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Activity Patterns

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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

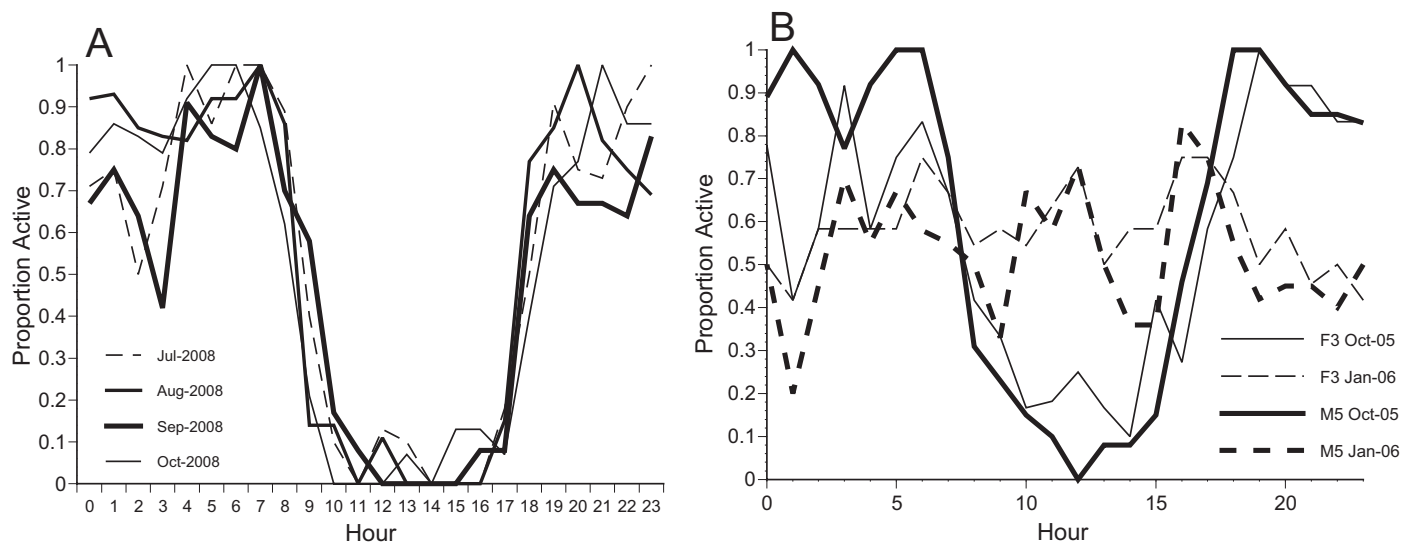


FIGURE 2.1. Average proportion of “active” intervals between hourly fixes (movement >50 m, see Materials and Methods), based on hourly GPS fixes recorded during three days of each week, with all fixes classed as either active (1) or inactive (0). (A) Monthly dry season averages for male M8, July–October 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).

