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Ranging Patterns

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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 km². MW varied their sequential nightly trajectories such that an average of 34 km² (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,

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 km² 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.

Animal (Site)	Collar	Data start	Data end	Fixes	Three-night samples	KHR, km²			
						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).

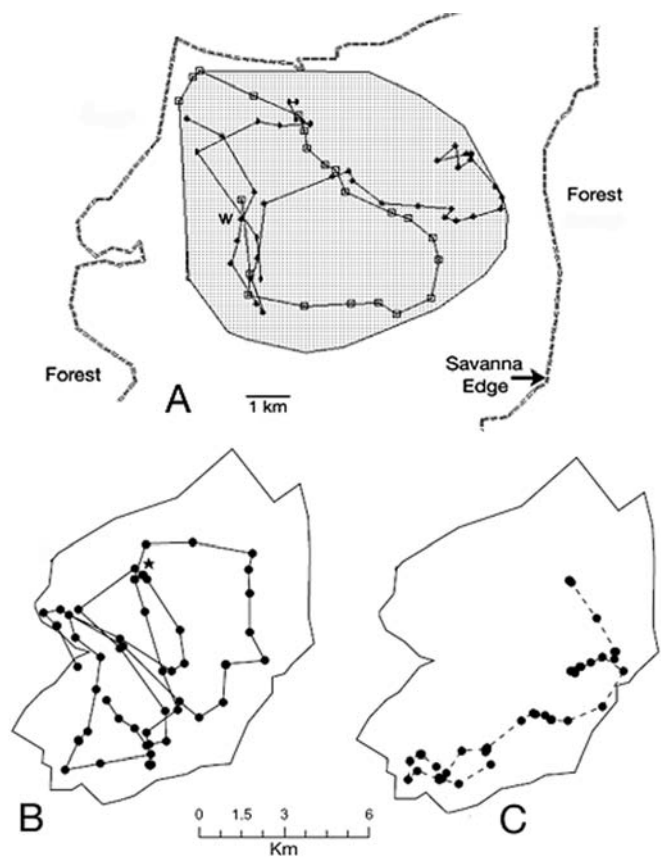### General Movement Patterns and Distance Traveled

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

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 3.2. 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.

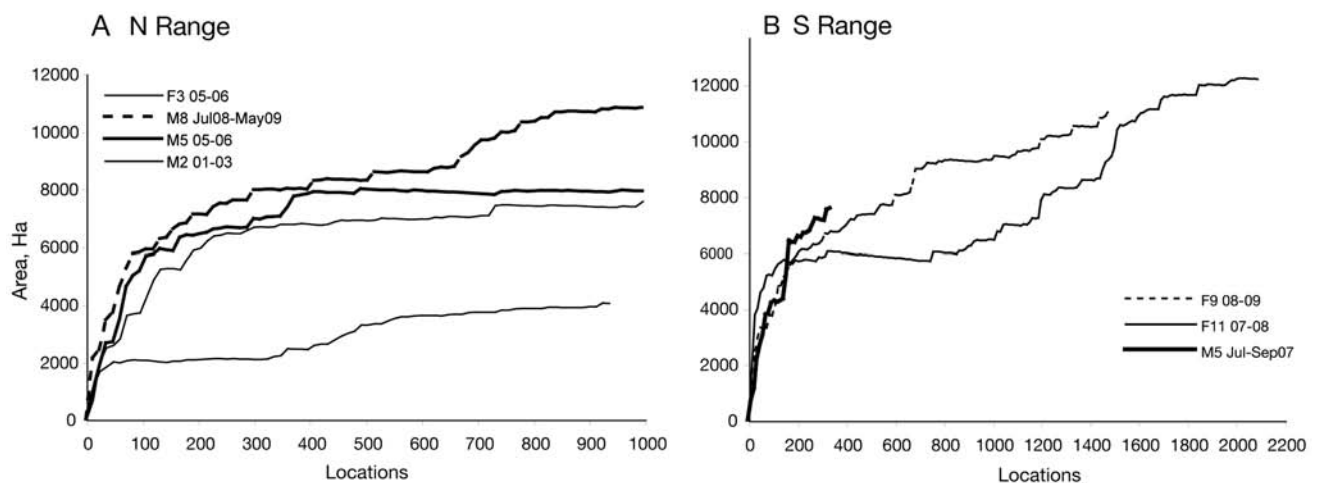| Month (N)	M5 (28)	M8 (16)	F3 (25)	F11 (14)	F9 (9)	Average (92)	SD
1 (9)	8.80	10.35	12.74	11.28	11.09	10.85	1.29
2 (8)	9.00	9.85	9.43	8.85	5.74	8.57	1.46
3 (8)	7.92	10.73	8.82	6.79	6.65	8.18	1.50
4 (4)	7.68	10.06	5.87	7.81	4.99	7.28	1.76
5 (4)	9.54	10.47	8.48	9.73	n/a	9.56	0.71
6 (3)	9.65	n/a	7.24	13.26	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	

