3)
M6 (1)	Negative	Crystals; no ova
M8 (1)	Positive	n/a
M10 (1)	Negative	n/a
F11 (1)	Positive	Crystals; no ova

between our male and female MW. Females had significantly lower PCV and higher TS values than males. One possible explanation for this difference was a chronic underlying infectious process in the females, which may have been responsible for the two low (22%) values for F3. Packed cell volume values in both male and female MW in our study were lower than both those for captive MW in North America, with values of 40.9 % ± 6.5 (sample size of 132 animals and 579 points) (International Species Information System [ISIS], 2002), and for free-ranging MW tested in Brazil (about 40%; May-Júnior et al., 2009).

On chemistry profile, only CK differed between males and females in our study, with males having a higher median value. This may be due to the high value in one male

TABLE 6.8. Findings from five MW (*C. brachyurus*) that died in the NKP during our study period of February 2000–July 2009.

Wolf	Date	Age	Cause(findings)
F1	March–Oct. 2000	Young (8 mo)	Disease epidemic?
M2	Feb. 2004	Old	Date of death during flooding in study area. Changes consistent with geriatric status. Most severe vertebral pathology lesions of all MW we have examined. Maxillary osteomyelitis. Multiple tooth loss.
M6	Jan. or Feb. 2006	Old	Date of death during flooding. Changes consistent with geriatric status. Many teeth missing with lytic bone surrounding, mandibular osteomyelitis, osteoporosis, vertebral pathology.
F9	16 April 2009	3 years	Date of death during flooding. Osteomyelitis of maxillae, zygomatic arch.
F11	22 March 2008	10 years	Date of death during flooding. There were no obvious bony lesions. Molars worn to gums. This female was small in stature.

FIGURE 6.3. Vertebrae of M6 showing severe bridging spondyloarthropathy. Photograph, L.H. Emmons.

(M5) (1,310 U/L) and the fact that both of the highest CK values were from males. Interestingly, in the Brazil study, there was also a difference in CK between males and females, with females having higher values than males (May-Júnior et al., 2009).

A number of differences were evident between chemistry profile results of our NKP MW and those in captivity and free-living MW in Brazil. The glucose mean value (68.5 mg/dL) in Bolivian MW was significantly lower than the ISIS value (114 mg/dL ± 25) and the value for MW in Brazil (106.4 mg/dL ± 5.0) (ISIS, 2002; May-Júnior et al., 2009). The glucose value in the MW of this study was low for a carnivore and warrants further investigation.

Serology and Endoparasites

Maned wolves in NKP were seropositive for parasitic and infectious diseases of concern in carnivore conservation, and known to cause high morbidity and mortality in captive MW. Our original hypothesis was that domestic dogs living at the perimeter of the park were the likely route of exposure for these MW. However, we did not find support for this, because high seroprevalence was found in MW for a number of pathogens that were at low prevalence in domestic dogs near the park (Table 6.5; Bronson et al., 2008). In 40 domestic dogs around NKP, seroprevalences were high for CDV (93%), CHV (70%), CPV (85%), *T. gondii* (80%), and *E. canis* (86%) (Bronson et al., 2008). In these dogs, CAV-II prevalence was low at 18% as compared to the 100% prevalence in the MW. Because the dogs were short lived and all young, their disease profiles may reflect short exposure times and be highly variable from one year to the next. We recommend further studies that include longer-term sampling and molecular testing for virus typing to determine the relationship between the viruses within the maned wolf and domestic dog populations.

All MW were seropositive for CAV-II with titers waxing and waning during the 10 year study period. Canine adenovirus is a known cause of pup mortality in captive MW (Barbiers and Bush, 1995) and is suspected to have caused hepatitis in one individual (Hammond, 2012). Although we cannot confirm an association based on these data, it is interesting to note that in the years when F3 (2008) and F11 (2007) had high adenovirus titers (4096 and 1024, respectively), neither had successful litters. The mate of F3 (M8) also had a CAV-II titer change from 768 (in 2008) to 3072 (in 2009). This litter died at about 16 days postpartum (August 2008), based on F3's abrupt cessation of movement behavior associated with lactation (Chapter 5).

Seven of the 11 MW tested were positive for the antigen of *D. immitis*, the causative agent of canine heartworm. This is a potentially fatal, mosquito-borne disease of domestic and wild carnivores. In captivity, MW are often maintained on a heartworm prophylactic because of the devastating effect of this parasite. The role of *D. immitis* in morbidity and mortality of free-ranging MW is not known, although one of the MW (M8) had high positive antigen to *D. immitis* and an IV/VI heart murmur during anesthetic events. At the beginning of our study in Los Fierros pampa, geriatric M2 was negative for *D. immitis* (2001), while F3 on the same territory, who was sampled yearly from 2003, was seronegative until she was four. At 5 years she had converted to antigen positive status, 2 years after acquiring a highly-positive mate (M5). Of six animals tested less than 1 year of age, four were antigen negative and two were already positive, one less than 6 months old, born of positive parents. All four adults captured for the first time after 2004 were antigen positive. This suggests an increase during our study to 100% adult prevalence. Thirty-three percent of the domestic dogs tested were also positive to *D. immitis* (Bronson et al., 2008). It is possible that a dog-mosquito-wild carnivore endemic cycle operates in the NKP region of Bolivia, but our data also suggest that currently heartworm may circulate between the MW and mosquitoes.

Many of the MW were positive for *T. gondii*, as in a study of captive MW in Brazil (Vitaliano et al., 2004). This is not surprising for a species that eats positive prey (rodents and other small mammals; Deem et al., 2009) and is sympatric with seven native felid species (the definitive host).

Free-ranging Canidae usually harbor enteric parasites (Kennedy-Stoskopf, 2003), including those found in the MW in this study. These parasites are not often present in high numbers and do not cause a clinical problem in healthy adult free-living canids. However, in animals immunocompromised because of factors such as concurrent disease or physiologic stress related to habitat or population modifications, enteric parasites may result in disease. The lungworm *Capillaria aerophila*, detected in the feces of six MW in this study, can cause clinical signs associated with bronchitis and pneumonia, but these animals had no overt respiratory signs. Eggs of pinworms, mites, and mite eggs from the rodent-specific family Listrophoridae were detected in three MW, probably ingested with their rodent prey (Chapter 4). Likewise, ascarid-like and strongyle-like eggs from bird parasites were found in three MW, indicating ingestion of avian prey. A tapeworm, likely *Spirometra* spp., also associated with rodents, was recovered from maned wolf feces in the savanna (Mike Kinsella, pers. comm.). One adult worm, *Toxocara canis*, was identified in a female maned wolf (F9) approximately 6 months prior to her death around 3.5 years of age. On postmortem evaluation, there was evidence of severe osteomyelitis of the skull, believed to be from a tooth infection (Figure 6.1). Thus F9 possibly succumbed to sepsis, confounded by heartworm and gastrointestinal parasite infestation.

ECTOPARASITES

Of the five definitively identified tick species collected during this study, only *Amblyomma cajennense*, which we earlier reported from the maned wolf (Robbins and Deem, 2002), is known to be of veterinary importance. This tick has been found infected with *Encephalitozoon*-like microsporidia (Barbosa Ribeiro and Guimarães, 1998) and, together with its congeners, may be a vector of filarial worms, such as *Yatesia hydrochaerus*, which is specific to capybaras (Yates and Lowrie, 1984). *Amblyomma cajennense* also causes paralysis in bovine, ovine, and caprine hosts in Brazil (Serra-Freire, 1983). In the medical literature, *A. cajennense* is recognized as the principal vector of so-called Rocky Mountain spotted fever in the Neotropics, and, given its vast range and propensity for attacking humans, is a known or suspected vector of arboviruses, Chagas disease, and even leprosy (Guglielmone et al., 2003). We note that eight of nine tested MW were positive for *Rickettsia rickettsii* (Rocky Mountain spotted fever; but the antisera may cross-react with a local variant).

Amblyomma spp. ticks were previously reported from free-living MW (Dietz, 1984); but the first documented *A. ovale* was from our study population (Robbins and Deem, 2002). In Brazil, *A. ovale* has been implicated as a vector of *Rickettsia parkeri*, strain Atlantic rainforest, a novel spotted fever agent pathogenic to humans (Sabatini et al., 2010). *Amblyomma pecarium* is an uncommonly collected parasite of Artiodactyla known from Mexico, Panama, and Bolivia (Fairchild et al., 1966; Robbins et al., 1998). It might occasionally transfer to carnivores that prey on these herbivores or their carrion. *Amblyomma tigrinum* adults are highly specific to wild and domestic carnivores, so its occurrence on a maned wolf is expected. Adult stage *Amblyomma triste* likewise parasitize carnivores. Our records (4♂, 3♀; Table 6.6) from NKP are the first for Bolivia.

URINARY HEALTH

Morbidity from the genetic disease cystinuria, and resulting cystine calculi with urinary blockage, has been a common problem estimated to affect up to 80% of both wild and captive MW and led to nutritional modifications to minimize the occurrence of these calculi among captive MW in the United States (Bovee et al., 1981; Fernandes and Marcolino, 2007; Norton, 1990). Similarly, 71% of MW we tested (n = 7) were cystinuric, but we found no evidence of cystine calculi or urinary blockage. This agrees with another study in a free-living maned wolf population (Dietz, 1984). An ancient mutation and founder effect has been proposed (Bovee et al., 1981; Dietz, 1984; Fernandes and Marcolino, 2007; Norton, 1990), and mutations in the renal basic amino acid transporter have been identified in Newfoundland and Labrador retriever dogs with type I cystinuria and an autosomal recessive trait. However, there are many other breeds with type I and non–type I cystinuria (only males are cystinuric) where the molecular defect has not yet been defined. Initial studies of MW did not identify a mutation in the renal basic amino acid transporter (Kehler et al., 2002). With the recent completion of the full canine and low-density wolf genome sequences, progress can be made in MW. Samples have been preserved for future DNA studies.

Our finding of *D. renale* ova in three MW was not surprising, as this parasite is a common pathogen of recently captive MW (Kumar et al., 1972). *Dioctophyme renale* is often associated with a hypoplastic right kidney in infected MW and could contribute to mortality, especially with concurrent disease (Kumar et al., 1972; Norton, 1990).

MORTALITY

Forty-two percent (5/12) of the MW in our study died before September 2009, with deaths throughout the study years. This mortality rate is similar to that recorded in Emas National Park, where the survival rate was estimated at 64% per year for all age classes (Sollmann et al., 2009). All deaths at Los Fierros occurred between February and April, the months of flooding when foraging and movement in the study area are limited and could contribute to poor nutrition, debilitation, and death. The fates of the two individuals that vanished after the October 2009 fire are uncertain, as they could have escaped to die elsewhere. One was about 8 years old (F3) and the other 7 years old (M8), the latter in good health but the former geriatric, with severe dental problems. One yearling female survived the fire and was alive in 2011 (Chapter 5, Postscript).

Three of the five (60%) MW that died before September 2009 were estimated at 8 to >10 years old and considered geriatric at the time of death. Two of these three (67%) had severe spondyloarthropathy. This pathologic finding was previously considered a disease of captivity, with an incidence of about 80% of geriatric captive MW (Elizabeth Hammond, pers. comm.; Rothschild et al., 2001). The two affected MW in our study (M2 and M6) had the most severe skeletal lesions among any of three wild-taken and seven zoo skeletons (NZP) evaluated at the National Museum of Natural History (evaluated by LHE). The one geriatric maned wolf (F11) with no vertebral lesions was unusually small (22 kg). We conjecture that the body structure of MW (e.g., long legs and short back) and hunting style, of pouncing on small prey, make MW prone to vertebral pathologies. Further investigation is needed into this pathologic condition of captive and free-living MW. The two animals with severe vertebral lesions had likely lived with the condition for years.

Three of the MW that died had indication of severe osteomyelitis of the maxillae (M2, F9) or mandible (M6; Figure 6.2B) that was most likely associated with a tooth root abscess. M6 was geriatric at the time of death and had evidence that osteomyelitis had spread into the postcranial skeleton. However, F9 was only 3 years old but had evidence of spread of infection into the adjoining zygomatic arch, above and below the eye (Figure 6.1). This female died when the study area was experiencing unusually prolonged and deep flooding, and we hypothesize that the oral infection and associated pain decreased appetite while flood waters made finding food difficult. Prior to death she traveled from her own flooded territory into the drier adjacent territory, where she may have also experienced social conflict and stress. These two factors, in addition to her positive status for *D. renale* and *D. immitis*, may have led to poor nutrition and possible sepsis as the proximate and definitive cause of death. The other young maned wolf that died (F1) was believed to have succumbed to an infectious agent, as the fox (*Cerdocyon thous*) population in the same section of NKP was also decimated at this time.

Necropsy results of 47 MW housed at the Smithsonian Conservation Biology Institute, Front Royal, Virginia, from 1975 to 2003, list the primary cause of death as follows: 17 perinatal, two urolithiosis (cystine calculi), three infectious agents (e.g., CDV, CPV, and *Escherichia coli*), one trauma, three digestive, one cardiomyopathy, and 19 euthanasias. The reasons stated for euthanasia included four neoplasia, two infectious (one pyometra and one rabies virus), one trauma, four kidney related (two of these were urolithiasis), two spondylosis, one postsurgical, one cull, one arthritis, two old age, and one digestive problems. Thirteen of these 19 (68%) euthanized MW were >10 years old at time of euthanasia, and there were 11 males and 8 females.

CONCLUSIONS

We found a surprising number of significant clinical and pathologic findings in this small population of free-living MW in Bolivia. The NKP maned wolf population was previously estimated at 120 pairs (Rumiz and Sainz, 2002), but we now believe it is closer to 20–30 pairs (see Chapter 3). On the basis of our findings for the 12 MW in our study, the health of the Los Fierros population may be rated as only moderate. The lower body weights, PCV, and glucose values compared to other maned wolf populations, as well as the many dental abnormalities, may indicate a lower plane of nutrition in this population. Recent evidence of rodent population declines indicates that the prey base for this population of MW declined over 94% in biomass during the study (Chapter 4; Emmons, 2009).

We had not anticipated such a high number of dental and bony lesions. The prevalence of dental disease was most likely associated with the dietary intake of acidic, sweet fruits such as *Alibertia edulis* and *Solanum gomphodes* (Chapter 4), and tooth fractures related to chewing fruits with hard stones and perhaps armadillos. The high prevalence of vertebral pathologies in the older MW that died was similar to that found in captive populations and may suggest that this pathology is more a function of body structure and behavior than a disease of captivity as previously thought (Rothschild et al., 2001).

Although there is no definitive diagnosis for the cause of death in the one maned wolf (F1) that died at less than 1.5 years of age; a concurrent large decline in crab-eating foxes implicates an infectious disease epidemic. We therefore recommend continued domestic dog health monitoring, domestic animal vaccination, and enforcement of the prohibition of all domestic animals within the park, especially of carnivores.

Our ability to conserve the growing number of endangered species will necessitate an understanding of the health of both captive and free-living populations. We anticipate that studies similar to this one will provide data necessary for the long-term conservation of animals in their natural habitats and proper captive care and propagation of endangered species in captivity.

ACKNOWLEDGMENTS

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7

Conservation

Matthew J. Muir and Louise H. Emmons

ABSTRACT. Maned wolves (MW) (*Chrysocyon brachyurus*) are classified as "Near Threatened" on the International Union for Conservation of Nature (IUCN) Red List. Twenty-two subpopulations have been identified in Brazil, Argentina, Paraguay, Bolivia, and Peru, with an estimated 80%–90% of all MW occurring in Brazil. Only 5%–10% of maned wolf range is globally protected, but to understand how unprotected wolves are faring, better population surveys are needed on land outside of national parks and reserves. Although agricultural expansion is responsible for a contraction in the species' southern range, field studies consistently show that MW can survive in agricultural land with sufficient refugia and prey. Publicized threats include disease transmission by domestic dogs, road mortality, and hunting for folk medicine and in retaliation for livestock deaths. To these, we add fire and fire suppression, clear-cut pasture for livestock, and the emerging threat of climate change. Despite these ongoing threats, MW do not require intensive management to remain in a human-dominated landscape, and this resilience is the best hope for their successful conservation. Nonetheless, habitat management of grasslands could increase the population density of MW in protected areas.

INTRODUCTION

Through our research, we wanted to learn enough about maned wolves (MW) (*Chrysocyon brachyurus*) to suggest how their needs might be better met by conservation efforts in Bolivia. In the preceding chapters, we have presented field data and results on many aspects of the ecology of the MW on our study area: some findings are well known and many are new. These descriptive results pertain to individual animals in a specific place and time, and they can be generalized only by comparison with the results from other times and places. Compared to ecology, conservation is a different kind of subject, as we can bring to it no specific field results from regional management efforts. Rather, we can apply what we have observed to predict the status of future maned wolf populations. To include the variability and flexibility found across

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the species' range, we start with a range-wide overview of issues that can determine if a population will thrive or dwindle.

Within the Canidae, MW are exceptional not only in their ecology and evolutionary history (Chapter 1) but also in their conservation status. They are listed as "Near Threatened" by the International Union for Conservation of Nature (IUCN) (a threat category below "Vulnerable"; IUCN, 2009), but they have life history traits that predict high extinction risk for other carnivores, such as low reproductive capacity and occurrence at low density (Purvis et al., 2000; Chapter 4). Canids of similar size (>15 kg) in monotypic genera are classified as "Endangered" (African wild dog, *Lycaon pictus*; dhole, *Cuon alpinus*; IUCN Red List). Because MW do not kill ungulate livestock or wild species valued by human hunters, they have not been subjected to the campaigns of deliberate extermination that have brought other carnivores to extinction (Falkland Island wolf) or to its brink. Of no threat to people, they have stayed below the radar of both publicity and of conservation efforts. For example, in a review of maned wolf global status, Rodden et al. (2004) cited no conservation strategies for MW. This deficiency was remedied by a recent maned wolf conservation workshop in Brazil (Paula et al., 2008), which outlined status and threats in all range countries but primarily highlighted the vast information gaps to be filled. Relatively few conservation-related papers have been published on MW (15% of citations) compared to other large canids like the African wild dog (38%), dhole (20%), and Ethiopian wolf (46%, *Canis simensis*; Web of Science, keyword search, i.e., *Chrysocyon brachyurus*: subject category, Biodiversity and Conservation, June 2010).

This chapter is thus an assessment of what is known about maned wolf conservation and management, including where populations occur, what threatens these populations, and what conservation actions might mitigate those threats. Our focus is range-wide, but we will end with specific management recommendations for our study area in Noel Kempff Mercado National Park (NKP), drawing on findings from our 10 year field study (Chapters 2–6).

WHAT IS KNOWN AND WHAT MORE NEEDS TO BE KNOWN?

New literature on MW has grown exponentially since the 1960s, increasing by 50%–75% per decade (Figure 7.1). Starting with Reginald Pocock's (1927) notes on MW held at the London Zoo, we estimate that by 2010, 235 citations existed in English, German, Czech, Spanish, and Portuguese.

Information on maned wolf biology has accumulated unevenly. Excluding general reviews ($N = 29$), over half of all maned wolf citations originate from observations of captive individuals ($N = 109$). In the 1960s and 1970s, studies on captive MW outnumbered field observations by a factor of 5 (Figure 7.1). Since 1997, publications on free-ranging MW have steadily become more prevalent until they have equaled or exceeded literature on *ex situ* MW (excepting 2001). Of the 80 citations on free-ranging MW, 35% focus on diet ($N = 28$); 23% concern health and disease ($N = 18$); 9% report ranging data ($N = 7$; home range, telemetry); and 6% deal with genetic analysis ($N = 5$). Literature highlighting MW as a conservation concern appeared as early as the 1960s (Carvahlo, 1968) and recent overviews include Rodden et al. (2004), Paula et al. (2008), and Pautasso (2009).

Planning for conservation action requires taking stock of what is known and what more needs to be known (Woodroffe et al., 2005). On the basis of current work, MW have the following requirements:

1. Diet: MW subsist primarily on fruit and small mammals (Chapter 4; Dietz, 1985) and consume most food items according to their availability (Rodrigues et al., 2007). We calculated the average daily energy needs of MW to be 1,580 kcal (Chapter 4). On the basis of the 50-50 prey-fruit diet generally reported for MW, this daily requirement can be met by two or three large rodents such as cavies (>250 g) and six to eight large, soft-pulped fruits such as *Solanum* spp. (Table 4.6, Chapter 4).
2. Space and habitat: maned wolf home ranges are from 25 to over 80 km^2 (Rodden et al., 2004; Jácomo et al., 2009; Chapter 3). Breeding pairs have little or no range overlap with other pairs (Dietz, 1985; Chapter 3) but can be associated with young adult females (Melo et al., 2007; Chapter 5). MW occur primarily in grassland and savanna and avoid areas where canopy cover exceeds 30% (Vynne, 2010). They can also be found in scrub forests, flooded habitats, livestock rangelands (Rodden et al., 2004), and cropland with refugia and prey (Vynne, 2010).
3. Population size and structure: Simulated populations of at least 50 MW were modeled to persist in the absence of harvest or habitat loss, while populations of over 250 MW were thought to be relatively robust to these threats (Paula et al., 2008).