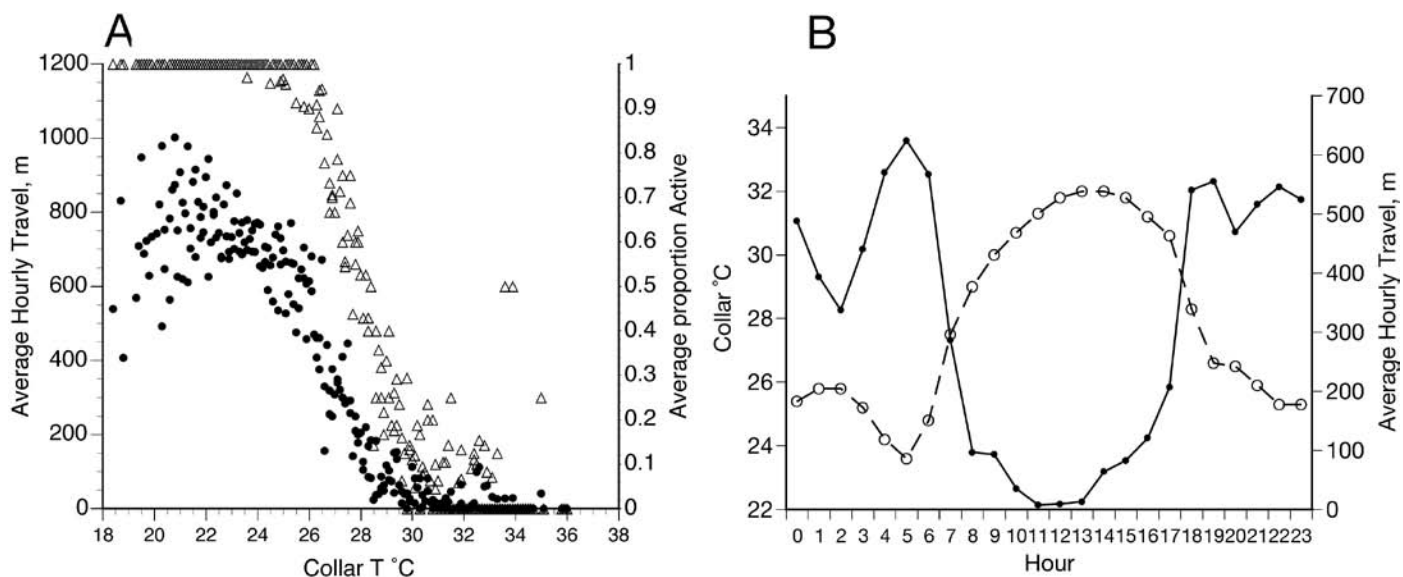


FIGURE 2.2. Activity and collar temperature for F3 October 2004–January 2005; T (°C) measured at each GPS fix by collar sensor (distance traveled is for the hour preceding the T reading; $N = 1,847$). (A) Raw data sets for distance traveled from the previous fix and temperature at that fix time (solid 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.