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 km², 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).
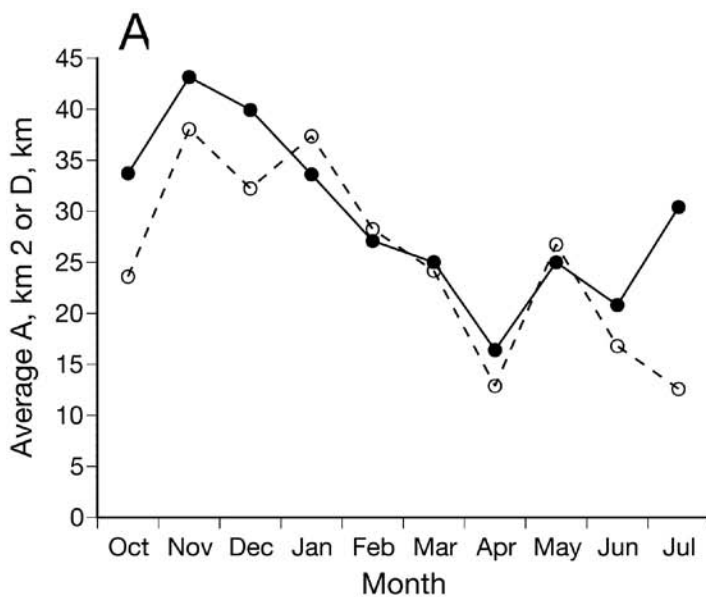
TABLE 3.4. Area and distance covered in three night samples. The mean minimum convex polygon area covered (calculated in R-Ade), and mean total distance and SD of distance traveled per three night sample, for individual MW with large data sets. Data are for M8 total and segregated into samples taken in different home range areas (SR, South Range; NR, North Range). Samples for F3 with newborn pups omitted.

Maned wolf	N samples	Mean area, km²	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
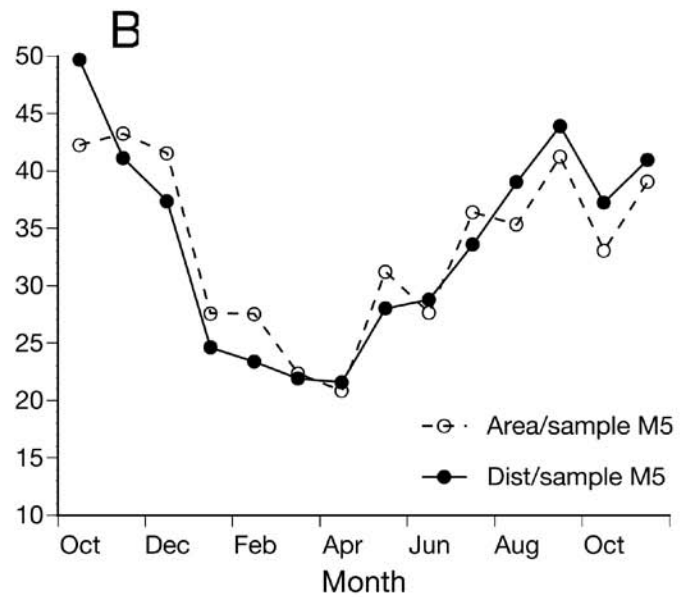