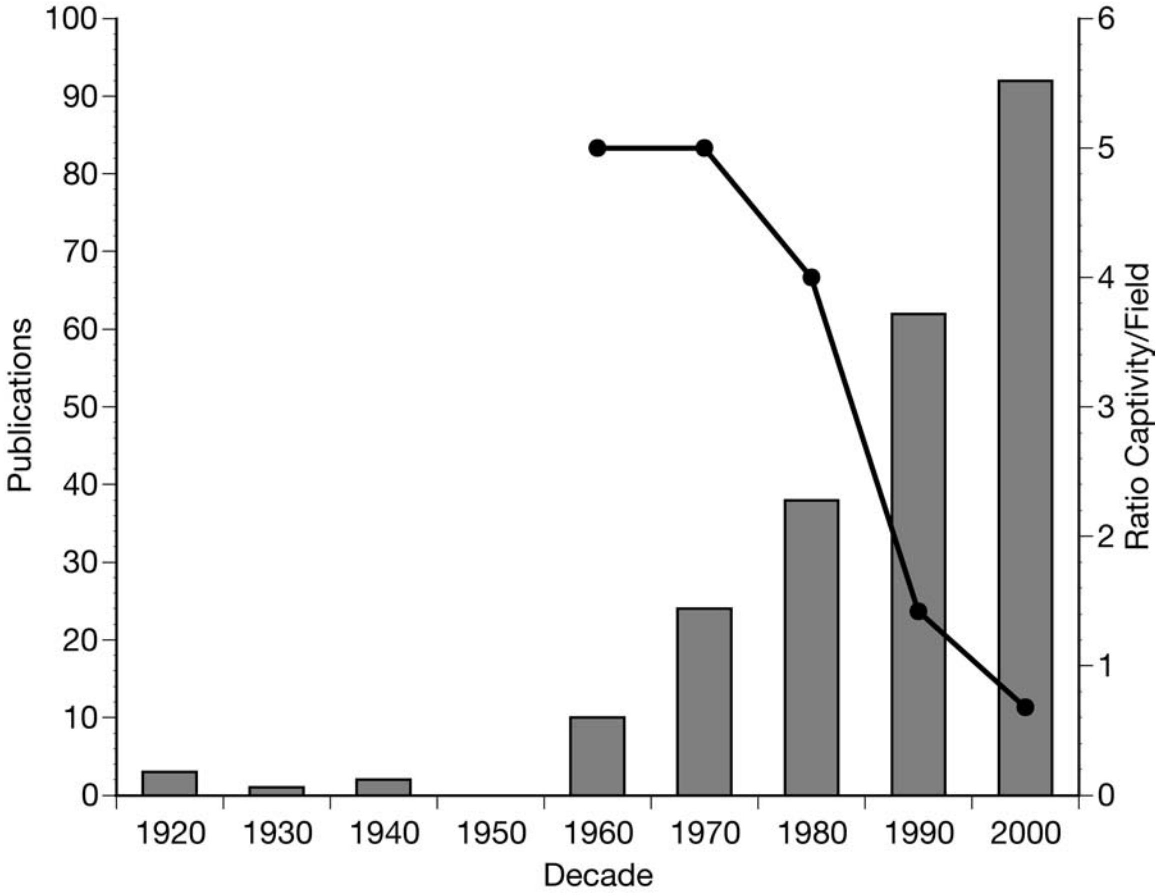

FIGURE 7.1. Publications on maned wolves (MW) by decade from 1927 to 2009. Secondary axis and point data show the ratio of publications on captive to field studies (Web of Science [keyword search = *Chrysocyon*] and personal libraries of L. H. Emmons and M. Rodden).

The persistence of MW populations is most sensitive to female mortality (Paula et al., 2008). No survivorship cost of inbreeding was found in captivity (Ralls et al., 1988).

4. Climate: Most areas in which MW occur receive 1,000–2,000 mm annual rainfall and the species' lower limit is likely between 600 and 1,000 mm (Quierolo et al., 2011). MW cease sustained activity when temperatures reach 30°C, probably to prevent water loss from panting, and in NKP they seemed to decrease travel below 20°C (Chapter 2).

Behavior (Dietz, 1984; Kleiman, 1972) and health (Bovee et al., 1981; Lamina and Brack, 1966) are relatively long- and well-studied aspects of maned wolf biology in captivity, but they are little known *in situ* (Chapters 5, 6). Information is scarce and scattered on the size and shape of populations, the scope and impact of threats, and the effectiveness of conservation strategies. Almost nothing is reported but anecdotal evidence on key life history parameters, such as litter size at birth, survivorship to weaning, or lifetime reproductive success of females.

Population and Geographic Distribution

The most definitive maned wolf distribution map is based on a collaborative effort that compiled all known point records of maned wolf occurrence (Queirolo et al., 2011). A 2005 population viability analysis (PVA) workshop held in Brazil identified maned wolf subpopulations in Brazil, Argentina, and Paraguay (Paula et al., 2008) with Bolivia and Peru evaluated later (R. C. Paula and

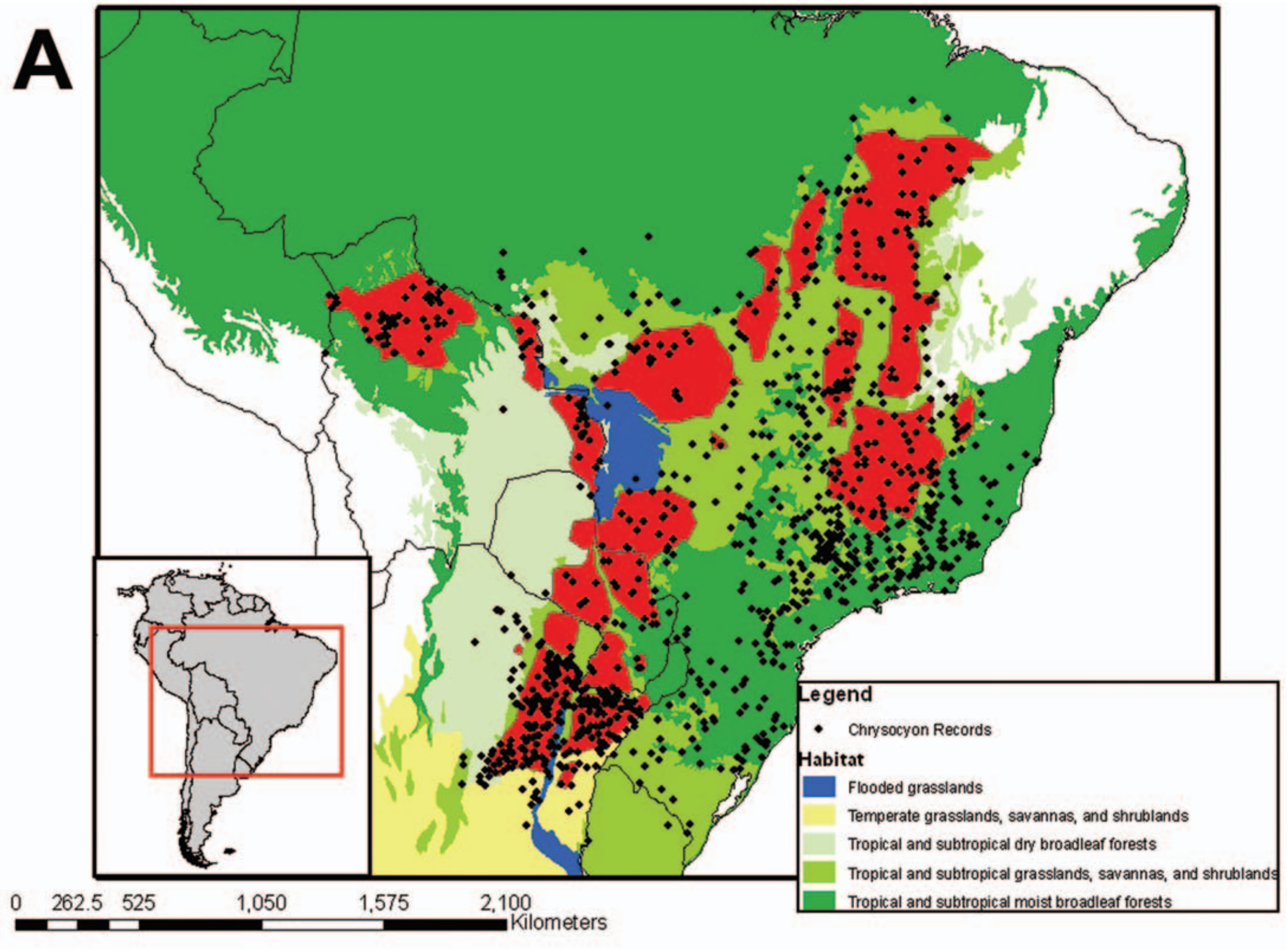

FIGURE 7.2. (A) Maned wolf distribution map and occurrence records. Point records from Queirolo et al. (2010) combined with 22 identified populations from Paula et al. (2008): red shading. Source for habitat coverage: WWF Terrestrial Ecoregions.

L. H. Emmons, unpublished). We here combine the two maps and hypothesize where discrete subpopulations still occur within the recent maned wolf distribution (Figure 7.2A, B). We emphasize that Figure 7.2B is hypothetical and that the existence and margins of subpopulations represented by polygons need both refining by local experts, and regular revision of maps, to track the collective understanding of where MW occur. Surveys of MW presence have included spoor identification, camera traps, informant interviews, and detection dogs (Vynne et al., 2011; Figure 7.3). Documenting absence is always problematic in conservation, and the maned wolf traits that increase detection probability (large-bodied, conspicuously colored, occasionally vocal) are countered by cryptic behavior (nocturnal, shy) and common names shared by other carnivore species (Queirolo et al., 2011).

Twenty-two subpopulations were identified in the 2005 workshop (Appendix A) and 1,126 occurrence records were collected by Queirolo et al. (2011). Approximately half of occurrence points fell within identified subpopulations ($N = 586$). Points falling outside of subpopulation polygons may represent transient individuals, an unidentified subpopulation or a more accurate margin of a nearby subpopulation, historical records from extirpated areas, or erroneous records of maned wolf presence. For example, subpopulations were not identified in the

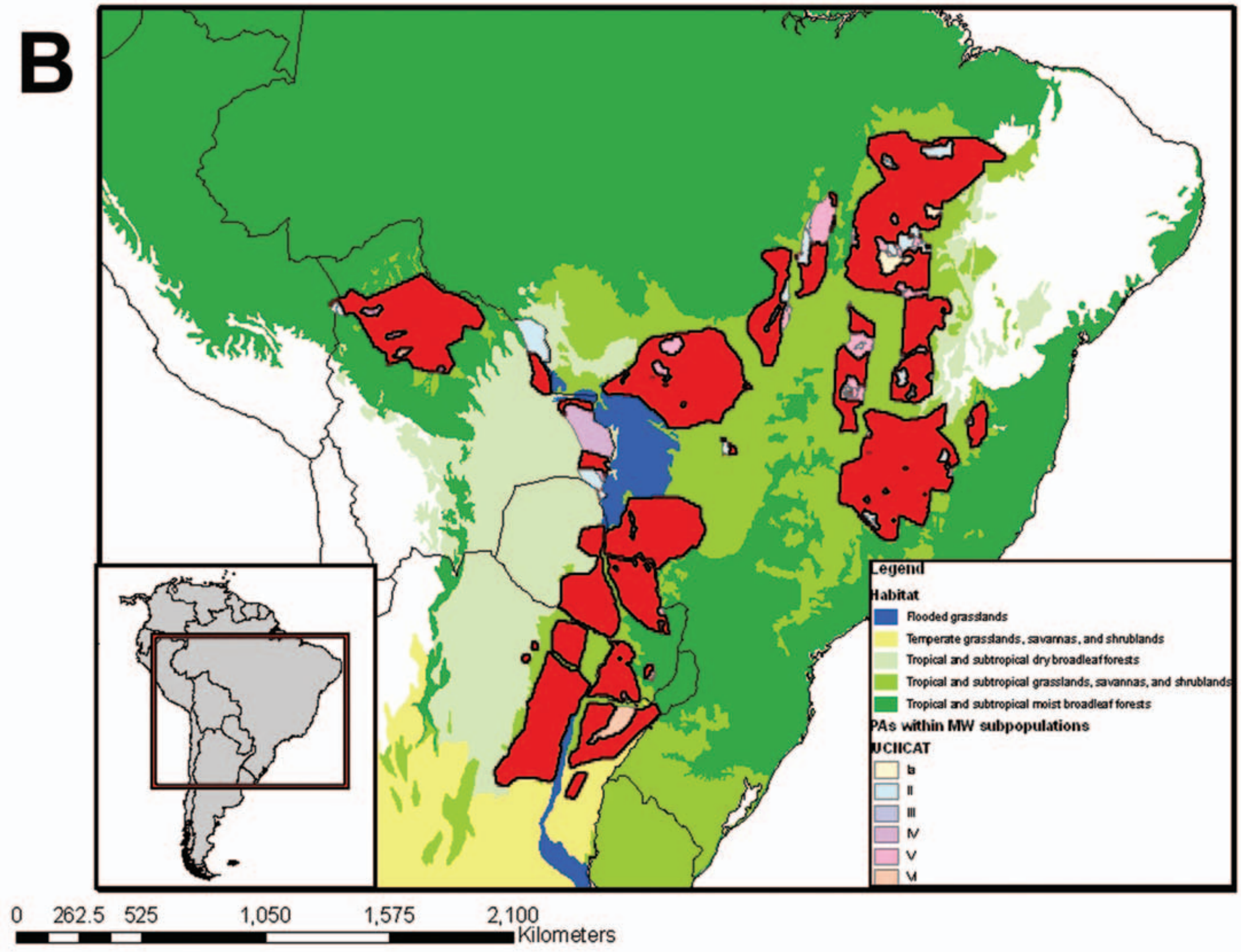

FIGURE 7.2. (B) Maned wolf distribution map and protected areas. Protected areas within populations from Paula et al. (2008): dark blue represents wetlands; red, subpopulations; paler shading, protected areas. Source for protected area coverage: World Database on Protected Areas (http://www.wdpa.org/ on 26 Jan 10). Source for habitat coverage: WWF Terrestrial Ecoregions.

Brazilian state of Sao Paulo or southern Brazil because workshop participants considered those populations “isolated and very small” (Paula et al., 2008). Thus the interstitial areas of Figure 7.2B may still contain resident MW. For example, there were no data available for a large area of potential habitat in the Beni savannas of Bolivia (Queirolo et al., 2011). See Appendix A for a description of each subpopulation and population estimate from Paula et al. (2008).

The available data suggest that more MW are found outside of formal conservation areas than within them. Only 5%–10% of occurrence records from Queirolo et al. (2011) are within a protected area ($N = 54$–117; range: IUCN Protected Area Categories Ia-IV to Ia-VI). Likewise, protected areas comprise only 7%–11% of the area included within identified subpopulations (Range: IUCN Ia-V to Ia-VI). Five subpopulations intersect no protected areas. If indigenous reserves are included, an additional 2% of both maned wolf records ($N = 18$) and area within subpopulations (34,000 km^2) are added.

There is no credible estimate of the global maned wolf population. Approximately 23,000 MW were counted

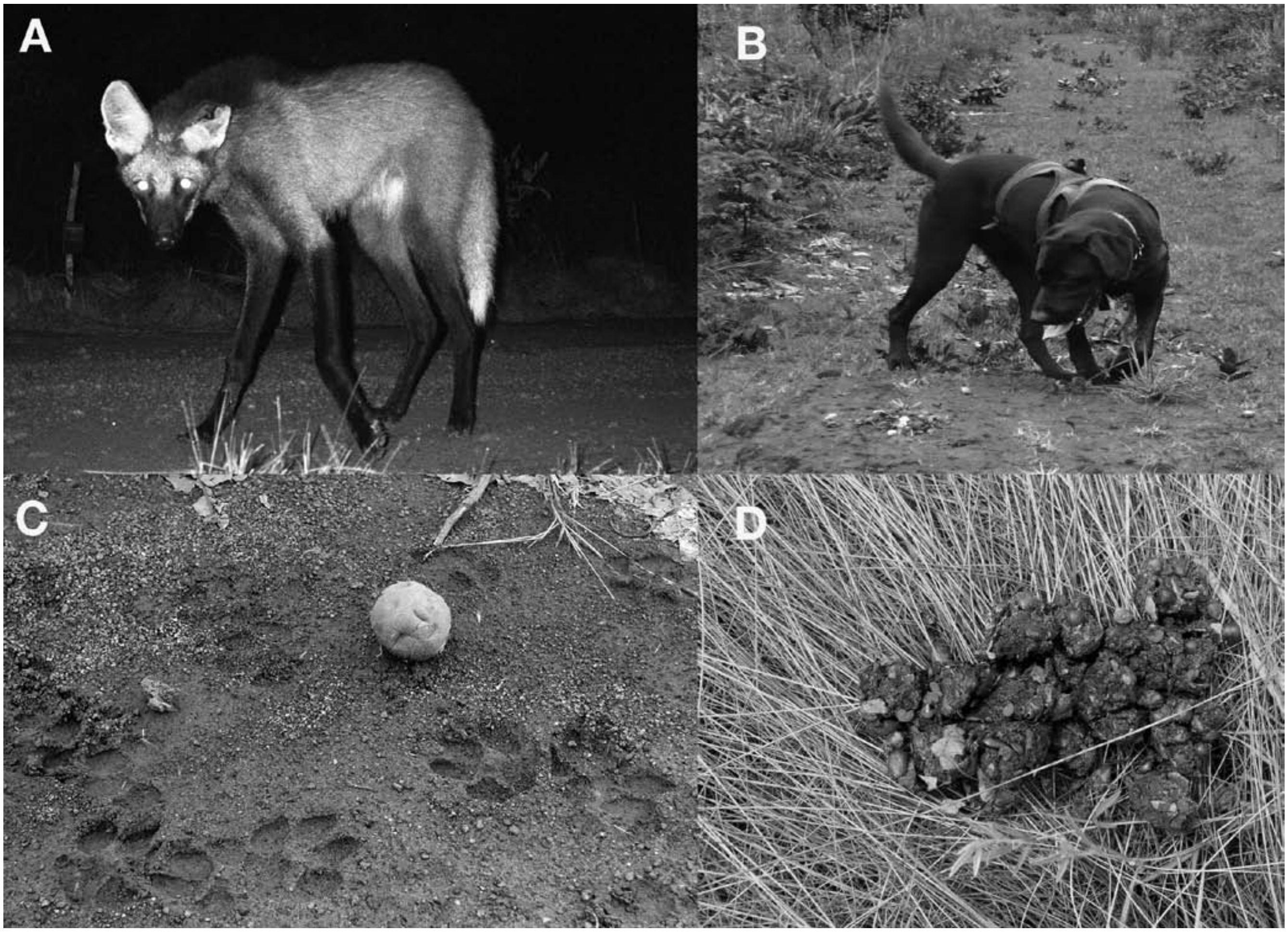

FIGURE 7.3. Methods to document maned wolf presence (top left, clockwise): (A) camera trap, unmarked individual with ear damage (NKP, photograph by M. Swarner), (B) scat-detection dog pointing at an old scat below right hind leg (Emas NP area; photograph by C. Vynne), (C) tracks and small (immature) *Solanum gomphodes* fruit with teeth marks, perhaps rejected as unripe (NKP, Bolivia; photograph by M. Swarner), (D) Scat with seeds of *Duguetia furfuracea, Solanum gomphodes, Emmotum nitens*, and other fruit, but no animal prey (NKP, photograph by L. Emmons).

in the summed efforts of the 2005 PVA workshop, with over 90% of them in Brazil (Paula et al., 2008: Brazil, *N* = 21,746; Argentina, *N* = 660; Paraguay, *N* = 830; Paula and L. H. Emmons, unpublished: Bolivia, *N* = 380). This estimate combined the best guesses of four national delegations and used extrapolations from density studies and informed speculation by local experts. For example, workshop participants from Brazil used a range of densities (2–10 individuals/100 km^2) to calculate a low and high estimate across the subpopulations there (Paula et al., 2008). Density estimates at individual sites, however, reach a maximum of 5.2 individuals/100 km^2 (Table 7.1). The range of published densities in Brazil (~1–5/100 km^2) suggests that the workshop estimates were overly optimistic. Using this published range instead, a revised population estimate for Brazilian MW is 11,820. Conversely, we now believe that the population in Bolivia was underestimated and that least 1,000 individuals may occur there. Combining these two revisions with the country estimates from Paula et al. (2008), we propose that approximately 14,700 MW occur in the wild.

Rodden et al. (2004) highlight the need for better population surveys. We suggest the following survey priorities: (1) censuses that distinguish breeding populations

TABLE 7.1. Densities reported for maned wolves (MW).

Density estimates (individuals /100 km^2)	Habitat and country	Estimate method	Citation
3.6 ± 0.8	Cerrado farm, Brazil	Camera traps	Trolle et al., 2007
1.6 ± 0.8	Protected pantanal, Brazil	Camera traps	Trolle et al., 2007
5.2	Protected grassland, Brazil	Mark-recapture trapped MW	Silveira et al., 2009
4	Protected grassland, Bolivia	Longitudinal study of marked	Emmons et al., this volume, Chapter 3
	MW + camera traps		

from transient individuals; (2) a refinement of the distribution maps by re-evaluating the subpopulations identified in the 2005 workshop with the data from Queirolo et al. (2011) and other newly reported maned wolf occurrences; and (3) more population surveys on agricultural land under different crop systems to understand the impact of human encroachment on maned wolf habitat suitability (Vynne, 2010).

THREATS

By prioritizing identified threats, conservation action can be focused on the most relevant human actors. The IUCN Species Account for MW (Rodden et al., 2008) identifies four threats: habitat conversion to cropland, road mortality, domestic dogs, and hunting for folkloric medicine. Participants in the 2005 workshop identified habitat loss (including conversion to cropland and pasture) and harvest (including hunting, road kill, and shooting of "problem animals") as the two greatest threats to maned wolf populations (Paula et al., 2008). In Argentina, conflict with humans is also considered a serious threat (Soler et al., 2005).

In the following section, we consider these threats in Bolivia and propose two additional threats (fire and climate change). We focus on population-level threats but note that wherever MW live in small isolated populations, any combination of threats that increase mortality may have population consequences.

Conversion to Cropland

Savannas in maned wolf range are threatened by industrial-scale monocultures of soya, sunflower, sugar cane, maize, sorghum, rice, and others (Ratter et al., 1997). More than half of the Brazilian Cerrado has been cleared for agriculture (Klink and Machado, 2005), and it is being lost at a higher rate than is the Amazon forest (1.1% per year, Machado in Butler, 2009). As the most significant threat to MW (Rodden et al., 2008), agricultural expansion is thought to destroy habitat needed for reproduction and dispersal, as well as to increase the risk of other anthropogenic pressures (hunting for folkloric medicine, road mortality, disease transmission by domestic animals). Habitat loss has been greatest in southern Brazil, Argentina, and Uruguay (where MW may be represented only by transient individuals), and populations in those regions are restricted to remnant pockets of habitat "hemmed in on all sides by fields of soy, corn, sunflower, and wheat" (Queirolo et al., 2011).