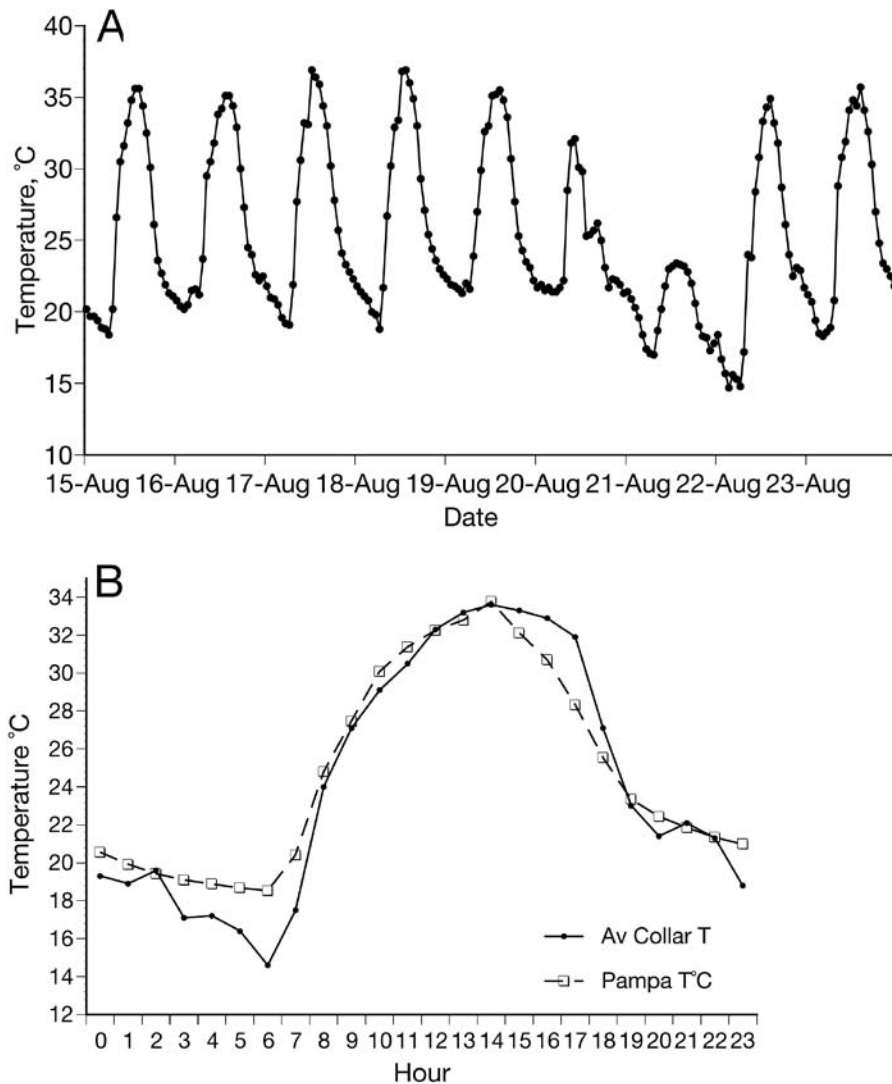


FIGURE 2.3. (A) Hourly ambient temperature 15–27 August 2009, with passage of a cold front 21–22 August (Kestrel® weather logger in open Los Fierros savanna) and (B) average hourly instrument temperature reading in savanna August 2009 during 13.5 days ($N = 322$ readings) (dashed line); and mean hourly 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 $T_{\max} = 32.0^{\circ}\text{C}$, $T_{\min} = 16.2^{\circ}\text{C}$) was colder than August 2009 (mean $T_{\max} = 33.6^{\circ}\text{C}$, $T_{\min} = 20.2^{\circ}\text{C}$), 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

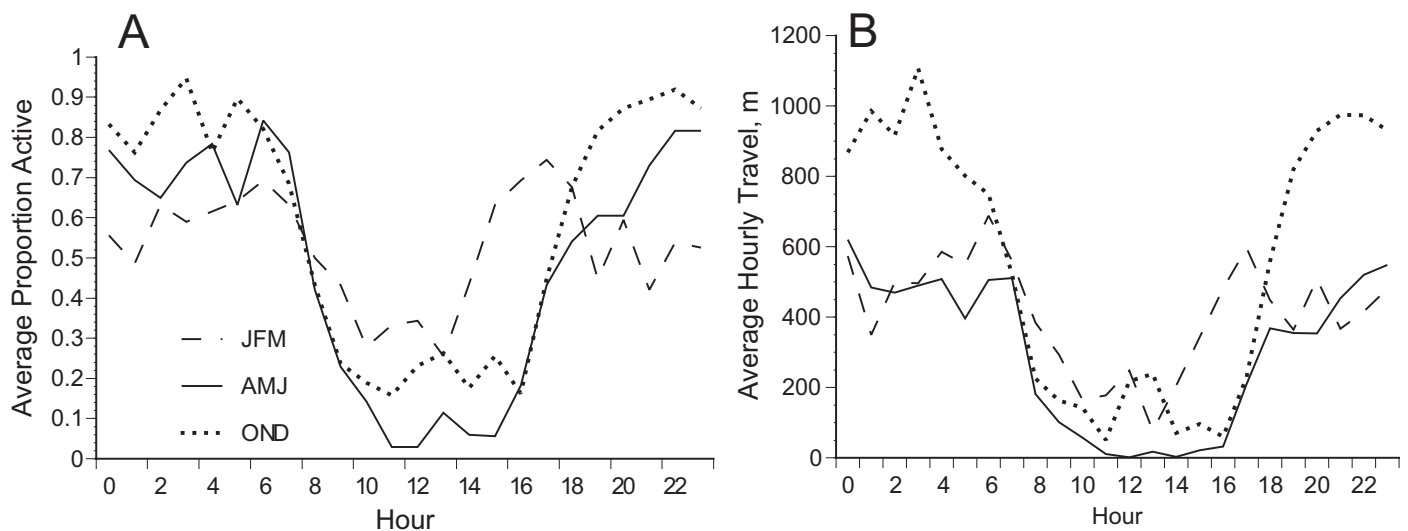


FIGURE 2.4. Hourly activity by season. (A) The average proportion of fixes for a given hour during which F3 was active (movement >50 m between fixes, nominal data active/inactive) and (B) the average distance traveled between hourly fixes from the same data set. On the basis of three-night weekly samples 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).

