

Synthesis

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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.

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, km ²	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 ($\text{g kg}^{0.75} \text{d}^{-1}$), 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 its 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 covies 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 covies 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 km² [Courtenay and Maffei, 2004]; MW, 5.2 per 100 km² 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 tree-lets 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

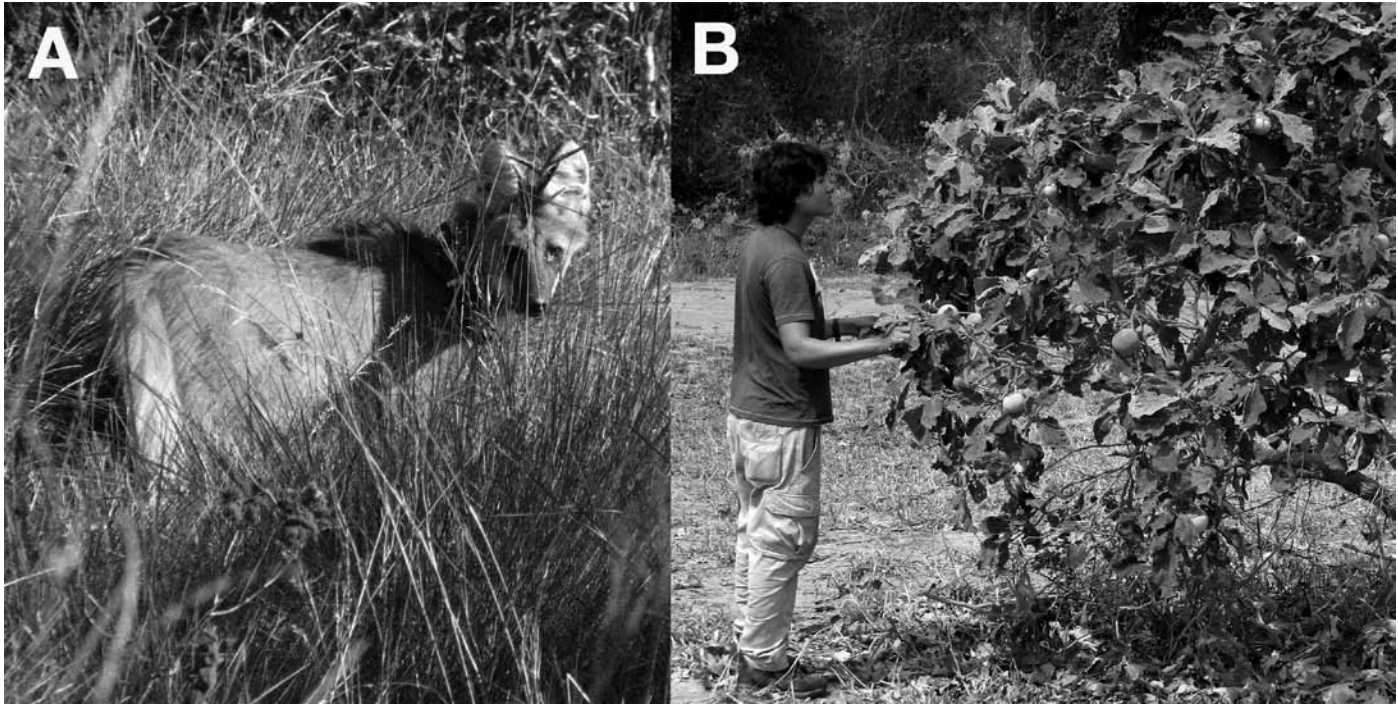


FIGURE 8.2. (A) Height of maned wolf M8 relative to long grass of Los Fierros savanna. (B) J. M. Castro inspects a tree of *Solanum gomphodes* on a roadside outside of Noel Kempff Mercado National Park. The many fruits are immature; note that some are higher than his head (Photographs by L Emmons).

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,

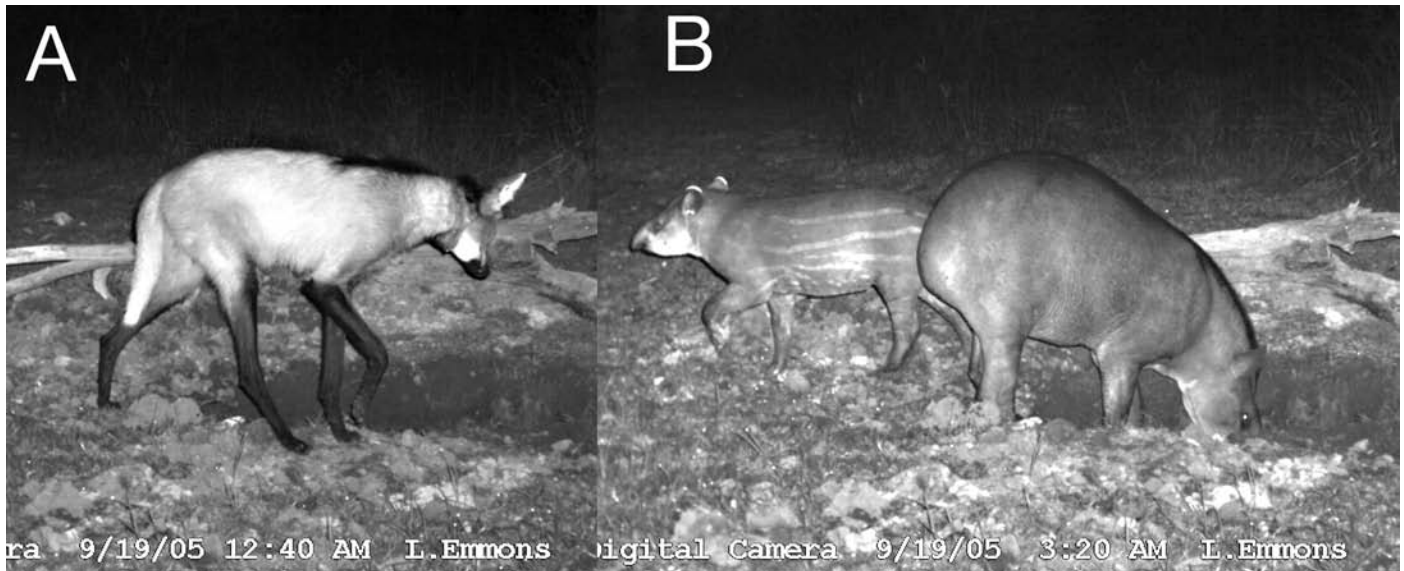


FIGURE 8.3. Relative heights of (A) maned wolf F3 and (B) a mother tapir with young (standing partly below ground level). Camera trap images taken 3 hours apart at the Pozo Matt water hole.

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 adaptive 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.