Several studies suggest cautious optimism for maned wolf survival in farmland (Courtenay, 1994; Dietz, 1984; Lyra-Jorge et al., 2008; Santos et al., 2003; Vynne, 2010). Outside Emas NP, Brazil, Vynne (2010) found that MW can even survive in mechanized cropland where there is adequate land management, including at least 20% set aside on each farm as a wildlife refuge, and low-growing crops (soya) with sufficient rodent prey. It was not shown, however, whether the croplands were merely a sink for animals emigrating from the park. Quierolo et al. (2010) reported some recent expansion of the maned wolf geographic range into grazing land created by deforestation of humid Atlantic Forest (Mata Atlantica) of Brazil. In Bolivia, however, there is no evidence of MW expanding into or surviving in agroindustrial croplands. Sugar cane for biofuel production is now rapidly expanding in Brazil (Rudorff et al., 2010), ballooning from 2.57 million ha in 2003 to 4.45 million ha in 2008, and it now accounts for almost a quarter of all agricultural crops (Klink and Machado, 2005; Rudorff et al., 2010). Because of its height and lack of foraging opportunities, sugar cane is likely inhospitable to MW, and its expansion rapidly threatens to reverse any range gains for MW from deforestation (Vynne, 2010).

In Bolivia, monoculture crops overlap current maned wolf range only to a moderate extent and populations are primarily separated by forest. The greatest threat to connectivity is the extensively cleared land in Brazil that separates Bolivian MW from maned wolf populations in the Brazilian state of Mato Grosso. For example, the border between Bolivia and Brazil (and the edge of the protected area where our maned wolf fieldwork was conducted) is clearly defined in satellite imagery by intensive agriculture on the Brazilian side (Figure 7.4). The threat posed by modern crop production is likely to increase dramatically in Bolivia, especially if the proposed dams and inland waterway (Hidrovía) on the Rios Madeira-Guaporé-Paraguay lead to rapid agricultural growth and development in the adjacent Beni grasslands and Bolivian Pantanal. Recent expansion of industrial rice into Beni savannas is already directly replacing maned wolf historical habitat.

FIGURE 7.4. Satellite image of NKP, indicating much more intensive deforestation for agroindustry (palest polygons) in Brazil compared with Bolivia. Natural grasslands are darker pale areas, while the darkest zones are forest. Our Los Fierros (LF) study area, blackened by fire, is in the center of the image, and the Huanchaca Meseta is the curved structure to its NE–SE. The border of Brazil follows the edge of the agroindustrial deforestation, and new colonization in Bolivia can be seen approaching NKP on the lower left edge. Image by NASA-Terra FAS-Bolivia, October 2009.

Domestic Dogs

Domestic dogs can threaten maned wolf populations by food competition, aggression, and disease transmission (Rodden et al., 2008). In Bolivia, where feral domestic dogs are rare in maned wolf habitat, we consider only disease to be a plausible population threat. Depending on the pathogen and its local dynamics, diseases can be actively maintained by the domestic dog population (such as distemper) or persist as a legacy threat (such as canine heartworm) where the disease has been historically introduced by domestic dogs but can persist in their absence via reservoir species. In our study area in NKP, MW have been exposed to many disease agents spread by domestic dogs (Chapter 6; Table 7.2; Deem and Emmons, 2005; Fiorello et al., 2004), via either hunting dogs entering maned wolf habitat or perhaps by crab-eating zorros (*Cerdocyon thous*) moving between human and natural communities (Bronson et al., 2008). Pathogens now endemic to MW (canine adenovirus, giant kidney worm: *Dioctophyme renale*) may not always be shared by domestic dogs and are not normally considered a population threat.

Road Traffic

Maned wolf mortality due to vehicle traffic (i.e., road kill) is, unsurprisingly, greatest in areas where high-speed roads intersect or border maned wolf habitat. Fischer et al. (2003) note that MW are killed “more than rarely” on both Pantanal and Cerrado roads. While road traffic is considered a significant threat to maned wolf populations in Brazil and Argentina, the density and quality of Bolivian roads is lower. Thus, while individual MW do die on Bolivian roads, we suggest that the severity of this threat is relatively minor. As an additional mitigating factor, protected areas in Bolivia are not subdivided by high-speed roadways as they are some in other countries.

Hunting for Folkloric Medicine

MW are killed for numerous uses in traditional folk medicine: bronchitis, epilepsy, dizziness, kidney disease, back pain, love potions, protection against snakebite, and to bring good luck (Alves et al., 2010; L. H. Emmons, unpublished interviews). Because trade in maned wolf body parts is not on a large commercial scale (Rodden et

TABLE 7.2. Infectious and parasitic agents of domestic dogs to which MW show serologic exposure or that have been identified in the species.

Pathogen	Lethality	Transmission
Canine adenovirus	Can cause mortality in neonatal MW	Direct contact with body fluids or urine
Canine coronavirus	Not lethal; can cause mortality in conjunction with other pathogens	Oral-fecal contact with feces
Canine distemper virus	Can cause mortality in MW; linked to serious population declines in other canid species	Respiratory and contact with body fluids
Canine parvovirus	Can cause mortality in MW	Oral-fecal; virus can survive for months in environment
Rabies virus	Fatal to MW	Bite of rabid animal
Sarcoptes scabiei (causative agent of mange)	Susceptibility varies	Direct and indirect contact
Dirofilaria immitis (causative agent of heartworm disease)	Can cause mortality in MW	Mosquito-borne

al., 2008), medicinal harvest is not judged to be a major conservation concern for MW or indeed, any canid species (Alves et al., 2010). Our impression, however, is that hunting MW for folk medicine is greater in Bolivia than elsewhere and can be a substantial source of mortality in areas where maned wolf parts can bring high prices due to strong local beliefs in sorcery and folklore (M. Herrera, pers. comm.; Figure 7.5). For example, in San Matias, Bolivia, the meat of MW was purported to improve a person's ability to withstand chemotherapy for cancer, the pelt and bones to cure rheumatism and prevent osteoporosis, and pieces of skin to block malicious attempts of witchcraft (V. Sandoval, pers. comm.).

Retaliatory Killing for Livestock Damage

Killing of "problem animals" is an important source of maned wolf mortality in some areas (Paula et al., 2008). Over about a dozen years, Dietz (1984) recorded 21 maned wolf deaths caused by people; 16 of which occurred while MW were preying on chickens. Methods varied: "seven were shot, five were run down and killed by dogs, [and] four were trapped" (Dietz, 1984:27). Because maned wolf predation on poultry can be prevented with nighttime enclosures and predation does not extend to high-value livestock (cattle), human–MW conflict does not seem to be a severe threat to the species. MW are perceived to kill hoofed stock in some areas, but the lack of evidence in studies of diet suggests that hoofed stock predation is extremely rare or folkloric legend. In Bolivia, some cattlemen believe that MW kill calves to drink their blood, and in the Beni Department, a few ranch owners pay a bounty

FIGURE 7.5. One of two maned wolf skins found on an estancia in Bolivia. The wolf was killed for medicinal use of body parts. (Photograph by Vanessa Sandoval)

for killing MW as well as for jaguar and puma (M. Herrera, pers. comm.).

Fire and Fire Suppression

Fire and fire suppression are human activities that threaten maned wolf habitat (Klink and Machado, 2005). Outside of protected areas, farmers set annual fires for weed control and pasture maintenance that can inhibit the fruiting of woody plants for several years, depriving MW of fruit resources (Chapter 4; Sanaiotti and Magnusson, 1995). Inside protected areas, managers prevent and suppress fires, leading to the total loss of the grassland habitat through overgrowth by woody shrubs and trees that shade out grasses. These grass-free shrublands are depauperate of the rodents on which MW feed (Chapter 4; Emmons, unpublished) and fire suppression can lead to a vast accumulation of dry plant matter. The resulting buildup can fuel infrequent but exceptionally destructive fires (Silveira et al., 1999). In Emas NP, where protected area management resisted the controlled use of fire, catastrophic fires killed hundreds of large mammals and "a maned wolf *Chrysocyon brachyurus* was observed alight, running along a fire line towards a dead end" (p. 111, Silveira et al., 1999). A territorial maned wolf pair on our study area disappeared without trace after a fire burned the entire area in October 2009 (Chapter 6, Figure 1.10). We do not know when or how the pair died, but it was the only year that more than one collared adult resident was presumed to have died.

Although the balance between too much and too little fire is a site-specific function of the flora, climate, and soil, we believe that the appropriate fire frequency for maned wolf habitat is about every 3 to 4 years. Prior to European colonization, burn intervals ranged from three to 10 years and savanna fruit productivity requires at least three years to recover to pre-burn levels (Hoffman, 1998; Sanaiotti and Magnusson, 1995). Silveira et al. (1999) suggest that after three years, the accumulated fuel load creates a high risk of a catastrophic fire. Because recovery times vary between savanna shrub species, a spatial and temporal heterogeneity is required to maintain maximal populations of woody fruiting plants (such as *Solanum* spp., Anonnaceae spp., *Alibertia edulis*, and *Miconia albicans*). Our data also hint that fruit production may start to decrease the fourth year after fires (Table 4.5), which we attribute to increased loads of insect parasites on fruits, coupled with the waning of effects of ash fertilizers.

At our study site in NKP, we suspect that fire contributed directly to short-term cavy and armadillo declines in the NKP savanna at Los Fierros (Chapter 4), and indirectly, to long-term declines. Emmons hypothesized that dense atmospheric smoke from large, regional fires raises nocturnal temperatures and prevents dew formation, decreasing an important water source for savanna rodents and microbiota during months of drought (Emmons, 2009). Whether fire-related or perhaps related to some broader climatic shift, the volatility of the maned wolf food base has emerged from our studies in NKP as a potentially important threat to maned wolf fitness, but one perhaps amenable to management.

Climate Change

MW do not survive in hot and dry climates. The geographic range of MW skirts around Chaco habitat in western Paraguay and Bolivia, where annual precipitation is 550–1000 mm annually and temperatures can reach 40°C in the hottest month of January. Pautasso (2009) estimated that more than 10% of MW die in periods of extreme drought in Santa Fe, Argentina (2008, 615 mm), including deaths due to thirst-driven MW killed at drinking points for cattle and poisoned by drinking from the only surface water available, toxic canals.

In the next 70 years, temperatures are projected to increase across the maned wolf geographic range (Table 7.3; Intergovernmental Panel on Climate Change [IPCC], 2007). Comparing seven models, Boulanger et al. (2006) estimate that the region will warm by as much as 4°C by 2075–2100. In Chapter 2, we showed that maned wolf activity had a clear relationship with temperature, abruptly decreasing above 27°C–29°C and nearly ceasing above 30°C (Figure 2.2A). In a +4°C scenario, MW are

TABLE 7.3. Projected changes in temperature and precipitation in Amazonia, 2020–2080. Source: Intergovernmental Panel on Climate Change (2007).

Year	Season	Projected temperature change (°C)	Projected precipitation change (%)
2020	Dry season	+0.7 to +1.8	–10 to +4
	Wet season	+0.5 to +1.5	–3 to +6
2050	Dry season	+1.0 to +4.0	–20 to +10
	Wet season	+1.0 to +4.0	–5 to +10
2080	Dry season	+1.8 to +7.5	–40 to +10
	Wet season	+1.6 to +6.0	–10 to +10

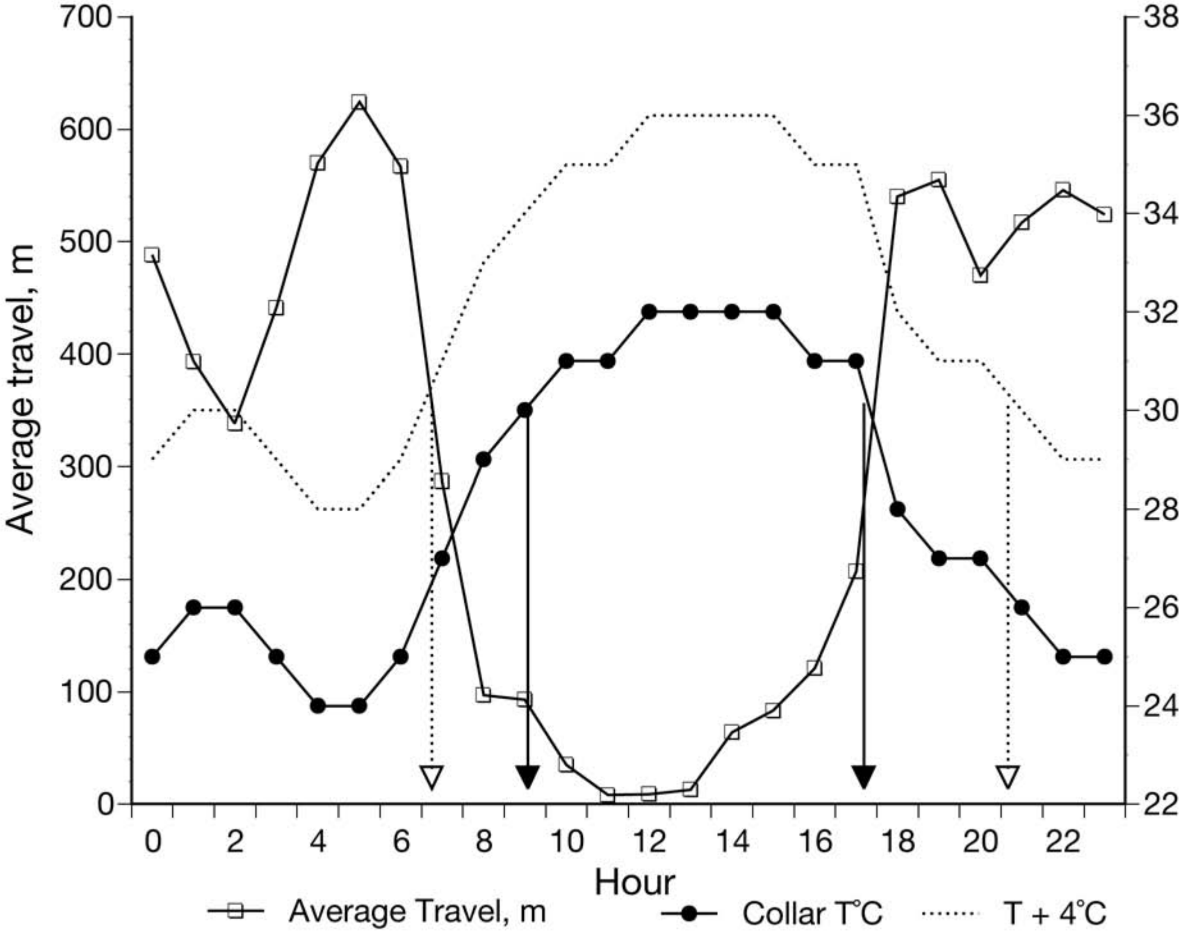

FIGURE 7.6. A modified Figure 2.2B (Chapter 2), illustrating a projected +4°C temperature change. Female maned wolf F3 2004–2005 average hourly travel (left axis, open squares) and average hourly collar temperature (right axis, closed circles); broken line is the collar T°C with 4°C added; vertical solid lines indicate the hour where the 2004–2005 collar temperature curve intersects 30°C (where travel nearly ceases); outer vertical dashed lines indicate where the same curve +4°C intersects 30°C. In the projected scenario, the temperature reaches at 30°C about 2.8 hours earlier in the morning (~0715) and goes below 30°C about 1.5 hours later in the evening (~2000), removing about 5 hours of peak travel time from the current maned wolf activity pattern.

projected to lose 5 hours of daily activity time (Figure 7.6). To compensate, all maned wolf behavior—foraging, social interactions, travel—would need to either become more efficient (i.e., accomplish the same amount in less time) or take place under heat stress that would require permanent proximity to water. In our study site at Los Fierros, the observed loss in body weight and reproductive failure of MW during a rodent decline is evidence that our study animals are living near their energetic limits. The stress of adapting to the new rhythms of a warmer climate is likely to push more marginal populations of MW to extinction.

Our +4°C adjustment (Figure 7.6) is an oversimplified representation of the complex climatic factors that will interact at a finer scale than the broad projections of the IPCC or Boulanger (2006). It also ignores all other environmental responses (vegetation change, reduction in rodent carrying capacity, water scarcity) to a 4° change in temperature. We believe, however, that our example illustrates the physiological limits that conservation biologists soon will be forced to consider, as well as the data that current behavioral ecology fieldwork can contribute to such scenarios. Precipitation and maned wolf water regulation will be even more difficult to predict and manage. The IPCC suggests that rainfall in the Amazonian region may increase or decrease from current levels. Given the great distances that MW traveled to seek water at NKP, we expect any decreases in precipitation to have at least as great, if not greater, an effect on maned wolf populations than would temperature increases alone.

Threats to Maned Wolf Habitat Integrity

As illustrated by the discussion of fire management, the health of maned wolf populations depends on the health and functionality of the ecosystems they inhabit. The major threats shared by species that co-occur with MW and are components of intact savanna ecosystems are also threats to MW, and the conservation of MW could likewise preserve those taxa.

To identify the species that share threats with MW, we used the search function of the IUCN Red List (Version 2009.2) and filtered species by country, habitat, and threat type. Of 1,080 terrestrial vertebrate species that share range countries and habitat types with MW, 4% are classified as Vulnerable (*N* = 46), 3% as Endangered (*N* = 29), and 1% as Critically Endangered (*N* = 15; IUCN Red List). Of the four threats identified for MW by Rodden et al. (2008), agriculture is the most widely shared threat, followed by hunting, roads, and nonnative species (Figure 7.7). While nonnative species likely refers to domestic dogs in the maned wolf species assessment, exotic grasses, introduced as pasture for cattle, are a major threat to Cerrado biodiversity and exacerbate the effects of other threats (fire: Klink and Machado, 2005).

Three other threats to savanna and grassland species are widespread (listed for more than 10% of IUCN-assessed species), but not identified in the IUCN maned wolf assessment (Rodden et al., 2008): fire or fire suppression, logging or wood harvesting, and livestock ranching. Maned wolves share fire as a threat, and its effect should be considered in conservation efforts across the species' range. In contrast, selective logging is unlikely to directly affect maned wolf populations. Wood harvest does not target the open vegetation or fruit species on which MW

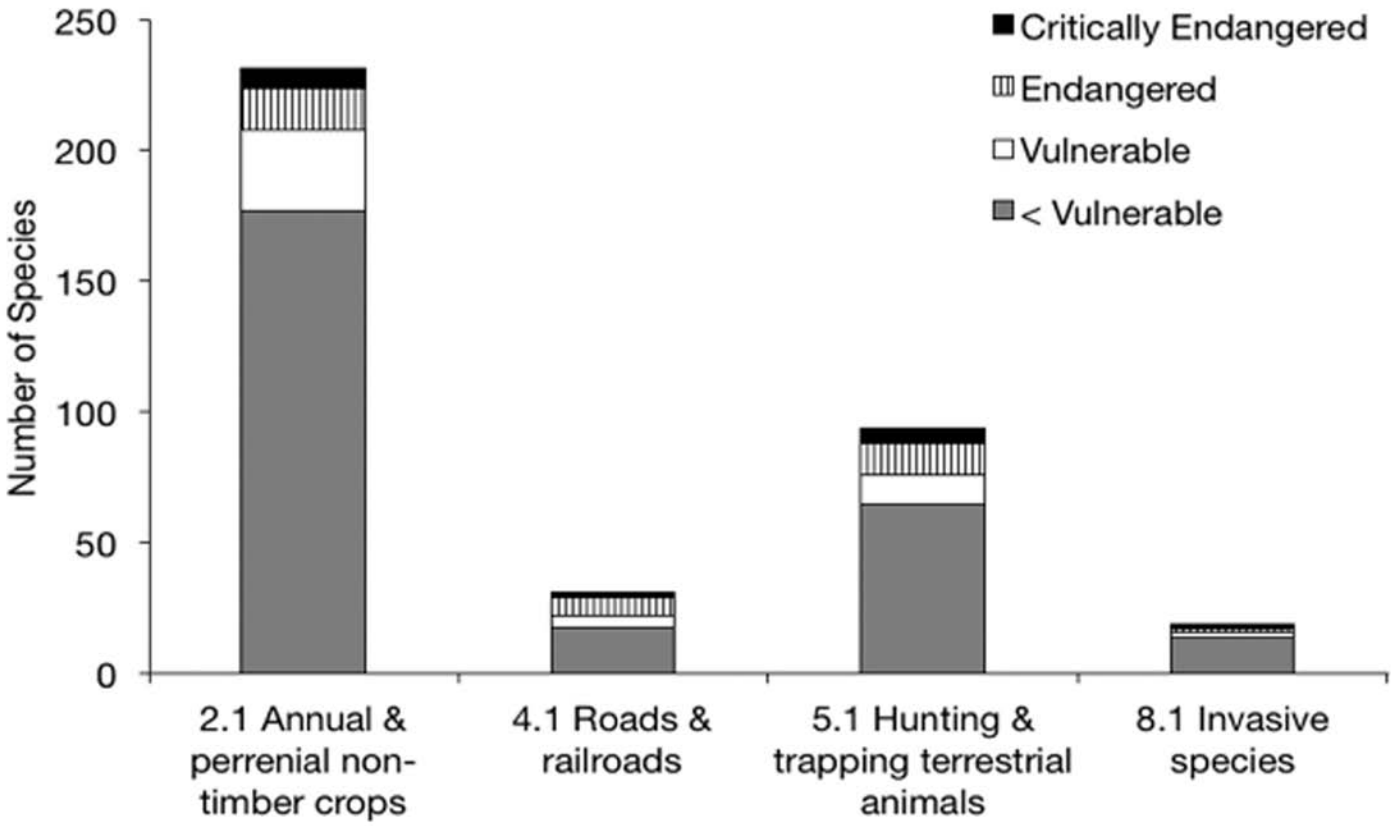

FIGURE 7.7. Number of savanna species that share IUCN threat categories (numbers) with MW by conservation status (IUCN Red List).

forage, so the fauna most likely to be affected are forest dwellers such as the monster rice rat (*Euryoryzomys lamia*) or tree nesters. Clear-cutting can increase available open habitat for MW (Quierolo et al., 2011).