FIGURE 3.3. Average distances (broken lines) and areas (solid lines) of three-night weekly samples for the male and female of a pair, by month, in 2005–2006. (A) Female F3, 10 months of continuous data (she had new pups in July); (B) Male M5, 14 months of continuous data.
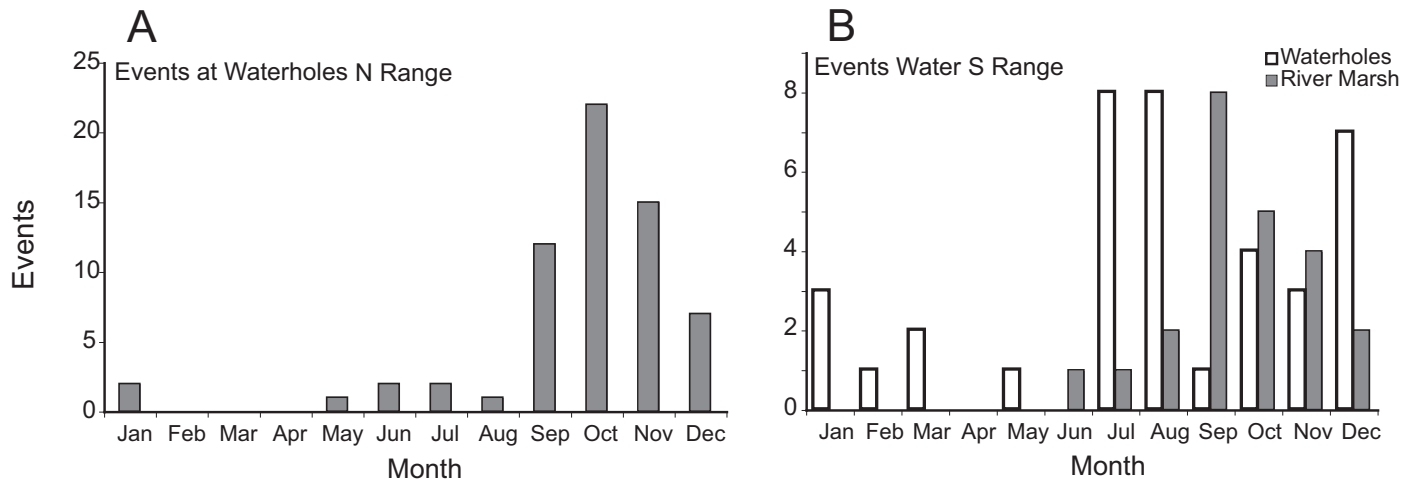
FIGURE 3.4. Proximity to water sources by month. (A) North Range, three, 11–12 month continuous data sets (35 months) from two males and a female ($N = 64$ events). (B) South Range, two, 11–12 month continuous data sets from two females ($N = 61$ events); river marsh, shaded bars. Only the first fix (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 km² strip near the SW boundary of her 52 km², 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
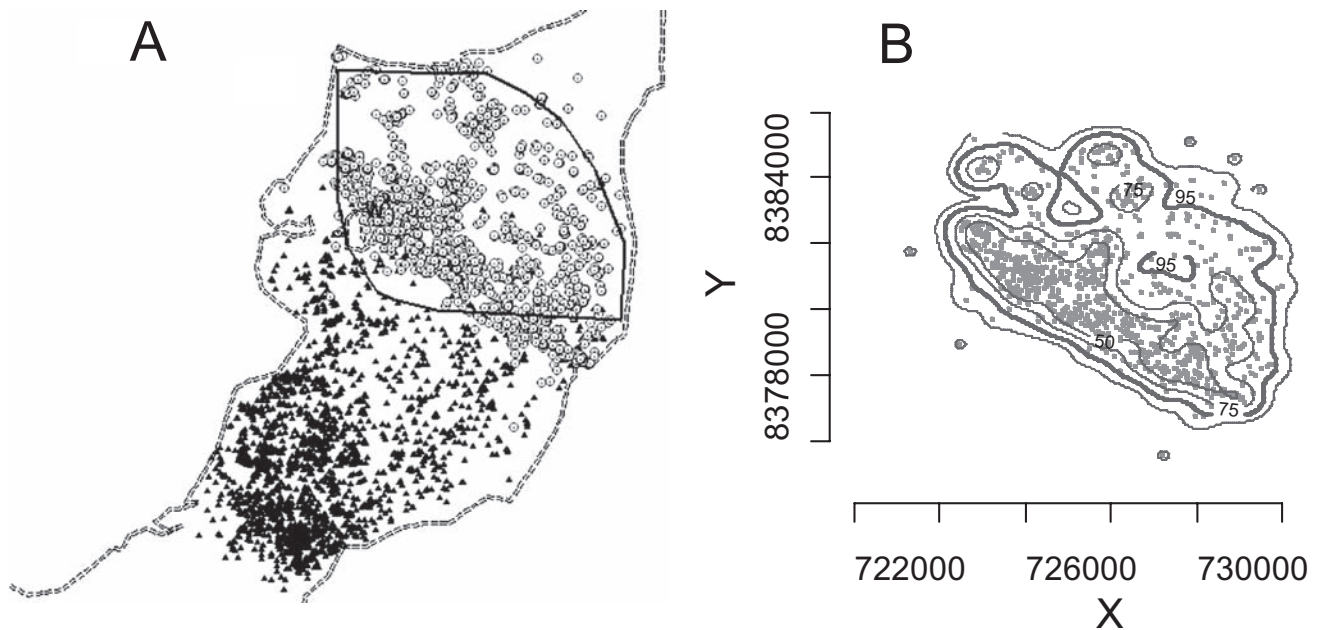
FIGURE 3.5. Positions of maned wolf ranges on the Los Fierros savanna from October 2001 to March 2005. (A) Los Fierros savanna outline with all October 2003 to January 2004 GPS locations of F3 (open circles), overlaid by M2 range polygon outline (dark pointed oval, 2001–2003 VHF locations); and M5 GPS 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.
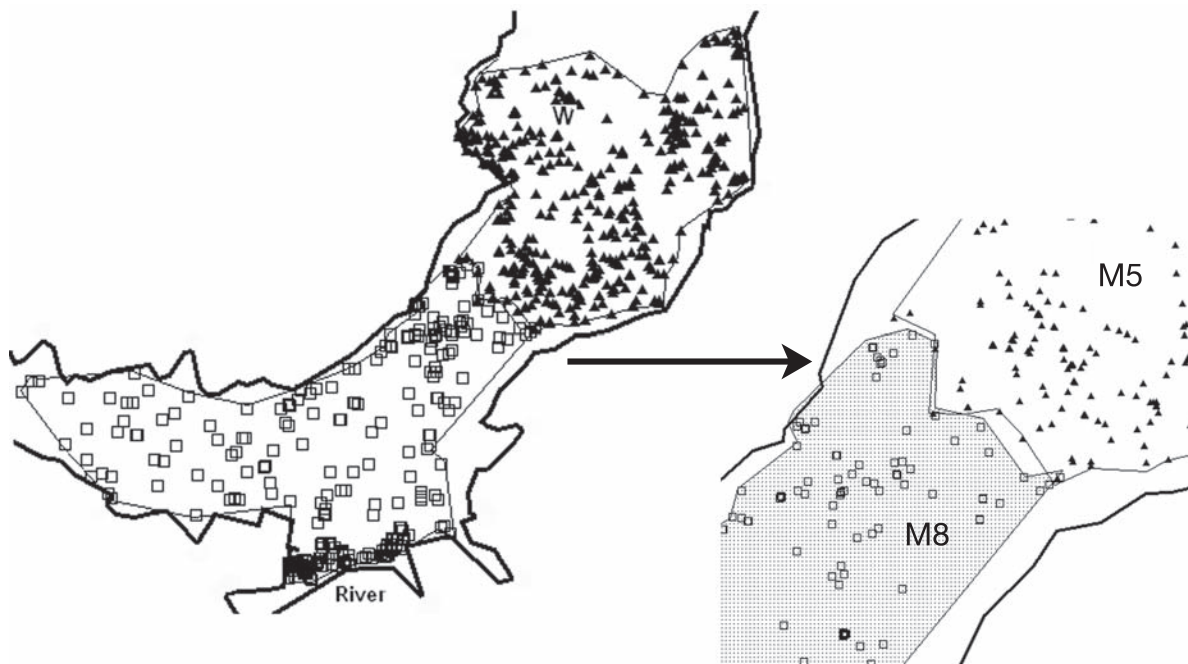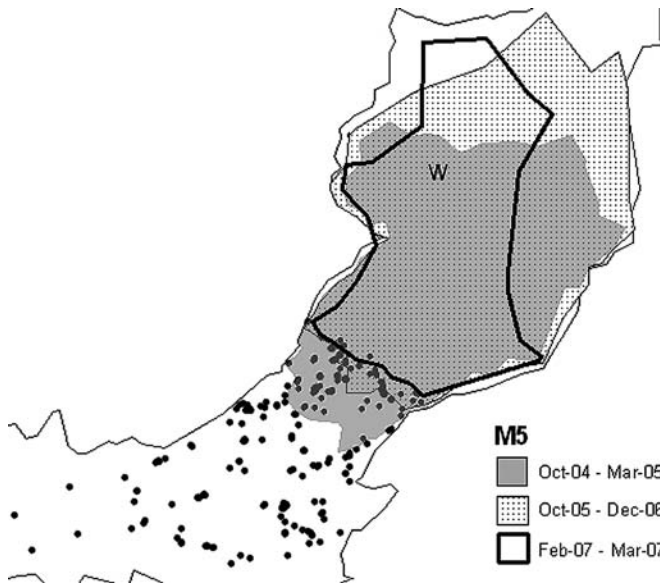