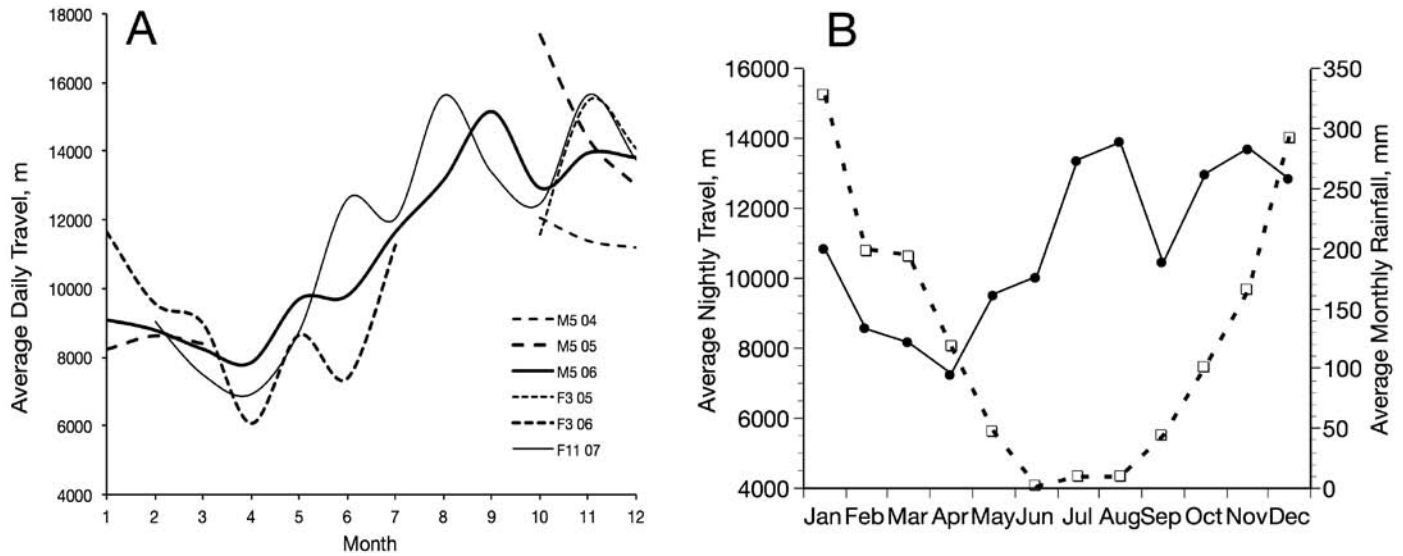


FIGURE 2.5. Average daily total travel distance (sums of average hourly travel) by month. (A) Six data sets from three individuals show the variation between individuals and months and (B) average daily travel of five adult MW combined from 40 monthly data sets 2003–2008 (solid line) and average monthly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

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 (*Cercopithecus thomasi*), 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

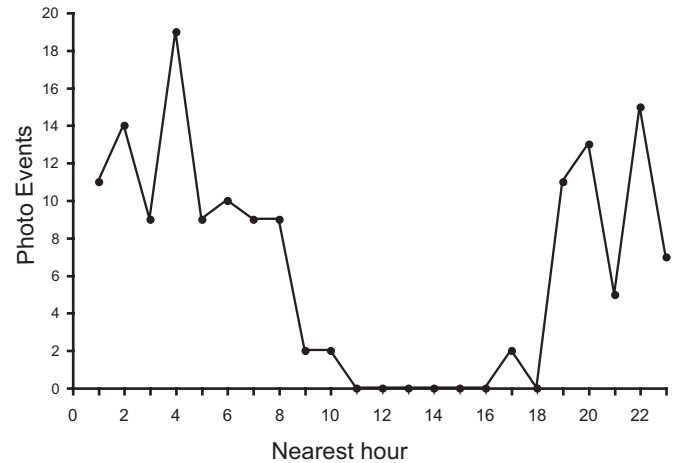


FIGURE 2.6. Circadian pattern of visiting water. Time to the nearest hour of photos of MW at water holes, including only the first photo (event) of a given individual in a given hour ($N = 158$ events).

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 km²). 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, caviies (*Cavia aperea*) were the main prey of MW, with about 80% occurrence in scats (Emmons, 2009; Chapter 4). Caviies are active in early morning and late afternoon, as are the numerically dominant mice of the savanna, *Necromys lenguarum* (Francisco et al., 1995). Caviies 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 caviies were

abundant. However, because caviies 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 mellifera*) 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.