Livestock ranching is likewise a mixed prospect for MW. Dietz (1984) found MW thriving on ranchland and Kawashima et al. (2007) suggested that MW may expand their range as forest is cut down for pasture, as has occurred in areas previously covered by Atlantic Forest (Queirolo et al., 2011; Santos et al., 2003). The lobeira fruit (*Solanum lypocarpum*) favored by MW can grow in abundance in rangelands and may even be facilitated by the disturbed areas associated with cattle ranching (Courtenay, 1994). Traditional cattle ranching on natural grasslands in Bolivia seems fully compatible with maned wolf survival, but conversely, “modern” ranching methods can destroy the plant and animal life on which MW depend. Pastures are bulldozed, burned, and seeded with invasive African grasses as forage (Klink and Machado, 2005). These grasses outcompete native vegetation and increase the intensity of fires, thus altering the system’s succession and recovery. Vynne (2010) detected few MW in the surveyed cattle pastures of Goiás, Brazil. Because some pastures have little biomass to support rodent populations and few fruiting woody species (Santos et al., 2003, Vynne, 2010), artificial pasture may present lower food availability for MW than natural areas or even some cropland. As planted pasture has become the most widespread land use across the maned wolf range (40% of the Cerrado biome: Klink and Machado, 2005), we are only beginning to learn how maned wolf ecology and population trends are affected by rangeland conditions and how land use interacts with other threats, such as increased exposure to ectoparasites, diseases, pesticides, and stressors (May-Júnior et al., 2009).

Our web sample does not reflect threats to Data Deficient species on the IUCN Red List, including three species of the rodent genus *Juscelinomys*. Two are endemic to the grasslands of NPK, where MW eat them (Chapter 4). These are the only known surviving populations of their genus, as the other species (*J. candango*, from a now-destroyed Brazilian Cerrado site), has no known populations (Emmons, 1999). *Juscelinomys* spp. and other rare cerrado grassland rodents such as *Kunsia tomentosus* and *Kerodon acrobata* are threatened by any destruction of their habitats. The local extinction of *Cavia aperea*, the chief rodent prey of MW at Los Fierros, shows that even common and widespread rodents can be sensitive to apparently small environmental variations (Emmons, 2009), as Magnusson et al. (2010) also found for *Necromys lasiurus*.

STRATEGIES TO REDUCE THREATS TO MW

Effective conservation action requires an understanding of the causal relationship between human activities and biodiversity threats. We constructed a conceptual model to diagram proximate and ultimate causes of maned wolf endangerment (Figure 7.8; Margoluis et al., 2009), based on the conservation issues known to affect MW and their habitat (Deem and Emmons, 2005; Dietz, 1984; Klink and Machado, 2005; Paula et al., 2008; Rodden et al., 2008).

More than describing how we understand the world to work, our conceptual model highlights which are the key threats and contributing factors where conservation efforts can intervene. We divide the effects of threats into those that directly affect MW (agriculture, domestic dogs, road traffic, and intentional mortality caused by people; Figure 7.8) and those that affect maned wolf grassland habitat (agriculture and fire management). Some contributing factors (maned wolf dispersal behavior, international demand for soya or biofuels) are unlikely to be influenced by a maned wolf conservation project and so would be unproductive as a focus for conservation efforts. Other factors, such as the perception that maned wolf body parts can cure sickness, can be mitigated by campaigns to change attitudes, values, and behaviors (Figure 7.9). Likewise, our veterinary team has worked to improve domestic dog health in the communities surrounding our maned wolf field site (Figure 7.10; Deem and Emmons, 2005; Bronson et al., 2009), as has been done by other maned wolf projects. Depending on the site and local capacity, programs can be developed to mitigate many causes of mortality (speed limits, incentives to provide legal frameworks to mitigate agricultural conversion).

RECOMMENDATIONS FOR NOEL KEMPFF MERCADO NATIONAL PARK

The conservation status of MW is tenuous within NKP. Because of the park’s relative isolation and protected status, MW are unlikely to suffer some threats (road kill), but the small and fragmented populations are susceptible to unpredictable factors such as the 2004–2007 rodent decline, droughts, flooding, and fires (Chapters 4, 5; Emmons, 2009). We present recommendations by scale: (1) local management within the park and (2), regional or country-wide management. Both are vital to maintaining the ecological resilience of the park and healthy maned wolf populations, but while regional leadership must prepare for and address an external dynamic (Hidrovía

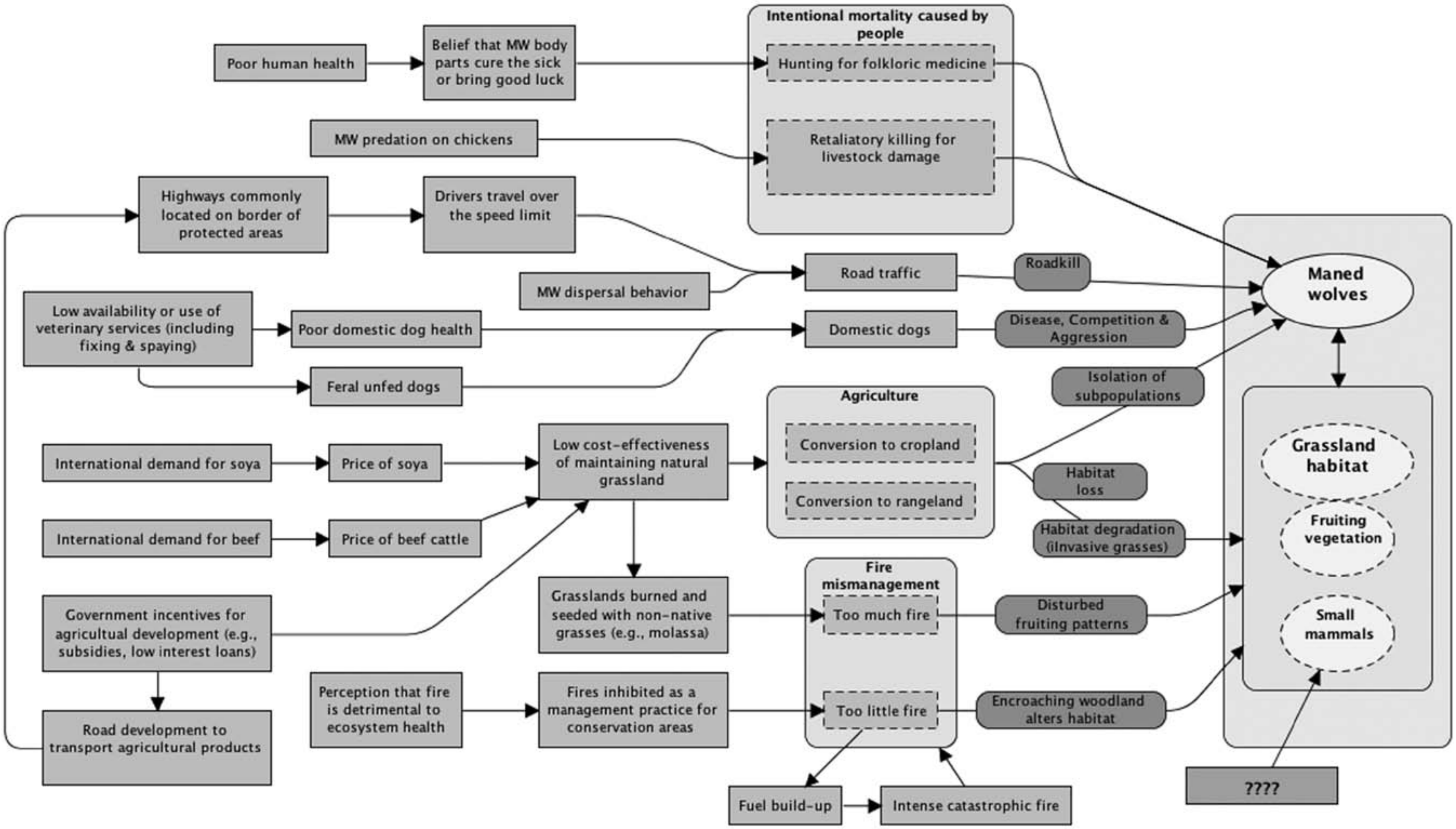

FIGURE 7.8. Conceptual model of the threats to maned wolf conservation and their contributing factors.

FIGURE 7.9. Public awareness poster about the ineffectiveness of animal parts as medicine, from Bolivia. The maned wolf in the lower right-hand corner is saying, "I'm not a pharmacy!" Color version of the poster is available at http://www.canids.org/species/Chrysocyon_brachyurus.htm. Artist: Alan Hesse.

FIGURE 7.10. Veterinarian Ellen Bronson monitoring domestic dog health in the community of Florida, outside NKP. Photograph by L. Emmons.

project and climate change), park management must tackle the on-the-ground direct threats to NKP MW (fire suppression and disease).

Local park management recommendations:

1. **Mitigate the effects of fire suppression and catastrophic fire by conducting yearly prescribed burns.** To maintain optimal habitat for MW, NKP lowland savannas will require burning with sufficient frequency to preserve the habitat as grassland, but in a spatial and temporal patchwork that maintains populations of woody fruiting plants (such as *Solanum* spp., Anonnaceae spp., *Alibertia edulis*, and *Miconia albicans*) in several stages of annual postfire regeneration on each maned wolf home range. In the flood-prone lowland savannas, prescribed burning in patches should occur on a 3–4 year rotation, and in months when conditions are not so dry that fires escape into nonprescribed areas. More urgently, overgrown savanna edges should be burned to restore the habitat's former extent. Existing roads can be cleared to act as fire breaks, as has been done in Emas NP, Brazil (Silveira et al., 1999). Savannas on the southern part of the Huanchaca Meseta burn regularly, perhaps too often, from fires started on fazendas in Brazil that propagate yearly across the tableland, but the northern part of the Meseta seems to be losing its grassland to overgrowth by shrubs.
2. **Suppress disease transmission between wildlife and domestic dogs and cats by excluding domestic animals from the park and vaccinating those on the periphery.** Exposure to a number of pathogens was found at high prevalence in domestic dogs near the park, but not simultaneously in the NKP maned wolf population (canine distemper and rabies; Bronson et al., 2008; Chapter 6). This encouraging result suggests that domestic dogs are not directly

exposing MW to disease. Maintaining this separation is extremely important and to continue to do so, we recommend two universal rules: "1) prohibit the release of individuals of wild species from captivity into wild populations, unless the wild populations are threatened and in need of augmentation for survival, and strict health and genetic evaluations have been performed before release; and 2) exclude all pets and other domestic animals from parks" (Deem and Emmons, 2005:196). While perhaps not by direct transmission from dogs, MW in NKP have been exposed to a number of potentially lethal diseases that are transmitted by domestic dogs and cats. We recommend regular rabies vaccination of local pets and livestock and distemper vaccination of dogs. Both diseases have effective vaccines and recur in multiyear cycles when new generations of susceptible animals are at sufficient density. Healthier pets also mean healthier children.

Regional-scale recommendations:

1. **Seek partnerships with adjacent ranchers to resist and mitigate the effects of agroindustrial development.** The proposed Hidrovía inland waterway and consequent traffic on the park border would be disastrous to maned wolf populations. Adjacent ranches, now in seminatural grassland, would likely be converted into agroindustry and isolate MW in the park. Buffers should be sought to maintain adjacent land in seminatural pasture with appropriate land management, including at least 20% set aside on each farm as an undeveloped refuge for wildlife (as per Brazilian land use laws). Partnerships should also be established with ranchers between the park and adjacent villages (e.g., Campamento) to create seminatural cerrado habitat for maned wolf subsistence and dispersal.
2. **Prepare for climate change by increasing connectivity to other grasslands.** The type of peripheral land connectivity described above is also thought to be one of the best strategies for protected areas to prepare for climate change (Hannah, 2008). Early interventions can be both more effective and less costly than delayed or no action (Hannah et al., 2008). If climate changes render some fragments of savanna unsuitable for MW (lack of dry season water), park managers should consider support for more intensive management interventions, such as maintaining water holes at several points in August–October.

CONCLUSION

Enabled by the technology of GPS telemetry, we are now in a golden age of maned wolf study. Insight into their ecology and daily lives is growing sharper and a growing cohort of researchers contributes information about wild maned wolf populations. We are also more acutely aware of the human activities that threaten them. The species as a whole is endangered by unmitigated agroindustry. Where populations are small and isolated, a number of threats and management actions have been identified for conservationists and park managers. The next challenge is to link maned wolf conservation to the emerging threats of climate change, invasive grasses, and biofuel production. Long-term field studies have never been more important, but funders want quick results. Only longitudinal research supplies the baseline for detection of emerging problems and helps identify environmental change early enough to pose research questions and eventually help mitigate them (rodent declines: Emmons, 2009; biofuels: Vynne, 2010; climate change: Chapter 2).

As understanding of maned wolf ecology grows, so, too, does the evidence that MW are resilient for a large canid. Dietz (1984) reported that although MW were highly sensitive to the physical presence of people, they were tolerant of agriculture and persisted where ranchers and farmers had earned a livelihood for generations. Vynne (2010) has found MW in soya fields, Lyra-Jorge et al. (2008) documented their presence in eucalyptus plantations, and Santos et al. (2003) showed them to thrive on dairy farms cut from Atlantic forest. If sufficient resources are available, MW do not need intensive management. Long-distance dispersal is crucial to the conservation success of species in fragmented landscapes (Trakhtenbrot et al., 2005) and fortunately, MW are far travelers. In rare events, they have been recorded crossing hundreds, even thousands, of kilometers of unsuitable habitat (Queirolo et al., 2011). Models, imperfect as they are, suggest that maned wolf populations have the potential to grow quickly (Paula et al., 2008) and that some populations are expected to persist for hundreds of years, even under worst-case scenarios (high inbreeding, high rates of habitat loss, and high population variability; Rodrigues and Diniz-Filho, 2007). Nonetheless, we should not diminish the evidence that in the past hundred years, MW have lost extensive habitat and geographic range, and the status of many subpopulations is desperate. However, it is also clear that if enough prey and fruit can be kept in the landscape, MW can live beside us for a long time to come.

ACKNOWLEDGMENTS

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APPENDIX A: MANED WOLF SUBPOPULATIONS

In October 2005, a PVA workshop was held in Serra da Canastra National Park, Brazil (Paula et al., 2008). National delegations identified 19 maned wolf subpopulations in Brazil, Argentina, and Paraguay. Bolivia and Peru were considered later (R. C. Paula and L. H. Emmons, unpublished) with three additional subpopulations being recognized. Here, we compile workshop results into one map (Figure 7.11). Each identified maned wolf subpopulation, or landscape, is represented as a numbered polygon. We know the map is incomplete. For example, subpopulations were not identified in the Brazilian state of São Paulo or southern Brazil because workshop participants considered

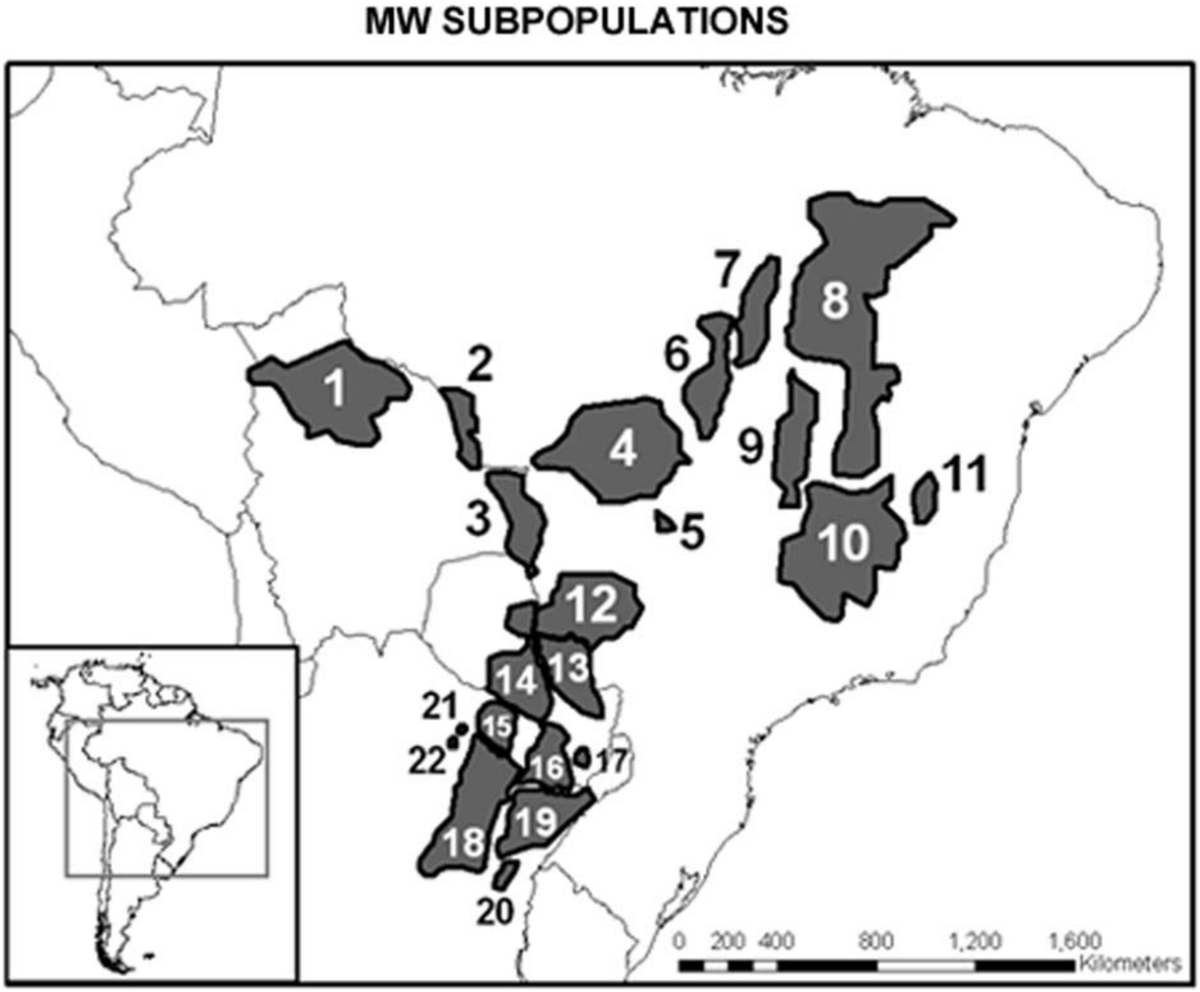

FIGURE 7.11. Twenty-two identified subpopulations (or landscapes) for MW. Source: Paula et al. (2008) and Quierolo et al. (2011).

those populations "isolated and very small" (Paula et al., 2008). We have also introduced a source of error by manually drawing the polygons in ArcGIS 9.1, based on the figures in Paula et al. (2008) and political and natural boundaries.

We tabulate the basic details of each subpopulation, including protected areas and population estimates given by Paula et al. (2008; Table 7.4). Workshop participants estimated that 23,631 MW exist in the wild. On the basis of the published range of maned wolf densities and our own upwardly revised estimate of MW in Bolivia, we propose that the number is likely closer to 15,000. The total estimated area of the 22 landscapes is approximately 1.5 million km^2. Within that, approximately 200,000 km^2 is included within a protected area under the most inclusive definition: all IUCN categories, plus uncategorized. The IUCN Protected Areas I–IV compose 102,000 km^2, IUCN Protected Areas V–VI contribute 63,000 km^2, and all others, 34,000 km^2. These are likely maximum estimates of protected coverage for MW because not all protected areas in the subpopulation margins likely support MW, and much of the habitat within them is not suitable (e.g., only a third of NKP is savanna).

We reemphasize that Figure 7.11 is hypothetical and that the existence and margins of subpopulations need verification by local experts. New data have already improved upon this map; for example, in Landscape 18, the distribution of MW has been refined into two areas of high density, one in Santa Fe Province, the other straddling the border of Córdoba and Santiago del Estero Province, and a larger, less dense zone of occupation that is fully joined with Landscapes 19 and 20 (Pautasso, 2009: fig. 9). Queirolo et al. (2010) also present more detail on connectivity and presence in individual states and provinces. For consistency we did not revise any subpopulations from the 2005 contributions. Revising the global distribution of MW is a continual necessity, and also a Herculean task that is best tackled by the community of all those interested in the status and future of MW. A campaign for mammals on the model of the Christmas Bird Counts in the United States, perhaps with the participation of schools, or a web tool like iNaturalist.org might yield better data on current distribution trends.

TABLE 7.4. Twenty-two identified subpopulations of MW in Brazil, Argentina, Paraguay, Bolivia, and Peru. Source: Paula et al. (2008).