FIGURE 3.6. Synchronous locations of neighboring males M5 (North) and M8 (South) during September and October 2006, home range polygons shown as thin lines. (Left) Whole ranges; (right) mutual boundary, enlarged. The cluster of locations at bottom center at left are along the river; cluster above the W on the NW side of the North Range is at Pozo Matt water hole.
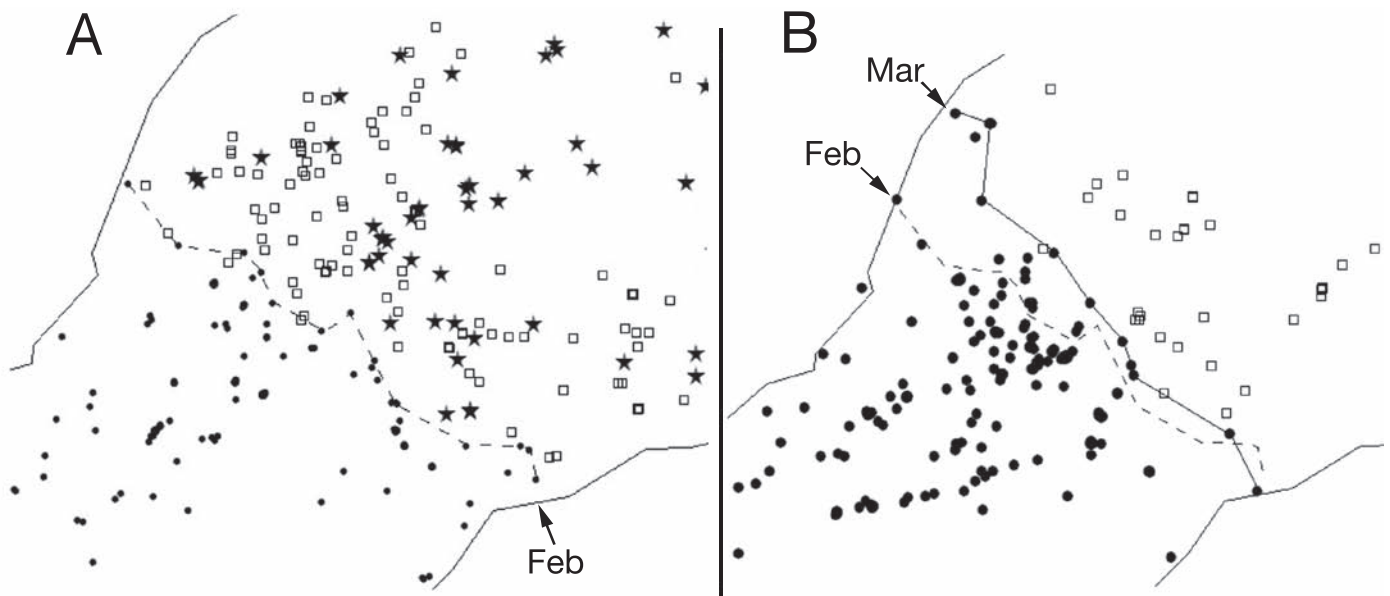
FIGURE 3.7. Home range shifts of M5, moving gradually north-westward over three years, and February 07 locations of F11 (black circles). Note that data sets are of unequal length (2 to14 months), the February–March 2007 range (heavy line) shows avoidance of a recently burned area on its NE side.