Landscape No.	Description	Representative Protected Areas (PAs)	Population estimate	Total Area	PA I–IV	PA V–VI	Other PAs	Total PAs
1	Bolivia and Peru. Includes populations in the grasslands of the Beni Department, Bolivia, and the tiny population in the Pampas del Heath National Sanctuary, Peru. Some exchange is expected with Noel Kempff Mercado population (2).	Estación Biológica del Beni (Biosphere Reserve, IUCN VI); Estancias San Rafael (Wildlife Refuge, IUCN IV); Estancias Elsner Espírir (Wildlife Refuge, IUCN IV); El Dorado (Wildlife Refuge, IUCN IV); Madidi National Park (IUCN II); Bahuaja Sonéné National Park (Peru, IUCN II).	130	150,343	5,259	1,440	3,130	9,829
2	Bolivia. Includes the populations in and around Noel Kempff Mercado National Park, Santa Cruz Department. Some exchange is expected with the Beni (1) and San Matías (3) populations.	Noel Kempff Mercado National Park (IUCN II).	180	25,229	14,377	0	0	14,377

(*continued*)

TABLE 7.4. *Continued*

Landscape No.	Description	Representative Protected Areas (PAs)	Population estimate	Total Area	PA I–IV	PA V–VI	Other PAs	Total PAs
3	Bolivia. Includes the populations in the Pantanal and in the two large protected areas (Otuquis National Park in the south and San Matías in the north) and associated reserves, Santa Cruz Department. Some exchange is expected with the Noel Kempff Mercado (2) and potentially with the Mato Grosso do Sul (12) and West Paraguay (14) populations.	San Matías Integrated Management Natural Area (IUCN IV); Otuquis National Park (IUCN II).	70	33,886	33,886	0	0	33,886
4	Brazil. Includes the populations in the cerrado of central and southern Mato Grosso State. Some exchange is expected with the Emas (5) and eastern Mato Grosso (6) populations.	Cabeceiras do Rio Cuiabá (State Environmental Protection Area, IUCN V); Chapada dos Guimarães (State Environmental Protection Area, IUCN V); Serra das Araras (State park, IUCN II); Dom Osório Stoffel (State Park, IUCN II); Serra Azul (State Park, IUCN II); Gruta da Lagoa Azul (State Park, IUCN II); several indigenous reserves (the largest: Parabubure Indigenous Area).	1,764	165,450	990	6,804	8,444	16,237
5	Brazil. Includes the cerrado populations in and around Emas National Park, southern Goiás State. Some exchange is expected with the southern Mato Grosso (4) and Mato Grosso do Sul (12) populations.	Emas National Park (IUCN II), associated buffer PAs around Emas National Park.	127	3,374	1,283		1,088	2,371
6	Brazil. Includes the populations in the cerrado of eastern Mato Grosso, which includes several indigenous reserves. Some exchange is expected with southern Mato Grosso (4) populations and potentially with the western Tocantins (7) population.	Rio das Mortes (State Wildlife Refuge, IUCN III); Meandros do Rio Araguaia (Environmental Protection Area, IUCN V); indigenous reserves with MW records: Pimentel Barbosa Indigenous Area, Areões Indigenous Area.	1,412	51,952	3,312	2,496	5,256	11,064

(*continued*)

TABLE 7.4. *Continued*

Landscape No.	Description	Representative Protected Areas (PAs)	Population estimate	Total Area	PA I–IV	PA V–VI	Other PAs	Total PAs
7	Brazil. Includes the populations in and around the cerrado and flooded grasslands of Bananal Island, the largest fluvial island in the world, western Tocantins State. Potential exchange is expected with eastern Mato Grosso (6) and Piauí and Maranhão (8) populations.	Araguaia National Park (IUCN II); also indigenous area, large adjacent to south of National Park: Parque do Araguaia Indigenous Area.	1,625	41,927	5,402	14,954	4,302	24,658
8	Brazil. Includes populations in the Cerrado of Piauí, Bahia, Maranhão, and eastern Tocantins States. Some exchange is expected with the Goiás (9) and central Minas Gerais (10) populations.	Mirador (State Park, IUCN II); Chapada das Mesas National Park (IUCN II); Uruçui-Una Ecological Station (IUCN Ia); Nascentes do Rio Parnaiba National Park (IUCN II); Cabeceira do Rio das Balsas, (State Environmental Protection Area, IUCN V); Serra Geral do Tocantins (IUCN Ia); Jalapão (State Park, IUCN II, and State Environmental Protection Area, IUCN V); Serra da Tabatinga (Environmental Protection Area, IUCN V); Bacia do Rio Janeiro (State Environmental Protection Area, IUCN V); Serra do Lajeado (State Environmental Protection Area, IUCN V); Cristópolis National Forest (IUCN VI); Veredas do Oeste Baiano (Wildlife Refuge, IUCN III); Grande Sertão Veredas (IUCN II); Veredas do Acari (State Park, IUCN II); Cavernas do Peruaçu (Environmental Protection Area, IUCN V); several indigenous areas, including Kraolandia Indigenous Area.	10,384	327,751	30,024	9,207	6,440	45,672

(*continued*)

TABLE 7.4. *Continued*

Landscape No.	Description	Representative Protected Areas (PAs)	Population estimate	Total Area	PA I–IV	PA V–VI	Other PAs	Total PAs
9	Brazil. Includes populations in the cerrado of Goiás. Some exchange is expected with the Bahia (8) and central Minas Gerais (10) populations.	Chapada dos Veadeiros National Park (IUCN II); buffer: Pouso Alto (State Environmental Protection Area (IUCN V); Planalto Central (Environmental Protection Area, IUCN V); Bacia do Rio São Bartolomeu (Environmental Protection Area, IUCN V); several other EPAs in this Planalto complex.	2,173	55,551	1,334	14,077	0	15,412
10	Brazil. Includes populations in the cerrado of central Minas Gerais. Many MW records from Queirolo et al. (2011) were identified to the south of this landscape, suggesting that its margins may be larger or that distinct subpopulations exist in southern Minas Gerais and São Paulo States. Some exchange is expected with the Bahia (8), Goiás (9), and northeastern Minas Gerais (11) populations.	Serra da Canastra National Park (IUCN II); Córrego Feio e Fundo e Areia (State Area of Special Protection, IUCN V); Confusão (State Area of Special Protection, IUCN V); Sempre-Vivas National Park (IUCN II); Biribiri State Park (IUCN II); Águas Vertentes (State Environmental Protection Area (IUCN V).	3,091	186,264	3,501	1,165	0	4,666
11	Brazil. Includes populations in the Cerrado of northeastern Minas Gerais. Some exchange is expected with the central Minas Gerais (10) populations.	Grão-Mogol State Park (IUCN II); Acauã State Ecological Station (IUCN Ia).	386	13,336	409	0	0	409
12	Brazil. Includes populations in the Pantanal and cerrrado of Mato Grosso do Sul. Some exchange is expected with the Emas (5) and potentially with eastern (13) and western (14) Paraguay.	Serra da Bodoquena National Park (IUCN II); Kadiwéu Indigenous Area; Cachoeirinha Indigenous Area; Taunay/Ipegue Indigenous Area; Buriti Indigenous Area; Nioaque Indigenous Area; Jatayvari Indigenous Area; Ñande Ru Marangatu Indigenous Area; Pirakua Indigenous Area; Dourados Indigenous Area; Panambizinho Indigenous Area	784	92,422	772	0	3,204	3,975

(*continued*)

TABLE 7.4. *Continued*

Landscape No.	Description	Representative Protected Areas (PAs)	Population estimate	Total Area	PA I–IV	PA V–VI	Other PAs	Total PAs
13	Paraguay. Includes populations in 12–20 cerrado and subtropical grassland areas scattered in eastern Paraguay. Potential exchange with Mato Grosso do Sul (12) and western Paraguay (14) populations.	Morombi Private Reserve (IUCN IV); Natural Reserve de Bosque Mbaracayú Private Reserve (IUCN V); Cerro Corá National Park (IUCN II); Arroyo Blanco Private Reserve (IUCN IV); Bella Vista National Park (IUCN II); San Luis National Park (IUCN II); Paso Bravo National Park (proposed).	150	50,674	653	545	993	2,191
14	Paraguay. Includes populations in the Pantanal and subtropical savanna in western Paraguay. Very little protected area coverage, but contains relatively low human density. Potential exchange with Mato Grosso do Sul (12), eastern Paraguay (13), and southern Paraguay (16).	Río Pilcomayo (IUCN II).	500	65,378	9	0	74	82
15	Argentina. Includes populations in the subtropical grasslands of Formosa Province. Few MW records from Queirolo et al. (2011) were identified within this landscape. Exchange is expected with Santiago del Estero (18) populations.	No protected areas identified.	100	22,671	0	0	0	0
16	Paraguay. Includes populations in the subtropical grasslands and wetlands of southern Paraguay. Exchange is expected with San Rafael (17) populations and potentially with western Paraguay (14), Corrientes Province (19), and Santa Fe Province (18) populations.	Yabebyry Wilderness Area (IUCN IV); Ybycuí National Park (IUCN II); Macizo Acahay National Monument (IUCN III); Ypacaraí National Park (IUCN II).	150	35,472	554	3	1,225	1,781

(*continued*)

TABLE 7.4. *Continued*

Landscape No.	Description	Representative Protected Areas (PAs)	Population estimate	Total Area	PA I–IV	PA V–VI	Other PAs	Total PAs
17	Paraguay. Includes a small population in and around the subtropical savannas of San Rafael NP. Exchange is expected with southern Paraguay (16) populations.	San Rafael Managed Resource Reserve (IUCN VI); Caaguazú National Park (IUCN II).	30	2,990	50	624	0	674
18	Argentina. Includes populations in the subtropical grasslands of Santa Fe, Córdoba, and Santiago del Estero provinces. Some exchange is expected with Formasa Province (15) and Chaquito (21) populations and potentially with southern Paraguay (16) and Corrientes (19) and Entre Ríos (20) province populations.	Chiquita Nature Reserve, (IUCN VI).	230	106,492	0	42	0	42
19	Argentina. Includes populations in the subtropical savannas and wetlands of Corrientes and Misiones provinces. Several MW records in Queirolo et al. (2011) were identified to the east of this landscape, suggesting that its margins may be larger or that distinct subpopulations exist in the Brazilian state of Rio Grande do Sul and possibly into northern Uruguay.	Iberá Nature Reserve, IUCN Category VI	300	60,718	0	11,190	0	11,190
20	Argentina. Includes populations in the subtropical savannas of Entre Ríos Province. Some exchange is expected with Corrientes Province (19) populations and potentially with Córdoba Province (18) populations.	No protected areas identified.	20	5,734	0	0	0	0

(*continued*)

TABLE 7.4. *Continued*

Landscape No.	Description	Representative Protected Areas (PAs)	Population estimate	Total Area	PA I–IV	PA V–VI	Other PAs	Total PAs
21	Argentina. Includes a small population, labeled Chaquito in Paula et al. (2008). Expected to exchange individuals with the Santiago del Estero (18) populations.	No protected areas identified.	10	844	0	0	0	0
22	Argentina. A newly described population in Paula et al. (2008). Potential exchange with Santiago del Estero (18) populations.	No protected areas identified.	15	1,119	0	0	0	0

8

Synthesis

Louise H. Emmons

BEHAVIORAL FLEXIBILITY OF MANED WOLVES AND ITS LIMITS

Our multiyear study uncovered features of maned wolf ecology and behavior that were unsuspected when we set out. Some may have been unique to our Los Fierros study site, while others might be general to the species but heretofore undescribed. Many patterns of behavior turned out to be quite variable, which is no surprise in a member of the Canidae. We studied too few individuals to assess which variable behaviors, if any, were the norm in the Los Fierros population, especially because averaging year-to-year data was precluded by unexpected and major environmental changes that occurred in the short decade of our research. These results mandate caution about generalizing to the species from patterns of ecology or behavior observed in either one season, one year, one place, or one set of individuals.

Maned wolves (MW) declined sharply at Los Fierros during our study, from three pairs with many helpers and young, to a solitary pair (Chapters 4, 5). By chance we may have witnessed the fragility of small populations faced with additive negative environmental events. Increasing dry season drought, unusually high and late flooding of the savanna, prey decline, and a catastrophic fire, all followed one another within 4 years. Lifetime residents of the zone had not witnessed equal drought or flooding, and the extinction of cavies from Los Fierros suggests a new change, as cavies had been present for decades, at least. These environmental events may or may not have been exacerbated by global warming, compounded by the El Niño–Southern Oscillation cycle and massive regional deforestation in Brazil, which yearly covers the sky with smoke for many weeks (Figure 7.4; Emmons, 2009). At the risk of "crying wolf," it seems safest to assume that major anthropic climatic changes are now damaging the Cerrado and that mitigation should be advanced.

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MW may be not flexible enough to adapt behaviorally to much environmental variation. Their historic habitat breadth and geographic range (Chapter 7) were both much smaller than those of most large, and many small, Canidae (e.g., bush dogs, crab-eating zorros, red foxes, coyotes, gray wolves, golden jackals, and formerly, both dholes and African wild dogs, among others; Sillero-Zubiri et al., 2004). Of the large Canidae, only the Critically Endangered Ethiopian wolf (IUCN Red List, 2009) is more habitat-restricted, and it may not be coincidental that it too, feeds on grassland rodents, albeit as a carnivore specialized on high-density diurnal alpine species (Sillero-Zubiri and Marino, 2004). Their geographical/ecological restriction to southern humid grasslands makes MW habitat specialists, compared to the latitudes achieved by many other Canidae.

IMPLICATIONS OF MANED WOLF OMNIVORY

Maned wolves differ from other large Canidae in their omnivorous diet, small litter size, group size of a pair plus one, and solitary foraging (Table 8.1). The postnatal growth rate of a maned wolf litter, in relation to maternal metabolic size, is lower by a factor of nearly 3 than that of the lowest among five other canid species, from gray wolf to red fox, placing MW close to black bears (Oftedal and Gittleman, 1989). The one character that sets MW into a class by themselves is their large body size. Their diet and social behavior resemble those of many small species such as *Cerdocyon thous* (crab-eating zorro), *Pseudalopex griseus* (chilla), and *Pseudalopex gymnocercus* (pampas fox), the common small Canidae of the Southern Temperate Grasslands (Courtenay and Maffei, 2004; González del Solar and Rau, 2004; Lucherini et al., 2004). All of these small species have much broader habitat and latitudinal ranges than do MW.

Carbone et al. (1999), based on an empirical model, hypothesized that carnivores above about 21 kg body mass cannot energetically be entirely supported by a diet of small prey. Maned wolves seem to validate this hypothesis. The Ethiopian wolf (*Canis simensis*), a strict predator on rodents (Sillero-Zubiri and Gottelli, 1995), is about 5 kg below this limit (Table 8.1). Paradoxically, the giant maned wolf can probably exist in its predatory role only because half of its diet is fruit. Carnivora that are omnivores, such as bears, can be very large, but this results in extremely low female reproductive output (Geffen et al., 1996).

Maned wolves probably could not capture enough small mice, arthropods, and birds to live and reproduce on these alone. Perhaps they could thrive uniquely on abundant cavies and armadillos, but they nowhere have diets primarily of prey (Chapter 4). Rodent abundance can roller-coaster wildly from year to year, and worldwide, mice are unpredictable resources (Branch et al., 1999;

TABLE 8.1. Characteristics of all large Canidae (>15 kg) and the smaller crab-eating zorro that is everywhere syntopic with maned wolves (MW). All listed species are said to be territorial, and all species with packs are said to include one breeding pair and helpers (their previous offspring or others). The disperser sex is usually the one that is not the helper sex. Data from Macdonald and Sillero-Zubiri, (2004,) and Sillero-Zubiri et al. (2004), except litter growth from Oftedal and Gittleman (1989) and weights of MW from Jácomo et al. (2009). Helpers have not been confirmed in zorros. Here n/a, not available.

Species	Male, kg	Female, kg	Social group	Litter size	Helper sex	Diet	Home range size, km²	Litter growth per MBS*(g/d)
Maned wolf	26.7	24.6	Pair, 0–1 helpers	1–3	Female	Small prey, 50% fruit	20–110	7.2 (76)
Gray wolf	20–80	16–55	pack 5–36	6	Both	Large mammals	75–2,500	67.3 (886)
Red wolf	29	24	pack 1–12	1–10	Both	Medium mammals	46–226	n/a
Ethiopian wolf	16	13	pack 3–13	2–10	Male	Diurnal rodents	6	n/a
Dhole	18	13	pack 5–25	5–10	Male	Large mammals	40–80	41.6 (298)
African wild dog	28	24	pack 2–40	7–10	Both	Large mammals	400–1,300	n/a
Crab-eating zorro	4	6	pair	3.1	n/a	Omnivore	1–5	n/a

*Postnatal growth rate of litter in relation to maternal metabolic size (gk $g^{0.75}d^{-1}$), and postnatal growth weight of litter (grams/day).

Emmons, 2009; Kelt et al., 2004). Armadillos were likewise present in some years in the maned wolf diet at Los Fierros but absent in others (Chapter 4). Some armadillos aestivate in dry periods, so that even if present, they can be unavailable (Erika Cuellar, pers. comm.). Fruit is also highly variable and unpredictable, especially in fire-prone savannas, and alone could not support a breeding maned wolf. Omnivory is thus a hedge against resource swings in both fruits and short-generation prey in a world of unpredictable climate. Frugivory may make life at its body size possible for MW, but in Noel Kempff Mercado National Park (NKP) it does not make life easy.

South America has no large-bodied, pack-hunting, predatory Canidae, although nearly a third of living taxa are found there. The only hypercarnivorous, pack-forming species on the continent, the bush dog, is the World's smallest (5–8 kg), and it feeds chiefly on armadillos and giant rodents (agoutis and pacas, 4–10 kg) that a pack can cooperate to run down or extract from their burrows (Zuercher et al. 2005), which MW cannot do. Guanacos (*Lama glama*), now the only large, high biomass, lowland South American grassland herbivores, have no range overlap with MW. The low large herbivore abundance and biomass of the Anthropocene (de Vivo and Carmignotto, 2004) thus provides no ecological place for a "South American Wild Dog," and MW probably owe their historical survival to their omnivory, whereas the Late Pleistocene dire wolf (*Canis dirus*) was extinguished in South America with is megafaunal prey (Cione et al., 2003).

SOCIAL GROUPINGS OR NOT?

In their excellent review of the forces shaping the sociobiology of Canidae, Macdonald et al. (2004a) note two situations that could allow selection for grouping in Canidae: (1) the home range contains sufficient resources to sustain additional individuals, without incurring prohibitive costs to the breeding female or pair; and (2) constraints on dispersal opportunities would favor the retention of young past maturity. We infer from the increase in territory size when cavies vanished from the Los Fierros study area that territories may not include much excess food supply, so condition 1 may limit grouping for MW in NKP. Because only MW with a territory are known to breed (Chapter 5), and all good habitat appears occupied, condition 2 certainly does apply to the MW of NKP. Possession of a suitable territory is an essential requirement for maned wolf reproductive success. That female helpers can inherit natal territories (Chapter 5) confirms condition 2 as a likely driver of young females remaining in the social group, while condition 1 may restrict their number to one. Moreover, small litters would limit the usefulness of more than one helper. Female MW appeared to be the "owners" of territories, and this might constrain helpers to females, as males would have no breeding future in a family. There is little evidence that grouping confers any foraging advantage to MW. Although Bestelmeyer and Westbrook (1998) apparently observed a maned wolf pair cooperate to hunt a deer and we recorded a pair often traveling together, cooperative hunting seems extremely rare, if it occurs at all.

The fruit moiety of the diet returns only about a third as much energy per kilogram consumed as does animal prey (Chapter 4; Table 4.6). A low rate of energy acquisition (herbivorous diet) in Carnivora is associated with low postnatal growth rates of the litter as a whole (Table 8.1; Oftedal and Gittleman, 1989). This is doubtless a factor underlying the tiny maned wolf litter size (mean 1.8, Oftedal and Gittleman, 1989; mean 3, Rodden et al., 2004), but there is little *in situ* litter data. Territorial females did not reproduce successfully each year, as also noted by Dietz (1984), and in the three cases we observed, females were 3 year olds before acquiring territories and mates. The dry season average travel of MW in our study area was about 14 km per night and MW were active (moving) for an average of 11–12 hours of each night (Chapters 2, 3; Table 2.2). At this activity level, a female may be unable to increase her energy intake to support more than three pups during pregnancy and lactation. Extra hours of foraging would force her into the hot hours of the day, incurring supplementary costs in thermoregulation and travel to water (Chapter 2). The loss in body weight of MW during the decline and disappearance of cavies at Los Fierros suggests that they are living near their energetic limits in NKP (Chapter 4). If so, just one helper offspring at a time, placed to inherit a territory, might supply important provisioning help without compromising the resource supply. Melo et al. (2007) reported a helper apparently guarding, but the quantitative roles of males and helpers in provisioning females and pups in free-ranging MW is unknown. It can be assumed to be important, if not critical, as it is in most or all Canidae with helpers (Macdonald and Sillero-Zubiri, 2004).

THE VALUE OF SIZE?

Size is the overriding biological characteristic of organisms. All aspects of functional morphology, physiology, ecology, and reproduction are tuned by evolution in relation to body size and shape. Ecological fine-tuning of size is on a precision scale: for example, congeners can coexist when feeding structures are separated by the magical size ratio of 1.2 or more (Hutchinson, 1959; Emmons, 1980). Size is the character that most rapidly responds to environmental selection (including interspecific interaction; Grant and Grant, 2002). To understand the nature of MW, we must understand their giant size and assume that it is particularly adapted to their current ecology. For this, it is instructive to compare the ecological role of MW to that of crab-eating zorros (*Cerdocyon thous*, "zorros" for brevity), with which they live side-by-side throughout their geographic range.

MANED WOLF VERSUS CRAB-EATING ZORRO

Large size is costly. Although larger mammals need relatively less fuel per kilogram than do equivalent, smaller ones, the larger they get, the more they need (Carbone et al., 1999, Geffen et al.,1996). Zorros in sympatry have about 75% dietary overlap with MW (Juarez and Marinho-Filho, 2002; Jácomo et al., 2004) at quarter of the body weight (Figure 8.1). Maned wolves are completely sympatric with *C. thous*, but not vice versa, as zorros have much wider habitat and geographic ranges. Zorros have slightly larger litters, 10- to 100-fold densities, and home ranges one sixteenth of the size of those of MW (zorros, 60–400 individuals per 100 km^2 [Courtenay and Maffei, 2004]; MW, 5.2 per 100 km^2 in Emas [Silveira et al., 2009]). The diet of MW includes a few more medium-sized prey (Jácomo et al., 2004; Juarez and Marinho-Filho, 2002), but most of the diet of both species is of many of the same taxa of small rodents and fruits acquired one by one. Zorros often travel and forage in pairs, when each usually gleans morsels independently; and if separated, they cry until rejoined (Emmons, pers. obs.). Along with their small body size, a higher fraction of dietary invertebrates may facilitate the small home range needs of zorros (Jácomo et al., 2004). We have a number of times seen adults and pups kilometers from any water source at the height of the dry season,

FIGURE 8.1. Height contrast between a maned wolf and a crab-eating zorro. (A) Unmarked maned wolf eating a sardine from a bait table used for occasional camera monitoring at El Refugio Huanchaca. (We did not provision maned wolves, but if water was too abundant to attract them, from time to time we lured them with treats to camera traps.) Note the long neck and that the sex cannot be determined. (B) Adult crab-eating zorro (*Cerdocyon thous*) at the same place (Photographs by L. Emmons).

so zorros may not require surface water (we saw one drinking morning dew from grass). Being smaller, their absolute water needs would be less, and unlike MW, zorros occupy the drier Chaco and Caatinga biomes, so perhaps they have physiological specialization for water conservation. Nonetheless, at Los Fierros every water hole has a resident zorro pair that visits many times a night.

By any usual measure (density, habitat breadth, geographic range, and reproductive output) *C. thous* is a more "successful" species than MW. Smallness confers the ability to easily meet energetic demands by consumption of small items; hence the fact that large Canidae (Carbone et al., 1999) and Felidae (Emmons, 1987) both "switch" to large prey at about 20 kg body weight. What advantage does a maned wolf accrue from its size?

The Tallness of Maned Wolves

Maned wolves have absolutely longer legs, and proportionally shorter backs, than do other large Canidae (Table 1.1), accompanied by a long neck (Figure 8.1). In predatory Canidae that track and run down their prey, the extreme being African wild dogs, the back is relatively long, and the hind foot is about 20% of head and body length (HBL). In MW the hind foot reaches nearly 30% HBL (Table 1.1). At normal speeds, the ipsilateral pace of MW is smooth, but their limb length precludes a diagonal trot. At a gallop they seem slightly ungainly, with much vertical motion (bouncing up and down) that must waste energy. Zorros traveled an average of 10.9 km during each of two, six hour half-nights (1900–0100 hours; Juarez and Marinho-Filho, 2002) or at a rate of 1.8 km per hour. This is within the highest range of nightly travel distances of MW but at a faster rate. When we briefly followed a VHF-collared zorro, it, too, moved much faster than is usual for MW (Emmons, unpublished data). Gray wolves in summer moved mean distances of 21 km per 24 hour day, at a mean rate of 830 m/h (Mills et al., 2006, data from GPS collars), with rests included in hourly rate calculations. Compared with our data, in which movement rates include only hours of active travel, Mills et al. (2006) would underestimate wolf travel speed. The long legs of MW thus are not associated with greater travel distances per night or per hour than those reported for shorter-limbed Canidae that travel with the efficient, long-distance, diagonal trot. However, we have found no data sets exactly comparable to ours (movements based on large sets of hourly locations, rests removed).

Tallness is intuitively an advantage for seeing above long grass or traversing tall grass or moderately flooded habitat without swimming (Figure 8.2A). In the tall dense grass on parts of our study savanna, pushing through the resistant grass at a trot would be impossible, but long legs can step over it. Tapirs use well-worn trackways, but MW have no fixed routes and travel ubiquitously (Chapter 3). We found it exhausting to drag our legs even 2–3 km through grass (like walking through thigh-deep water or worse). Maned wolves forage for the same small rodent prey hidden under the grass as do the syntopic zorros and four small felids in NKP, and height confers no evident advantage in prey capture. Small Carnivora such as zorros, jaguarundis, and grisons can travel below the canopy of tall grasses, between the grass bunches, or on the networks of armadillo trails, in the realm of mice and cavies. Dubost (1979) developed an hypothesis that the height classes of African forest duikers are fitted to the structural density of fine undergrowth stems through which they must push to travel. His vegetation measurements confirmed that duikers occurred in the discrete height classes where stems presented the least resistance. Perhaps the optimal sizes for travel in the tall-grass savannas are either below the intertwined bunch-grass canopy (jaguarundis, rails, armadillos) or stepping over it with long slender legs (maned wolf, marsh deer, pampas deer, rhea). To feed on mice and invertebrates, the smaller size would seem advantageous.

Selection for large gape size and strength to tackle armadillos or medium-size prey is not associated with hypertrophy of the legs in other canine predators (bush dogs have the shortest legs). The reduced agility, and greater predator-mass/prey-mass ratio resulting from size, puts MW at an energetic disadvantage, where the night may be too short to catch enough prey to meet their needs (Carbone et al., 1999; Macdonald et al., 2004a). Because prey capture does not seem to be enhanced by their size, we conjecture that the height of MW facilitates the frugivore half of their diet.

Height gives MW access to fruits of shrubs and treelets that are out of reach of competing foxes, armadillos, peccaries, agoutis, and tapirs (Figures 8.1, 8.2B). On its hind legs, a female maned wolf reached to a height of 170 cm to grasp a treat (trial in captivity, J. McLaughlin and M. Rodden, pers. comm). The "wolf fruit" that dominates the maned wolf diet in Cerrado ("lobeira": *Solanum lycocarpum,* in Brazil; *S. gomphodes,* in NKP; review in Rodden et al., 2004), is 10–15 cm in diameter, and in NKP, many *S. gomphodes* fruits hang well above the reach of zorros (Figure 8.2B). Although the ripe fruits drop, MW can choose them beforehand. Tapirs also eat *S. gomphodes*, but at Los Fierros, marked fruits stay on the plant until ripe, so tapirs apparently do not take immature

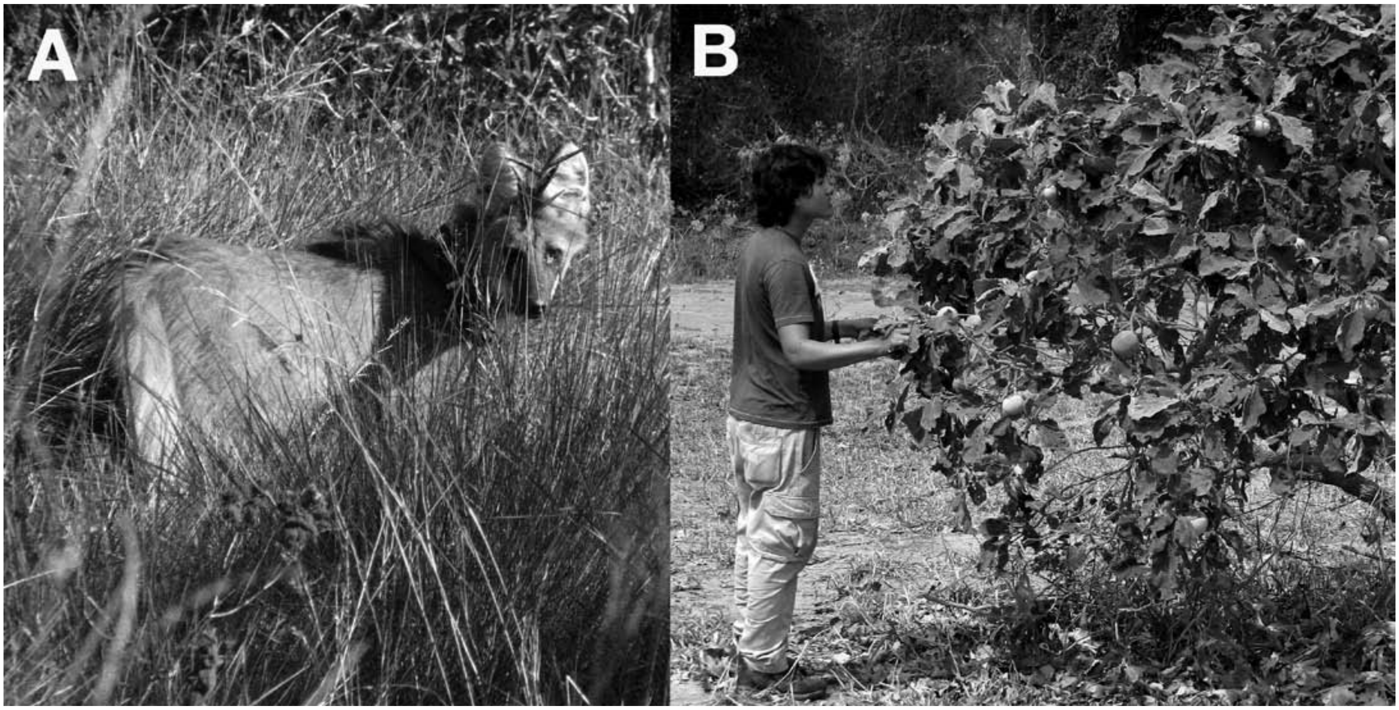

FIGURE 8.2. (A) Height of maned wolf M8 relative to long grass of Los Fierros savanna. (B) J. M. Castro inspects a tree of *Solanum gomphodes* on a roadside outside of Noel Kempff Mercado National Park. The many fruits are immature; note that some are higher than his head (Photographs by L Emmons).

fruits (J. M. Castro, unpublished data). The chief dietary fruit in NKP, *Alibertia edulis*, grows to above 6 m, and if not picked, it is opened *in situ* by bats and birds, or dries on the plant, so few ever fall (Emmons, pers. obs.). Fruits grow at all levels on the plant, which puts many out of reach of terrestrial mammals (*A. edulis* are yellow-green, mammal-dispersed fruits, Chapter 4). The few, large, nutritious, fruits per plant of *Annona coriacea* can hang above the reach of tapirs, which regularly bend over or break down the tops of the plants to reach them (Emmons, pers. obs.). On their hind legs, MW can reach higher than tapirs (Figure 8.3). In Emas Park, lobeira was 18% of all items eaten by MW, but only 2% of those eaten by zorros; for Annonaceae, the numbers were 12% and 6% (Jácomo et al., 2004). Of the possible reasons for this, one is that MW get the fruit first, another is that few fox territories are large enough to include the fruit species in their areas. Pampa fruits are scattered in a matrix of grassland, and height above the grass canopy could confer MW an olfactory or visual advantage for detecting them at a distance across tall grasslands (Figure 8.2A), as well as the height to outreach other mammals for them, and legs long enough to step over grass to travel efficiently.

Evolution for tallness, to reach tree leaves, has occurred repeatedly and with extraordinary diversity of structure throughout the history of vertebrate herbivores. In contrast, mammalian frugivores either feed on the ground on fallen fruits or climb trees to reach them; this includes the many frugivorous/omnivorous Carnivora, such as gray foxes (*Urocyon cinereoargenteus*), Procyonidae (coatis, kinkajous), Viverridae (palm civets), Mustelidae (tayras), and even Ursidae (black bears). Campo Cerrado trees and shrubs with mammal-dispersed fruits are usually short (<10 m), slender, and often brittle-stemmed from fire adaptation, thus poorly suited for climbing. The fruit of *Annona coriacea* dangles from long stems, while branches of the large-fruited *Solanum* spp. are heavily armed with spines. Dispersers must pick the fruits from a stance on the ground or wait for fruits to fall, unless they break the plant (tapirs). If the unique tallness of MW gives them a competitive feeding access to large, high-return, savanna fruit species that are dispersed over a large home range,

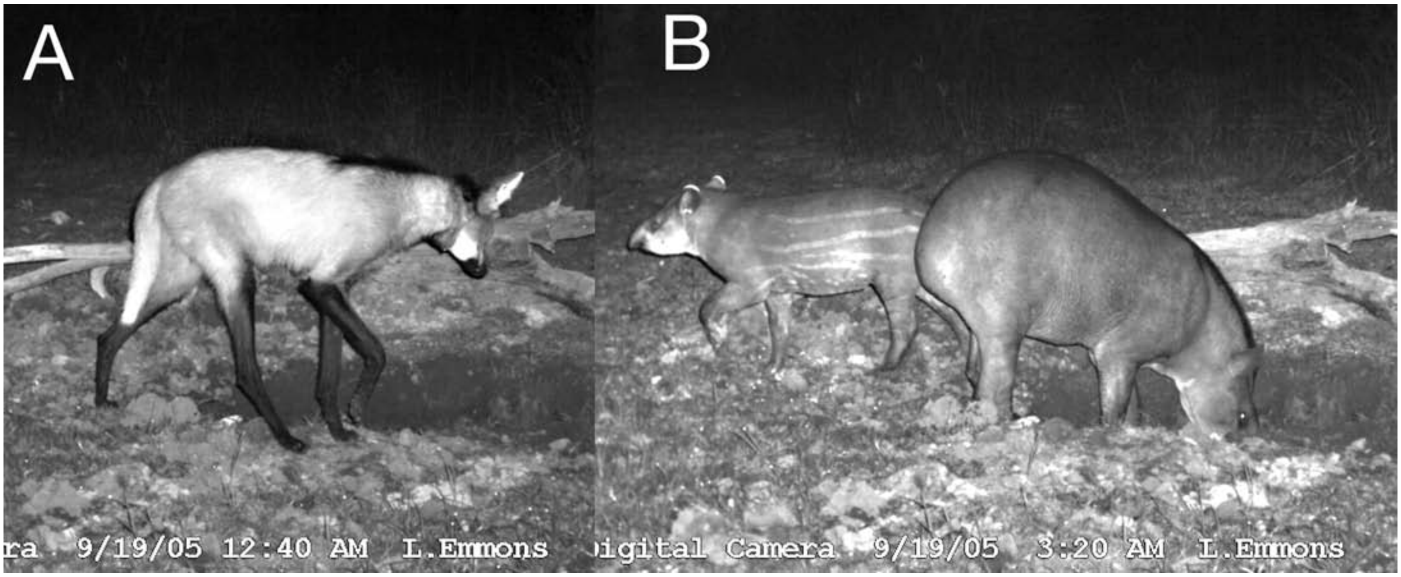

FIGURE 8.3. Relative heights of (A) maned wolf F3 and (B) a mother tapir with young (standing partly below ground level). Camera trap images taken 3 hours apart at the Pozo Matt water hole.

without compromising predation skills, then their anomalous characters as giant canids form a consistent suite of associated traits that places them into a unique canid category. They may also represent a unique adaptative type among living mammalia.

QUESTIONS FOR FUTURE RESEARCH

Our research on MW has sprouted many questions. The few animals we studied varied in characteristics such as male behavior after parturition, togetherness of pairs, and breeding season. Canidae in general respond flexibly to changing environmental conditions (Macdonald and Sillero-Zubiri, 2004), but these behaviors in MW all need clarification with larger sample sizes. Conditions leading to socioecological variations need to be teased apart. Particular areas where we think research would be most fruitful include the following:

Studies of field metabolic rates: Does the low muscle mass of MW correlate with low metabolic needs?

Studies of passage times of whole prey and fruit parts through the digestive tract: How exactly do scats represent numbers and biomass of items consumed?

Studies of resource abundances and territory sizes: What is the relative importance for home range size of prey and fruit? What is the inter- and intra-annual turnover of individual resources? How can land best be managed to maintain optimal habitat? What is the optimal fire regime?

Studies of the epidemiology of episodic diseases and their possible control: Which diseases are now established *in situ*? What is the current transmission of pathogens between domestic animals and MW (rabies, distemper, heartworm, etc.)? What is the disease ecology in relation to syntopic savanna mammals such as raccoons, ocelots, and zorros and those of forests? What is the reproductive cost of disease?

Studies of helpers: How often do pairs have helpers? Are helpers always female? Does the abundance of resources influence their numbers? Do helpers help provision pups? How long do they usually stay? Does food resource density influence retention of helpers? Does the breeding female choose to accept or reject presence of a helper?

Studies of reproductive cycles: Are there really February–March births? If so, can a female ever have a second estrous cycle within the same year? What are the triggers for estrus? Is there a method to accurately age youngsters between 8 and 18 months so birth date can be calculated? What is the litter size and survival to weaning in free-ranging MW?

Studies of populations: Where do maned wolf breeding populations still occur? Can MW be surveyed efficiently to distinguish between transient and breeding individuals? Under what conditions do MW successfully breed on agricultural land?

It is nearly impossible to acquire detailed behavioral data on many animals at once. The pioneering and best known behavioral ecology studies followed single social groups or small populations, where researchers could follow the relationships of individually known animals with each other and with the environment (e.g., the chimps of Gombe Stream, the lions of the Serengeti, the wolves of Isle Royale, and the elephants of Lake Manayra). Studies that began in the 1960s are in many cases still in progress, and they have acquired data on many animals by accumulating generations of longitudinal data. We followed far too few individuals for statistical inference of most parameters, but we relate for the first time the stories of a few free-living MW for a full maned wolf generation. We hope that these stories will inspire others to look more closely into the complex lives of individual families.

References

Ackerman, B. B., F. G. Lindsey, and T. P. Hemker. 1984. Cougar Food Habits in Southern Utah. *Journal of Wildlife Management*, 48:147–155. doi:10.2307/3808462.

Alves, R. R. N., R. R. D. Barboza, and W. M. S. Souto. 2010. A Global Overview of Canids Used in Traditional Medicines. *Biodiversity and Conservation*, 19:1513–1522. doi:10.1007/s10531-010-9805-1.

Aragona, M., and E. Z. F. Setz. 2001. Diet of the Maned Wolf, *Chrysocyon brachyurus* (Mammalia: Canidae), During Wet and Dry Seasons at Ibitipoca State Park, Brazil. *Journal of Zoology, London*, 254:131–136. doi:10.1017/S0952836901000620.

Asa, C. S. 1997. "Hormonal and Experiential Factors in the Expression of Social Behavior in Canids." In *Cooperative Breeding in Animals,* ed. N. G. Solomon and J. A. French, pp. 129–149. Cambridge: Cambridge University Press.

Asher, M., E. Spinelli de Oliviera, and N. Sachser. 2004. Social System and Spatial Organization of Wild Guinea Pigs (*Cavia aperea*) in a Natural Population. *Journal of Mammalogy,* 85:788–796. doi:10.1644/BNS-012.

Barbiers, R., and M. Bush. 1995. "Medical Management of Maned Wolves." In *Husbandry Manual for the Maned Wolf,* Chrysocyon brachyurus, ed. N. Fletchall, M. Rodden, and S. Taylor, pp. VII-1–VII-7. Grand Rapids, Mich.: John Ball Zoo.

Barboza, P. S., M. E. Allen, M. Rodden, and P. Kim. 1994. Feed Intake and Digestion in the Maned Wolf (*Chrysocyon brachyurus*): Consequences for Dietary Management. *Zoo Biology*, 13:375–381. doi:10.1002/zoo.1430130410.

Barbosa Ribeiro, M. F., and A. M. Guimarães. 1998. *Encephalitozoon*-like Microsporidia in the Ticks *Amblyomma cajennense* and *Anocentor nitens* (Acari: Ixodidae). *Journal of Medical Entomology,* 35:1029–1033.

Belentani, S. C. S., J. C. Motta-Junior, and S. A. Talamoni. 2005. Notes on the Food Habits and Prey Selection of the Maned Wolf (*Chrysocyon brachyurus*) (Mammalia, Canidae) in Southeastern Brazil. *Biociencias*, 13:95–98.

Beldomenico, P. M., D. Hunzicker, J. L. Taverna, and P. K. Rejf. 2002. Capillariidae Eggs Found in the Urine of a Free-Ranging Maned Wolf from Argentina. *Memórias do Instituto Oswaldo Cruz,* 97:509–510.

Berta, A. 1987. Origin, Diversification, and Zoogeography of the South American Canidae. *Fieldiana Zoology, New Series,* 39:455–471.

Bestelmeyer, S. V. 2000. Solitary, Reproductive, and Parental Behavior of Maned Wolves (*Chrysocyon brachyurus*) Ph.D. diss., Colorado State University, Fort Collins.

Bestelmeyer, S. V., M. Berman, K. Gipe, and L. Dotterer. 1996. Parturition Behavior in Captive Maned Wolves (*Chrysocyon Brachyurus*). *American Zoo and Aquarium Association Regional Conference Proceedings,* 1996:434–41.

Bestelmeyer, S. V., and C. Westbrook. 1998. Maned Wolf (*Chrysocyon brachyurus*) Predation on Pampas Deer (*Ozotoceros bezoarticus*) in Central Brazil. *Mammalia,* 62:591–595.

Bevilaqua, E., M. I. Machado, M. J. S. Mundim, A. V. Mundim, and A. M. Borges. 1993. Occurrence of *Dioctophyme renale* in Maned Wolves (*Chrysocyon brachyurus*) in the Area of Uberlandia, Brazil. *Animal Keepers Forum,* 20:324–329.

Beyer, H. L. 2004. *Hawth's Analysis Tools for ArcGIS.* http://www.spatialecology.com/htools (accessed 2005–2009).

Biewener, A. A. 2003. *Animal Locomotion.* Oxford: Oxford University Press.

Blatt, C. M., C. R. Taylor, and M. B. Habal. 1972. Thermal Panting in Dogs: The Lateral Nasal Gland, A Source of Water for Evaporative Cooling. *Science,* 177:804–805. doi:10.1126/science.177.4051.804.

Boniface, J. 1998. Dietary Control of Cysteinuria in Maned Wolves (*Chrysocyon brachyurus*). Master's thesis, University of Maryland, College Park.

Boulanger, J., F. Martinez, and E. C. Segura. 2006. Projection of Future Climate Change Conditions Using IPCC Simulations, Neural Networks and Bayesian Statistics. Part 1: Temperature Mean State and Seasonal Cycle in South America. *Climate Dynamics*, 27:233–259. doi:10.1007/s00382-006-0134-8.

Bovee, K.C., M. Bush, J. Dietz, P. Jezyk, and S. Segal. 1981. Cystinuria in the Maned Wolf of South America. *Science,* 212:919–920. doi:10.1126/science.7233184.

Brady, C. A. 1979. "Observations on the Behavior and Ecology of the Crab-Eating Fox (*Cerdocyon thous*)." In *Vertebrate Ecology in the Northern Neotropics*, ed. J. F. Eisenberg, pp. 161–171. Washington, D.C.: Smithsonian Institution Press.

———. 1981. The Vocal Repertoires of the Bush Dog (*Speothos venaticus*), Crab-Eating Fox (*Cerdocyon thous*), and Maned Wolf (*Chrysocyon brachyurus*). *Animal Behaviour,* 29:649–669. doi:10.1016/S0003-3472(81)80001-2.

Branch L., J. L. Hierro, and D. Villareal. 1999. Patterns of Plant Species Diversity Following Local Extinction of the Plains Viscacha in Semi-arid Scrub. *Journal of Arid Environments*, 41:173–182. doi:10.1006/jare.1998.0480.

Bridgewater, S., J. A. Ratter, and J. Felipe Ribeiro. 2004. Biogeographic Patterns, Beta-Diversity and Dominance in the Cerrado Biome of Brazil. *Biodiversity and Conservation,* 13: 2295–2317. doi:10.1023/B:BIOC.0000047903.37608.4c.

Bronson, E., L. H. Emmons, S. Murray, E. J. Dubovi, and S. L. Deem. 2008. Serosurvey of Pathogens in Domestic Dogs on the Border of Noël Kempff Mercado National Park, Bolivia. *Journal of Zoo and Wildlife Medicine*, 39:28–36. doi:10.1638/2006-0046.1.

Bueno, A. D. A., and J. C. Motta-Junior. 2004. Food Habits of Two Syntopic Canids, the Maned Wolf (*Chrysocyon brachyurus*) and the Crab-Eating Fox (*Cerdocyon thous*), in Southeastern Brazil. *Revista Chilena de Historia Natural*, 77:5–14.

———. 2006. Small Mammal Selection and Functional Response in the Diet of the Maned Wolf, *Chrysocyon brachyurus* (Mammalia, Canidae) in Southeast Brazil. *Mastozoología Neotropical,* 13:11–19.

———. 2009. Feeding Habits of the Maned Wolf, *Chrysocyon brachyurus* (Carnivora: Canidae), in Southeast Brazil. *Studies on Neotropical Fauna and Environment,* 44:67–75.

Burger, I. H., and J. V. Johnson. 1991. Dogs Large and Small: The Allometry of Energy Requirements within a Single Species. *Journal of Nutrition,* 121:S18–S21.