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.
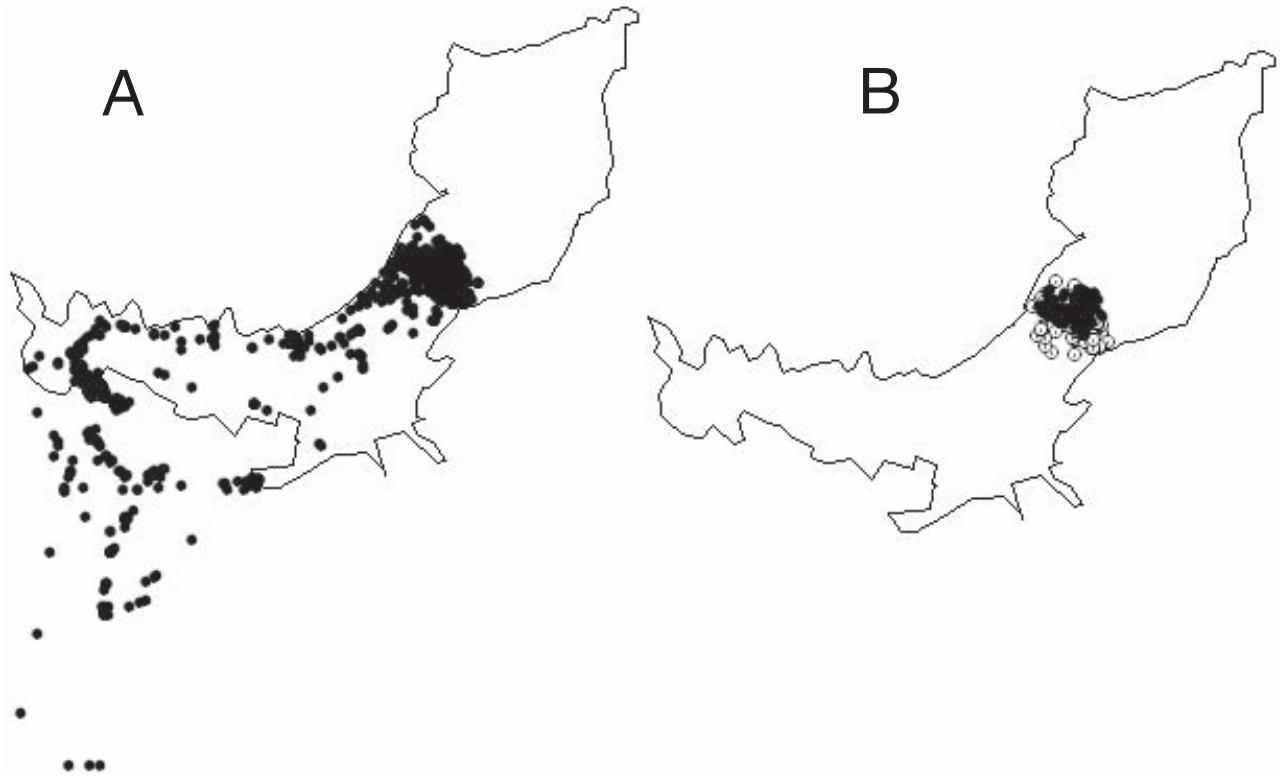
Exceptions to Territoriality

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 km²). (B) Locations in January 2006 (open circles, area = 9.2 km²), and 1–22 February 2006 (black circles, 4.8 km²), 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 km²). 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 km² (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 km² and mean 50% KHR areas of 13.8 km²: close to our mean values of 74.9 and 19.0 km² 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 km² (VHF, perhaps an underestimate) and 52 km²: more like the smaller ranges of 20–40 km² reported by Dietz (1984) and 40–50 km² 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 km²; Melo et al., 2009), additive factors that will underestimate travel distances. We note, however, that our male M2, also with a 40 km² range size, moved 11 km/night (*N* = 15 nights of VHF tracking), while F3 on a 52 km² 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 km², to a 6% difference in one of 75 km² 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.