Butler, R. A. 2009. Brazil to Step Up Efforts to Save the Cerrado Grassland. *Mongabay*, 11 September 2009. http://news.mongabay.com/2009/0911-cerrado.html (accessed 22 August 2010).

Calenge, C. 2006. The Package Adehabitat for the R Software: A Tool for the Analysis of Space and Habitat Use by Animals. *Ecological Modelling*, 197:516–519. doi:10.1016/j.ecolmodel.2006.03.017.

Carvalho, C. T., and L. E. M. Vasconcellos. 1995. Disease, Food and Reproduction of the Maned Wolf–*Chrysocyon brachyurus* (Illiger) (Carnivora, Canidae) in Southeast Brazil. *Revista Brasileira de Zoologia*, 12:627–640. doi:10.1590/S0101-81751995000300018.

Carbone C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. Energetic Constraints on the Diet of Terrestrial Carnivores. *Nature*, 402:286–288. doi:10.1038/46266.

Castro, J. M. 2010. Dieta estacional del borochi (*Chrysocyon brachyurus*) en el Parque Nacional Noel Kempff Mercado (PNK)—Reserva Biológica el Refugio Huanchaca (ERH) y posibles causas de su variación temporal. Lic. thesis, Licenciado en Ciencias Biológicas, Universidad Autónoma "Gabriel René Moreno," Santa Cruz.

Childs-Sanford, S. E. 2005. The Captive Maned Wolf (*Chrysocyon brachyurus*): Nutritional Considerations with Emphasis on Management of Cystinuria. Master's thesis. University of Maryland, College Park.

Childs-Sanford, S. E., and C. R. Angel. 2006. Transit Time and Digestibility of Two Experimental Diets in the Maned Wolf *(Chrysocyon brachyurus*) and Domestic Dog (*Canis lupus*). *Zoo Biology*, 25:369–381. doi:10.1002/zoo.20095.

Cione, A. L., E. P. Tonni, and L. Soibelzon. 2003. The Broken Zig-Zag: Late Cenozoic Large Mammal and Tortoise Extinction in South America. *Revista Museo Argentino de Ciencias Naturales, n.s.* 5:1–19.

Coelho, C. M., L. F. B. De Melo, M. A. l. L. Sábato, E. M. V. Magni, A. Hirsch, and R. J. Young. 2008. Habitat Use by Wild Maned Wolves (*Chrysocyon brachyurus*) in a Transition Zone Environment. *Journal of Mammalogy,* 89:97–104. doi:10.1644/06-MAMM-A-383.1.

Coelho, C. M., L. F. B. de Melo, M. A. L. Sábato, D. l. N. Rizel, and R. J. Young. 2007. A Note on the Use of GPS Collars to Monitor Wild Maned Wolves *Chrysocyon brachyurus* (Illiger 1815) (Mammalia, Canidae). *Applied Animal Behaviour Science*, 105:259–264. doi:10.1016/j.applanim.2006.04.024.

Courtenay, O. 1994. Conservation of the Maned Wolf: Fruitful Relations in a Changing Environment. *Canid News,* 2:41–43.

Courtenay, O., and L. Maffei. 2004. "Crab-Eating Fox *Cerdocyon thous* (Linnaeus, 1766)." In *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan*, ed. C. Sillero-Zubiri, M. Hoffmann, and D. W Macdonald. pp. 32–38. Gland: IUCN/SSC Canid Specialist Group.

Creel, S., and N. M. Creel. 2002. *The African Wild Dog: Behavior Ecology, and Conservation*, *Monographs in Behavior and Ecology*. Princeton: Princeton University Press.

de Vivo, M., and A. P. Carmignotto. 2004. Holocene Vegetation Change and the Mammal Faunas of South America and Africa. *Journal of Biogeography*, 31(6):943–957. doi:10.1111/j.1365-2699.2004.01068.x.

Deem, S. L., E. Bronson, S. Angulo, and L. H. Emmons. 2008. Monitoreo Sanitario del Borochi (*Chrysocyon brachyurus*) en el Parque Nacional Noel Kempff Mercado, Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental*, 21:41–50.

Deem, S. L., and L. H. Emmons. 2005. Exposure of Free-Ranging Maned Wolves (*Chrysocyon brachyurus*) to Infectious and Parasitic Disease Agents in the Noel Kempff Mercado National Park, Bolivia. *Journal of Zoo and Wildlife Medicine,* 36:192–197. doi:10.1638/04-076.1.

Deem, S. L., A. J. Noss, C.V. Fiorello, A. L. Manharth, R.G. Robbins, and W. B. Karesh. 2009. Health Assessment of Free-Ranging Three-Banded (*Tolypeutes matacus*) and Nine-Banded (*Dasypus novemcinctus*) Armadillos in the Gran Chaco, Bolivia. *Journal of Zoo and Wildlife Medicine*, 40:245–256. doi:10.1638/2007-0120.1.

DeMatteo, K. E., I. J. Porton, D. G. Kleiman, and C. S. Asa. 2006. The Effect of the Male Bush Dog (*Speothos venaticus)* on the female reproductive cycle. *Journal of Mammalogy*, 87:723–732. doi:10.1644/05-MAMM-A-342R1.1.

Dierenfeld, E. S., H. L. Alcorn, and K. L. Jacobsen. 2002. Nutrient Composition of Whole Vertebrate Prey (Excluding Fish) Fed in Zoos. U.S. Department of Agriculture. http://www.nal.usda.gov/awic/zoo/WholePreyFinal02May29.pdf (accessed 29 March 2010.

Dietz, J. M. 1984. Ecology and Social Organization of the Maned Wolf (*Chrysocyon brachyurus*). *Smithsonian Contributions to Zoology*, 392:1–51.

———. 1985. *Chrysocyon brachyurus*. *Mammalian Species*, 234:1–4. doi:10.2307/3503796.

Dubost, G. 1979. The Size of African Forest Artiodactyls as Determined by the Vegetation Structure. *African Journal of Ecology,* 17:1–17. doi:10.1111/j.1365-2028.1979.tb00452.x.

Dunnum, J. L., and J. Salazar-Bravo. 2010a. Phylogeny, Evolution, and Systematics of the *Galea musteloides* Complex (Rodentia: Caviidae). *Journal of Mammalogy,* 91:243–259. doi:10.1644/08-MAMM-A-214R1.1.

———. 2010b. Molecular Systematics, Taxonomy and Biogeography of the Genus *Cavia* (Rodentia: Caviidae). *Journal of Zoological Systematics and Evolutionary Research*, 48:376–388. doi:10.1111/j.1439-0469.2009.00561.x.

Emmons, L.H. 1980. Ecology and Resource Partitioning among Nine Species of African Rainforest Squirrels. *Ecological Monographs,* 50:31–54. doi:10.2307/2937245.

———. 1987. Comparative Feeding Ecology of Felids in a Neotropical Rainforest. *Behavioral Ecology and Sociobiology*, 20:271–283. doi:10.1007/BF00292180.

———. 1988. A Field Study of Ocelots in Peru. *Revue Ecologique*, 43:133–157.

———. 1999. Two New Species of *Juscelinomys* (Rodentia: Muridae) from Bolivia. *American Museum Novitates*, 3280:1–15.

———. 2000a. Mammal Fauna of Parque Nacional Noel Kempff Mercado. *RAP Working Papers*, 10:129–135.

———. 2000b. *Tupai: A Field Study of Bornean Treeshrews*. Berkeley: University of California Press.

———. 2009. Long-Term Variation in Small Mammal Abundances in Forest and Savanna of Bolivian Cerrado. *Biotropica,* 41:493–502. doi:10.1111/j.1744-7429.2009.00500.x.

Emmons, L. H., V. Chávez, N. Rocha, B. Phillips, I. Phillips, L. F. del Aguila, and M. J. Swarner. 2006a. The Non-flying Mammals of Noel Kempff Mercado National Park (Bolivia). *Revista Boliviana de Ecología y Conservación Ambiental*, 19:23–46.

Emmons, L. H., S. Deem, M. Rodden, and J. E. Maldonado. 2004. The Secret Wolf. *Zoogoer*, 33:14–21.

Emmons, L. H., R. Peña F., S. Angulo A., and M. J. Swarner. 2005. Bathing Behavior of Giant Anteaters (*Myrmecophaga tridactyla*). *Edentata*, 2005:41–43.

Emmons, L. H., M. J. Swarner, A. Vargas-Espinoza, M. Tschapka, H. Azurduy, and E. K. V. Kalko. 2006b. The Forest and Savanna Bat Communities of Noel Kempff Mercado National Park (Bolivia). *Revista Boliviana de Ecología y Conservación Ambiental*, 19:47–57.

Ewer, R. F. 1973. *The Carnivores*. Ithaca: Cornell University Press.

Fairchild, G. B., G. M. Kohls, and V. J. Tipton. 1966. "The Ticks of Panama (Acarina: Ixodoidea)." In *Ectoparasites of Panama*, ed. R. L. Wenzel and V. J. Tipton, pp. 167–219. Chicago: Field Museum of Natural History.

Fenn, M. G. P., and D. W. Macdonald. 1995. Use of Middens by Red Foxes: Risk Reverses Rhythms of Rats. *Journal of Mammalogy*, 76:130–136. doi:10.2307/1382321.

Fernandes, L. T. O., and M. G. M. Marcolino. 2007. Urolithiasis in the Maned Wolf (*Chrysocyon brachyurus*): Assessment of Four Clinical Cases in Captivity. *Brazilian Journal of Veterinary Research and Animal Science*, 44:352–357.

Fiorello, C. V., S. L. Deem, M. E. Gompper, and E. J. Dubovi. 2004. Seroprevalence of Pathogens in Domestic Carnivores on the Border of Madidi National Park, Bolivia. *Animal Conservation,* 7:45–54. doi:10.1017/S1367943003001197.

Fischer, W. A., M. B. Ramos-Neto, L. Silveira, and A. T. A. Jácomo. 2003. Human Transportation Network as Ecological Barrier for Wildlife on Brazilian Pantanal-Cerrado Corridors. Report. Road Ecology Center, John Muir Institute of the Environment, University of California, Davis.

Fletcher, K. C., A. K. Eugster, R. E. Schmidt, and G. B. Hubbard. 1979. Parvovirus Infection in Maned Wolves. *Journal of the American Veterinary Medical Association*, 175:897–900.

Floyd, T. J., L. D. Mech, and P. A. Jordan. 1978. Relating Wolf Scat Content to Prey Consumed. *The Journal of Wildlife Management,* 42:528–532. doi:10.2307/3800814.

Francisco, A. L., W. E. Magnusson, and T. M. Sanaiotti. 1995. Variation in Growth and Reproduction of *Bolomys lasiurus* (Rodentia: Muridae) in an Amazonian Savanna. *Journal of Tropical Ecology,* 11:419–428. doi:10.1017/S0266467400008889.

Furtado, M. M., C. K. Kashivakura, C. Ferro, A. Jacomo, L. Silveira, S. Astete, and F. M. Lopes. 2007. Prevalence of Crown Trauma in Free-Ranging Maned Wolves (*Chrysocyon brachyurus*) in Central Brazil. *Journal of Veterinary Dentistry,* 24:231–234.

Geffen, E., M. E. Gompper, J. L. Gittleman, H.-K. Luh, D. W. MacDonald, and R. K. Wayne. 1996. Size, Life-History Traits, and Social Organization in the Canidae: A Reevaluation. *American Naturalist*, 147:140–160. doi:10.1086/285844.

Gese, E. M. 2004. "Coyotes. Coyotes in Yellowstone National Park: The Influence of Dominance on Foraging, Territoriality, and Fitness." In *Biology and Conservation of Wild*

Canids, ed. D. W. Macdonald and C. Sillero-Zubiri, pp. 271–283.. Oxford: Oxford University Press.

Gipson, P. S., W. B. Ballard, R. M. Nowak, and L. D. Mech. 2000. Accuracy and Precision of Estimating Age of Gray Wolves by Tooth Wear. *The Journal of Wildlife Management,* 64:752–758. doi:10.2307/3802745.

González del Solar, R., and J. Rau. 2004. "Chilla *Pseudalopex griseus* (Gray, 1837)". In *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan*, ed. C. Sillero-Zubiri, M. Hoffmann, and D. W. Macdonald, pp. 56-63. Cambridge: IUCN/Species Survival Commission Canid Specialist Group.

Gorman, M. L., M. G. Mills, J. P. Raath, and J. R. Speakman. 1998. High Hunting Costs Make African Wild Dogs Vulnerable to Kleptoparasitism by Hyaenas. *Nature*, 391:479–481. doi:10.1038/35131.

Goszczynski, J. 1986. Locomotor Activity of Terrestrial Predators and Its Consequence. *Acta Theriologica*, 31:29–95.

Gottsberger, G., and I. Silberbauer-Gottsberger. 2006. *Life in the Cerrado, A South American Tropical Seasonal Ecosystem*. Vol. I–Origin, Structure, Dynamics and Plant Use, 277 pp.; Vol. II – Pollination and Seed Dispersal, 383 pp. Illust. Ulm: Reta Verlag.

Grant, P. R., and B. R. Grant. 2002. Unpredictable Evolution in a 30-Year Study of Darwin's Finches. *Science,* 296:707–711. doi:10.1126/science.1070315.

Guglielmone, A. A., A. Estrada-Peña, J. E. Keirans, and R. G. Robbins. 2003. "Ticks (Acari: Ixodida) of the Neotropical Zoogeographic Region." In *International Consortium on Ticks and Tick-borne Diseases*, 173 pp. Atalanta: Houten.

Hammond, E. 2012. "Medical Management of Maned Wolves (*Chrysocyon brachyurus*)." In *Zoo and Wild Animal Medicine*, vol. 7, ed. R. E. Miller and M. E. Fowler, p. 451. St. Louis: Elsevier.

Hannah, L. 2008. Protected Areas and Climate Change. *Annals of the New York Academy of Sciences*, 1134:201–212. doi:10.1196/annals.1439.009.

Hannah, L., G. Midgley, S. Andelman, M. Araújo, G. Hughes, E. Martinez-Meyer, R. Pearson, and P. Williams. 2008. Protected Area Needs in a Changing Climate. *Frontiers in Ecology and the Environment*, 5:131–138.

Hill, K., K. Hawkes, M. Hurtado, and H. Kaplan. 1984. Seasonal Variance in the Diet of Ache Hunter-Gatherers in Eastern Paraguay. *Human Ecology,* 12:101–135. doi:10.1007/BF01531269.

Hoffman, W. A. 1998. Post-burn Reproduction of Woody Plants in a Neotropical Savanna: The Relative Importance of Sexual and Vegetative Reproduction. *Journal of Applied Ecology*, 35:422–433.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why Are There So Many Kinds of Animals? *American Naturalist,* 93(1959):145–159. doi:10.1086/282070.

Intergovernmental Panel on Climate Change (IPCC). 2007. "Climate Change 2007: Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007," ed. M. L. Parry, O. F. Canziani, J. P. Palutikof, P.J. van der Linden, and C.E. Hanson. Cambridge: Cambridge University Press.

International Species Information System (ISIS). 2002. *Physiological Data Reference Values*. ISIS: Minneapolis.

International Union for Conservation of Nature and Natural Resources (IUCN). 2009. IUCN *Red List of Threatened Species*. Version 2009.2.

Jácomo, A. T. A. 1999. Nicho alimentar do lobo guará (*Chrysocyon brachyurus* Illiger, 1811) no Parque Nacional das Emas- Go. Thesis, Instituto de Ciencias Biológicas. Universidade Federal de Goiás.

Jácomo, A. T. A., C. K. Kashivakura, C. Ferro, M. F. Furtado, S. P. Astete, R. S. Tôrres, and L. Silveira. 2009. Home Range and Spatial Organization of Maned Wolves in the Brazilian Grasslands. *Journal of Mammalogy*, 90:150–157.

Jácomo, A. T. A., L. Silveira, and J. A. F. Diniz-Filho. 2004. Niche Separation Between the Maned Wolf (*Chrysocyon brachyurus*), the Crab-Eating Fox (*Ducicyon thous*) and the Hoary Fox *(Dusicyon vetulus*) in Central Brazil. *Journal of Zoology, London,* 262:99–106.

Jenness, J. 2007. Distance and Bearing between Matched Features (distbyid.avx) Extension for ArcView 3.x, v. 2.1. Jenness Enterprises. http://www.jennessent.com/arcview/distance_by_id.htm (accessed 18 February 2004).

Jones, E. K., C. M. Clifford, J. E. Keirans, and G. M. Kohls. 1972. The Ticks of Venezuela (Acarina: Ixodoidea) with a Key to the Species of Amblyomma in the Western Hemisphere. *Brigham Young University Science Bulletin, Biological Series,* 17:1–40.

Juarez, K. M., and J. Marinho-Filho. 2002. Diet, Habitat Use, and Home Ranges of Sympatric Canids in Central Brazil. *Journal of Mammalogy,* 83:925–933. doi:10.1644/1545-1542(2002)083<0925:DHUAHR>2.0.CO;2.

Kawashima, R. S., M. F. Siqueira, and J. E. Mantovani. 2007. Data from Monitoring Vegetation via NDVI by Modeling the Potential Geographical Distribution of the Maned Wolf (*Chrysocyon bracyurus*)/Dados do monitoramento da cobertura vegetal por NDVI na modelagem da distribuição geográfica potencial do lobo-guará (*Chrysocyon bracyurus*). *Anais XIII Simpósio Brasileiro de Sensoriamento Remoto, Florianópolis, Brasil, INPE*, 3983–3990.

Kehler, J., S. Gilbert, J. Liu, U. Giger, and P. Henthorn. 2002. "The Genetic Characterization of Cystinuria in Maned Wolves." In *Proceedings of the Faculty Research Retreat 2002,* Philadelphia, Pa.: University of Pennsylvania School of Veterinary Medicine.

Kelly, B. T., and E. O. Garton. 1997. Effects of Prey Size, Meal Size, Meal Composition, and Daily Frequency of Feeding on the Recovery of Rodent Remains from Carnivore Scats. *Canadian Journal of Zoology,* 75:1811–1817. doi:10.1139/z97-810.

Kelt, D. A., P. L. Meserve, L. K. Nabors, M. L. Forister, and J. R. Gutiérrez. 2004. Foraging Ecology of Small Mammals in Semiarid Chile: The Interplay of Biotic and Abiotic Effects. *Ecology,* 85:383–397. doi:10.1890/02-4065.

Kennedy-Stoskopf, 2003. "Canidae". In *Zoo and Wild Animal Medicine*, 5th ed., ed. M. E. Fowler and R.E. Miller, pp. 482–491. St. Louis: W.B. Saunders.

Kenward, R. E. 1987. *Wildlife Radio Tagging: Equipment, Field Techniques, and Data Analysis*. London: Academic Press.

Killeen, T., and T. Schulenberg. 1998. A Biological Assessment of Parque Nacional Noel Kempff Mercado, Bolivia. *RAP Working Papers,* 10:1–372.

Kleiman, D. G. 1972. Social Behavior of the Maned Wolf (*Chrysocyon brachyurus*) and Bush Dog (*Speothos venaticus*): A

Study in Contrast. *Journal of Mammalogy*, 53:791–806. doi:10.2307/1379214.

Klink, C., and R. B. Machado. 2005. Conservation of the Brazilian Cerrado. *Conservation Biology*, 19:707–713. doi:10.1111/j.1523-1739.2005.00702.x.

Kohls, G. M. 1956. Concerning the Identity of *Amblyomma maculatum*, *A. tigrinum*, *A. triste*, and *A. ovatum* of Koch, 1844. *Proceedings of the Entomological Society of Washington,* 58:143–147.

Kumar, V., J. Vercruysse, and R. Vandestreene. 1972. Studies in Two Cases of *Dioctophyma renale* Infection in *Chrysocyon brachyurus*. *Acta Zoologica et Pathologica Antverpiensia*, 56:83–89.

Lamina, J., and M. Brack. 1966. The Kidney Worm *Dioctophyme renale* (Goeze, 1782 Stiles, 1901) as a Cause of Death in a Maned Wolf (*Chrysocyon jubatus*). *Zeitschrift für Parasitenk*, 27:336–340. doi:10.1007/BF00260031.

Leung, W-T. W. 1968. *Food Composition Table for Use in Africa*. Rome: Food and Agriculture Organization/U.S. Department of Agriculture.

Lilienfeld C., M. D. 2000. Determinación de los hábitos alimenticios del aguará guazú (*Chrysocyon brachyurus*) en dos zonas del Parque Nacional Noël Kempff Mercado. Licenciado en Ciencias Biológicas, Universidad Autónoma "Gabriel René Moreno", Santa Cruz.

Lindenmayer, D. B., and J. Fischer. 2003. Sound Science or Social Hook—A Response to Brooker's Application of the Focal Species Approach. *Landscape and Urban Planning*, 62:149–158. doi:10.1016/S0169-2046(02)00147-0.

Lucherini, M., M. Pessino, and A. A. Farias. 2004. "Pampas Fox *Pseudalopex gymnocercus* (G. Fischer, 1814)". In *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan*, ed. C. Sillero-Zubiri, M. Hoffmann, and D. W. Macdonald. Gland: IUCN/SSC Canid Specialist Group.

Lyra-Jorge, M. C., G. Ciocheti, and V. R . Pivello. 2008. Carnivore Mammals in a Fragmented Landscape in Northeast of São Paulo State, Brazil. *Biodiversity Conservation,* 17:1573–1580. doi:10.1007/s10531-008-9366-8.

Macdonald, D. W., and O. Courtenay. 1996. Enduring Social Relationships in a Population of Crab-Eating Zorros, *Cerdocyon thous,* in Amazonian Brazil (Carnivora, Canidae). *Journal of Zoology, London*, 239:329–355. doi:10.1111/j.1469-7998.1996.tb05454.x.

Macdonald, D. W., S. Creel, and G. L. Mills. 2004a. "Society." In *Biology and Conservation of Wild Canids,* ed. D. W. Macdonald and C. Sillero-Zubiri, pp. 85–106. Oxford: Oxford University Press.

Macdonald, D. W., A. J. Loveridge, and R. P. D. Atkinson. 2004b. Jackals. A Comparative Study of Side-Striped Jackals in Zimbabwe: The Influence of Habitat and Congeners. In *Biology and Conservation of Wild Canids,* ed. D. W. Macdonald and C. Sillero-Zubiri, pp. 85–106. Oxford: Oxford University Press.

Macdonald, D. W., and C. Sillero-Zubiri, eds. 2004. *The Biology and Conservation of Wild Canids*. Oxford: Oxford University Press.

Magnusson, W. E., V. M. G. Layme, and A. P. Lima. 2010. Complex Effects of Climate Change: Population Fluctuations in a Tropical Rodent Are Associated with the Southern Oscillation Index and Regional Fire Extent, but Not Directly with Local Rainfall. *Global Change Biology,* 16(9):2401–2406. doi:10.1111/j.1365-2486.2009.02140.x.

Maia, O. B., and A. M. G. Gouveia. 2002. Birth and Mortality of Maned Wolves *Chrysocyon brachyurus* (Illiger, 1811) in Captivity. *Brazilian Journal of Biology*, 62:25–32. doi:10.1590/S1519-69842002000100004.

"Maned Wolf Species Survival Plan." 2007. In *Maned Wolf Husbandry Manual*. Silver Spring, Maryland: Association of Zoos and Aquariums, 97 pp.

Margoluis, R., C. Stem, N. Salafsky, and M. Brown. 2009. Using Conceptual Models as a Planning and Evaluation Tool in Conservation. *Evaluation and Program Planning*, 32:138–147. doi:10.1016/j.evalprogplan.2008.09.007.

Marinho-Filho, J. S., F. H. G. Rodrigues, and K. M. Juarez. 2002. "The Cerrado Mammals: Diversity, Ecology and Natural History." In *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, ed. P. S. Oliveira and R. J. Marquis, pp. 266–284. New York: Columbia University Press.

Martin, P. S., and R. G. Klein, eds. 1984. *Quaternary Extinctions: A Prehistoric Revolution*. Tucson: University of Arizona Press.

Martins, B. de A. 2006. Avaliação físico-química de frutos do cerrado in natura e processados para a elaboração de multimisturas. Master's thesis, Programa de Mestrado em Ecologia e Produção Sustentáve, Universidade Católica de Goiás.

Marucco, F, D. H. Pletscher, and L. Boitani. 2008. Accuracy of Scat Sampling for Carnivore Diet Analysis: Wolves in the Alps as a Case Study. *Journal of Mammalogy,* 89:665–673. doi:10.1644/07-MAMM-A-005R3.1.

May-Júnior, J. A., N. Songsasen, F. C. Azevedo, J. P. Santos, R. C. Paula, F. H. G. Rodrigues, M. D. Rodden, D. E. Wildt, and R. G. Morato. 2009. Hematology and Blood Chemistry Parameters Differ in Free-Ranging Maned Wolves (*Chrysocyon brachyurus*) Living in the Serra da Canastra National Park Versus Adjacent Farmlands, Brazil. *Journal of Wildlife Diseases*, 45:81–90.

Mech, L. D. 1970. *The Wolf: The Ecology and Behavior of an Endangered Species*. Garden City, N. Y.: Natural History Press.

Melo, L. F. B. de, M. A. L. Sábato, E. M. V. Magni, and C. M. Coelho. 2007. Secret Lives of Maned Wolves *Chrysocyon brachyurus* Illiger 1815): As Revealed by GPS Tracking Collars. *Journal of Zoology,* 271:27–36. doi:10.1111/j.1469--7998.2006.00176.x.

Melo, L. F. B. de, M. A. L. Sabato, E. M. V. Magni, R. J. Young, and C. M. Coelho. 2009. First Observations of Nest Attendance Behavior by Wild Maned Wolves, *Chrysocyon brachyurus*. *Zoo Biology*, 28:69–74.

Mills, M. G. L. 1989. "The Comparative Behavioral Ecology of Hyenas: The Importance of Diet and Food Dispersion." In *Carnivore Behavior, Ecology and Evolution,* ed. J. L. Gittleman, pp. 125–142. Ithaca, N. Y.: Comstock Publishing Associates.

Mills, K. J., B. R. Patterson, D. L. Murray, and J. Bowman. 2006. Effects of Variable Sampling Frequencies on GPS Transmitter Efficiency and Estimated Wolf Home Range Size and Movement Distance. *Wildlife Society Bulletin,* 34:1463–1469. doi:10.2193/0091-7648(2006)34[1463:EOVSFO]2.0.CO;2.

Moehlman, P. D., and H. Hofer. 1997. “Cooperative Breeding, Reproductive Suppression, and Body Mass in Canids.” In *Cooperative Breeding in Animals*, ed. N. G. Solomon and J. A. French, pp. 76–128. Cambridge: Cambridge University Press.

Motta-Junior, J. C., and K. Martins. 2002. “The Frugivorous Diet of the Maned Wolf, *Chrysocyon brachyurus*, in Brazil: Ecology and Conservation.” In *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*, ed. D. J. Levey, W. R. Silva, and M. Galetti, pp. 291–303. Wallingford: CAB International.

Motta-Junior, J. C., S. A. Talamoni, J. A. Lombardi, and K. Simokomaki. 1996. Diet of the Maned Wolf, *Chrysocyon brachyurus*, in Central Brazil. *Journal of Zoology*, 240:277–284.

Navarro, G., and M. Maldonado. 2002. *Geografía Ecológica de Bolivia: Vegetación y Ambientes Acuáticos*. Cochabamba: Editorial Simon I. Patino.

Norton, T.M. 1990. “Medical Management of Maned Wolves.” In *Proceedings: American Association of Zoo Veterinarians*, ed. R. C. Cambre, J. E. Whitney, C. L. Garrett, M. Zoller, and J. Nordstrom, pp. 61–63. Denver: American Association of Zoo Veterinarians.

Oftedal, O. T., and J. L. Gittleman. 1989. “Patterns of Energy Output during Reproduction.” In *Carnivore Behavior, Ecology, and Evolution*, ed. J. L. Gittleman, pp. 355–78. Ithaca, N. Y.: Cornell University Press.

Paula, R. C., P. Medici, and R. G. Morato. 2008. *Plano de ação para conservação do lobo-guará: Análise de vaibilidade populacional e de hábitat (PHVA)*. Brasilía: Ediçoes Ibama.

Pautasso, A. A., ed. 2009. Estado de conocimiento y conservación del aguará guazú (*Chrysocyon brachyurus*) en la provincia de Santa Fe, Argentina. *Biologica 11*.

Petrie, A., and P. Watson. 2006. *Statistics for Veterinary and Animal Science*. Ames: Blackwell Publishing.

Pocock, R. I. 1927. The External Characters of a Bush-Dog (*Speothos venaticus*) and of a Maned Wolf (*Chrysocyon brachyurus*) Exhibited in the Society’s Gardens. *Proceedings of the Zoological Society of London*, 1927:307–321. doi:10.1111/j.1096-3642.1927.tb02263.x.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting Extinction Risk in Declining Species. *Proceedings of the Royal Society B*, 267:1947–1952. doi:10.1098/rspb.2000.1234.

Queirolo, D., J. R. Moreira, L. Soler, L. H. Emmons, F. H. G. Rodrigues, A. A. Pautasso, J. L. Cartes, and V. Salvatori. 2011. Historical and Present Geographic Distribution of *Chrysocyon brachyurus* (Carnivora: Canidae). *Oryx*, 45:296–303. doi:10.1017/S0030605310000372.

Queirolo, D., and J. C. Motta-Junior. 2007. Prey Availability and Diet of Maned Wolf in Serra da Canastra National Park, Southeastern Brazil. *Acta Theriologica*, 52:391–402. doi:10.1007/BF03194237.

Ralls, K., J. D. Ballou, and A. Templeton. 1988. Estimates of Lethal Equivalents and the Cost of Inbreeding in Mammals. *Conservation Biology*, 2:185–193. doi:10.1111/j.1523-1739.1988.tb00169.x.

Rasmussen, J. L., and R. L. Tilson. 1984. Food Provisioning by Adult Maned Wolves (*Chrysocyon Brachyurus*). *Zeitschrift fur Tierpsychologie,* 65:346–352.

Ratter, J. A., J. F. Ribeiro, and S. Bridgewater. 1997. The Brazilian Cerrado Vegetation and Threats to Its Biodiversity. *Annals of Botany*, 80:223–230. doi:10.1006/anbo.1997.0469.

Redford, K. H., and G. A. B. da Fonseca. 1986. The Role of Gallery Forests in the Zoogeography of the Cerrado’s Non-volant Mammal Fauna. *Biotropica,* 18:126–135. doi:10.2307/2388755.

Reichard, U. H., and C. Boesch, eds. 2003. *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*. Cambridge: Cambridge University Press.

Reid, H. L., S. L. Deem, and S. B. Citino. 2005. Extraosseous Osteosarcoma in a Maned Wolf (*Chrysocyon brachyurus*). *Journal of Zoo and Wildlife Medicine*, 36:523–526. doi:10.1638/04-043.1.

Robbins, R. G., and S. L. Deem. 2002. Ticks of the Genus *Amblyomma* (Acari: Ixodida: Ixodidae) from a Maned Wolf, *Chrysocyon brachyurus*, with the First Report of *A. ovale* from This Endangered Canid. *Entomological News,* 113:25–28.

Robbins, R. G., Karesh, W. B., Painter, R. L. E., and S. Rosenberg. 1998. Ticks of the Genus *Amblyomma* (Acari: Ixodida: Ixodidae) from White-Lipped Peccaries, *Tayassu pecari*, in Northeastern Bolivia, with Comments on Host Specificity. *Entomological News*, 109: 172–176.

Robertshaw, D. 2006. Mechanisms for the Control of Respiratory Evaporative Heat Loss in Panting Animals. *Journal of Applied Physiology*, 101:664–668. doi:10.1152/japplphysiol.01380.2005.

Rodden, M., F. Rodrigues, and S. Bestelmeyer. 2004. “Maned Wolf *Chrysocyon brachyurus* (Illiger, 1815).” In *Status Survey and Conservation Action Plan: Canids: Foxes, Wolves, Jackals and Dogs*, ed. C. Sillero-Zubiri, M. Hoffmann, and D. W. Macdonald, pp. 38–43. Cambridge: IUCN.

———. 2008. “*Chrysocyon brachyurus*.” In *IUCN 2010. IUCN Red List of Threatened Species*. Version 2010.2. http://www.iucnredlist.org (accessed 22 August 2010).

Rodgers, A. R., and A. P. Carr. 1998. *HRE: The Home Range Extension for ArcView*. Ontario: Centre for Northern Forest Ecosystem Research.

Rodrigues, F. H. G. 2002. Biologia e conservação do lobo-guará na Estação Ecológica de Águas Emendadas, DF. Ph.D. diss. Universidade Estadual de Campinas, Campinas, Brazil.

Rodrigues, F. H. G., A. Hass, A. C. R. Lacerda, R. L. S. C. Grando, M. A. Bagno, A. M. R. Bezerra, and W. R. Silva. 2007. Feeding Habits of the Maned Wolf (*Chrysocyon brachyurus*) in the Brazilian Cerrado. *Mastozoologia Neotropical*, 14:37–51.

Rodrigues, F. M., and J. A. F. Diniz-Filho. 2007. Extinction of Canid Populations by Inbreeding Depression Under Stochastic Environments in Southwestern Goiás State: A Simulation Study. *Genetics and Molecular Biology*, 30:121–126. doi:10.1590/S1415-47572007000100021.

Rothschild, B. M., C. Rothschild, and J. R. Woods. 2001. Inflammatory Arthritis in Canids: Spondyloarthropathy. *Journal of Zoo and Wildlife Medicine*, 32:58–64.

Rumiz, D., and L. Sainz. 2002. Estimación del hábitat útil y la abundancia potencial del lobo de crin o borochi (*Chrysocyon brachyurus*) en Huanchaca, Santa Cruz. *Revista Boliviana de Ecologia y Conservación,* 11:3–16.

Rudorff, B. F. T., D. A. de Aguiar, W. F. da Silva, L. M. Sugawara, M. Adami, and M. A. Moreira. 2010. Studies on the Rapid Expansion of Sugarcane for Ethanol Production in São Paulo State (Brazil) Using Landsat Data. *Remote Sensing*, 2:1057–1076. doi:10.3390/rs2041057.

Sabatini, G. S., A. Pinter, F. A. Nieri-Bastos, A. Marcili, and M. B. Labruna. 2010. Survey of Ticks (Acari: Ixodidae) and Their *Rickettsia* in an Atlantic Rainforest Reserve in the State of São Paulo, Brazil. *Journal of Medical Entomology*, 47:913–96. doi:10.1603/ME10073.

Sanaiotti, T., and W. E. Magnusson. 1995. Effects of Annual Fires on the Production of Fleshy Fruits Used by Birds in a Brazilian Amazonian Savanna. *Journal of Tropical Ecology*, 11:53–65. doi:10.1017/S0266467400008397.

Santos, E. F., E. Z. F. Setz, and N. Gobbi. 2003. Diet of the Maned Wolf (*Chrysocyon brachyurus*) and Its Role in Seed Dispersal on a Cattle Ranch in Brazil. *Journal of Zoology,* 260:203–208. doi:10.1017/S0952836903003650.

Serra-Freire, N.M. 1983. Tick Paralysis in Brazil. *Tropical Animal Health and Production,* 15:124–126.

Shih, V.E. 1973. *Laboratory Techniques for the Detection of Hereditary Metabolic Disorders*, pp. 12–13. Boca Raton, Fla.: CRC Press..

Sillero-Zubiri, C., and D. Gottelli. 1995. Diet and Feeding Behavior of Ethiopian Wolves (*Canis simensis*). *Journal of Mammalogy*, 76:531–541. doi:10.2307/1382361.

Sillero-Zubiri, C., M. Hoffmann, and D. W. Macdonald, eds. 2004. *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan*. Gland: IUCN/SSC Canid Specialist Group.

Sillero-Zubiri, C., and J. Marino. 2004. "Ethiopian Wolf." In *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan*, ed. C. Sillero-Zubiri, M. Hoffmann, and D. W. Macdonald, pp. 167–74. Gland: IUCN/SSC Canid Specialist Group.

Silva, J. A., and S. A. Talamoni. 2003. Diet Adjustments of Maned Wolves, *Chrysocyon brachyurus* (Illiger) (Mammalia, Canidae), Subjected to Supplemental Feeding in a Private Natural Reserve, Southeastern Brazil. *Revista Brasileira de Zoologia,* 20:339–345. doi:10.1590/S0101-81752003000200026.

———. 2004. Core Area and Centre of Activity of Maned Wolves, *Chrysocyon brachyurus* (Illiger) (Mammalia, Canidae), Submitted to Supplemental Feeding. *Revista Brasileira de Zoologia*, 21:391–395. doi:10.1590/S0101-81752004000200038.

Silveira, L. 1999. Ecologia e conservação dos mamíferos carnívoros do Parque Nacional das Emas, Goiás. MS Thesis, Universidade Federal de Goiás, Goiás.

Silveira, L., M. M. Furtado, N. M. Tôrres, R. Sollmann, G. Uhl, and A. T. A. Jácomo. 2009. Maned Wolf Density in a Central Brazilian Grassland Reserve. *Journal of Wildlife Management,* 73:68–71. doi: 10.2193/2008-051.

Silveira, L., H. G. Rodrigues, A. T. A. Jácomo, and J. A. F. D. Filho. 1999. Impact of Wildfires on the Megafauna of Emas National Park, Central Brazil. *Oryx*, 33:108–114. doi:10.1017/S0030605300030362.

Simberloff, D. 1998. Flagships, Umbrellas, and Keystones: Is Single-Species Management Passé in the Landscape Era? *Biological Conservation*, 83:247–257. doi:10.1016/S0006-3207(97)00081-5.

Slater, G. J., O. Thalmann, J. A. Leonard, R. M. Schweizer, K.-P. Koepfli, J. P. Pollinger, N. J. Rawlence, J. J. Austin, A. Cooper, and R. K. Wayne. 2009. Evolutionary History of the Falklands Wolf. *Current Biology,* 19:R937–R938. doi:10.1016/j.cub.2009.09.018.

Soler, L., J. M. Carenton, D. Birochio, V. Salvatori, M. M. Orozco, M. S. Rosso, M. Carpinetto, S. H. Fortabat, L. Steiman, M. L. Díaz, M. C. Pino, V. Chávez C., A. M. Kina, G. T. Jiménez, P. Prates, and G. Solís. 2005. Problems and Recommendations for the Conservation for the Maned Wolf in Argentina. *Endangered Species UPDATE*, 22:3–9.

Sollmann, R., M. M. Furtado, A. T. A. Jácomo, N. M. Tôrres, and L. Silveira. 2010. Maned Wolf Survival Rate in Central Brazil. *Journal of Zoology,* 282:207–213. doi:10.1111/j.1469-7998.2010.00727.x.

Sollmann, R., L. Silveira, A. Jácomo, N. M. Tôrres, and M. M. Furtado. 2009. Population Ecology of the Maned Wolf of Central Brazil. Abstracts, IMC-10, Mendoza, Argentina.

Tedford, R. H., X. Wang, and B. E. Taylor. 2009. Phylogenetic Systematics of the North American Caninae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History,* 325:1–218. doi:10.1206/574.1.

Tobler, M. 2009. New GPS Technology Improves Fix Success for Large Mammal Collars in Dense Tropical Forests. *Journal of Tropical Ecology,* 25:217–221. doi:10.1017/S0266467409005811.

Trakhtenbrot, A., R. Nathan, G. Perry, and D. M. Richardson. 2005. The Importance of Long-Distance Dispersal in Biodiversity Conservation. *Diversity and Distributions*, 11:173–181. doi:10.1111/j.1366-9516.2005.00156.x.

Trolle, M., A. Noss, E. D. S. Lima, and J. C. Dalponte. 2007. Camera-Trap Studies of Maned Wolf Density in the Cerrado and the Pantanal of Brazil. *Biodiversity and Conservation*, 16:1197–1204. doi:10.1007/s10531-006-9105-y.

Van Valkenburgh, B. 1989. "Carnivore Dental Adaptations and Diet: A Study of Trophic Diversity Within Guilds." In *Carnivore Behavior, Ecology and Evolution*, ed. J. L. Gittleman, pp. 410–436. Ithaca, N. Y.: Cornell University Press.

Varela, O., and E. H. Bucher. 2006. Passage Time, Viability, and Germination of Seeds Ingested by Foxes. *Journal of Arid Environments,* 67:566–578. doi:10.1016/j.jaridenv.2006.03.013.

Velloso, A. L., S. K. Wasser, S. L. Monfort, and J. M. Dietz. 1998. Longitudinal Fecal Steroid Excretion in Maned Wolves (*Chrysocyon Brachyurus*). *General and Comparative Endocrinology,* 112:96–107. doi:10.1006/gcen.1998.7147.

Vitaliano, S. N., D. A. O. Silva, T. W. P. Mineo, R. A. Ferreira, E. Bevilacqua, and J. R. Mineo, 2004. Seroprevalence of *Toxoplasma gondii* and *Neospora caninum* in Captive Maned Wolves (*Chrysocyon brachyurus*) from Southeastern and Midwestern Regions of Brazil. *Veterinary Parasitology,* 122:253–260. doi:10.1016/j.vetpar.2004.04.004.

Vitt, L. J. 1978. Caloric Content of Lizard and Snake (Reptilia) Eggs and Bodies and the Conversion of Weight to Caloric Data. *Journal of Herpetology,* 12:65–72. doi:10.2307/1563505.

Vucetich, J. A., and R. O. Peterson. 2004. "Grey Wolves-Isle Royale." In *Biology and Conservation of Wild Canids,* ed. D. W. Macdonald and C. Sillero-Zubiri, pp. 285–296. Oxford: Oxford University Press.

Vynne, C. 2010. Landscape Use by Wide-Ranging Mammals of the Cerrado, Ph.D. diss., Department of Biology, University of Washington, Seattle.

Vynne, C., J. R. Skalski, R. B. Machado, M. J. Groom, A. T. A. Jácomo, J. Marinho-Filho, M. B. R. Neto, C. Pomilla, L. Silveira, H. Smith, and S. K. Wasser. 2011. Effectiveness of Scat-Detection Dogs in Determining Species Presence in a Tropical Savanna Landscape. *Conservation Biology*, 25:154–162. doi:10.1111/j.1523-1739.2010.01581.x.

Wallace, R.B. 2005. Seasonal Variations in Diet and Foraging Behavior of *Ateles chamek* in a Southern Amazonian Tropical Forest. *International Journal of Primatology,* 26:1053–1075.

Wang, X., R. H. Tedford, and M. Anton 2008. *Dogs: Their Fossil Relatives and Evolutionary History*. New York: Columbia University Press.

Wayne, R. K., E. Geffen, D. J. Girman, K. P. Koepfli, L. M. Lau, and C. R. Marshall. 1997. Molecular Systematics of the Canidae. *Systematic Biology,* 46:622–653. doi:10.1093/sysbio/46.4.622.

Wilson, D. E., and D. M. Reeder 2005. *Mammal Species of the World*. Third Edition. Baltimore: Johns Hopkins University Press.

Woodroffe, R., J. M. André, B. Andulege, F. Bercovitch, A. Carlson, P. Coppolillo, H. Davies-Mostert, A. Dickman, P. Fletcher, J. Ginsberg, M. Hofmeyr, M. K. Laurenson, K. Leigh, P. A. Lindsey, R. Lines, J. Mazet, K. McCreery, J. W. McNutt, M. G. L. Mills, M. Msuha, L. Munson, M. N. Parker, A. Pole, G. Rasmussen, R. Robbins, C. Sillero-Zubiri, M. J. Swarner, and M. Szykman. 2005. *Tools for the Conservation of the African Wild Dog. Do We Know Enough? What More Do We Need to Know?* New York: IUCN Canid Specialist Group, Wildlife Conservation Society.

Xu, L., A. Samanta, M. E. L. Costa, S. Ganguly, R. Nemani, and R. Myneni. 2011. Widespread Decline in Greenness of Amazonian Vegetation Due to the 2010 Drought. *Geophysical Research Letters,* 38:1–4. doi:10.1029/2011GL046824.

Yates, J. A., and R. C. Lowrie. 1984. Development of *Yatesia hydrochoerus* (Nematoda: Filaroidea) to the Infective Stage in Ixodid Ticks. *Proceedings of the Helminthological Society of Washington,* 51:187–190.

Zuercher, G. L., P. S. Gipson, and O. Carrillo. 2005. Diet and Habitat Associations of Bush Dogs *Speothos venaticus* in the Interior Atlantic Forest of Eastern Paraguay. *Oryx,* 39:86–89.

Index

Figures in **bold**; Tables in *italics*.

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