Ecological predictors of African wild dog ranging patterns in northern Botswana

Matthew A. Pomilia, J. Weldon McNutt, and Neil R. Jordan*

Faculty of Biological Sciences, University of Leeds, Willow Terrace Road, Leeds, West Yorkshire LS2 9JT, United Kingdom (MAP)
Botswana Predator Conservation Trust, Private Bag 13, Maun, Botswana (MAP, JWM, NRJ)
Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales (UNSW), Kensington Campus, Botany Street, Sydney, NSW 2052, Australia (NRJ)
Taronga Conservation Society Australia, Taronga Western Plains Zoo, Wildlife Reproduction Centre, Obley Road, Dubbo, NSW 2830, Australia (NRJ)

* Correspondent: neil.jordan@unsw.edu.au

Extinction risk in African wild dogs (*Lycaon pictus*) has been linked to their wide-ranging movement behavior. However, drivers of variability in African wild dog ranging are not well understood. This study examines the effects of intrinsic and extrinsic factors on ranging patterns and describes scale-dependent and intra-annual variation in the ranging of 5 packs of African wild dogs in the Okavango Delta from 2007 to 2010. 95% fixed kernel home ranges ($\bar{X} = 739 \pm 81$ km^2) and daily step lengths ($\bar{X} = 8.5 \pm 0.5$ km) in this study are larger than have generally been reported for African wild dogs elsewhere. Little seasonal variation in daily ranging distances was observed despite home-range contractions during denning to 27% of packs' ranges outside the denning period. During nondenning periods, litter size was the most influential driver of ranging patterns, with large litters associated with reduced pack movements and smaller home ranges at all temporal scales. Pack size was also a significant driver of home-range size (but not daily distance travelled) at weekly timescales, where larger packs utilized smaller ranges. Daily temperatures were inversely related to home-range size and step length at short timescales, while higher flood levels were related to reduced ranging distances at intermediate timescales. Our results indicate that extrinsic drivers of African wild dog ranging behavior tend to be scale dependent, while intrinsic factors may be more influential for ranging patterns than previously reported.

Key words: ecological drivers, endangered species, home range, Okavango Delta, spatial ecology

Home range is the most commonly used measure of animal space use, and since Burt's (1943) 1st definition, considerable effort has been expended in conceptualizing home ranges and determining the factors which influence their size and utilization. Intraspecific variation in home-range size has been documented in many species (e.g., brown bear, *Ursus arctos*— McLoughlin et al. 2000) with variation often related to extrinsic factors (e.g., habitat and food availability—Tufto et al. 1996; but see Massei et al. 1997). However, in general, and for wide-ranging species in particular, both extrinsic and intrinsic factors are likely to influence home-range size and use, although relatively few studies have considered the effects of these factors together (but see Börger et al. 2006; Naidoo et al. 2012; Godsall et al. 2014). Investigating the role that these factors play in shaping home ranges is essential for wildlife management, particularly in predicting a minimum area required for the effective conservation of a given species.

Generally speaking, food abundance and distribution represent important extrinsic determinants of home-range size both in herbivores (e.g., roe deer, *Capreolus capreolus*—Tufto et al. 1996; moose, *Alces alces*—van Beest et al. 2011) and some carnivore species (e.g., bobcat, *Lynx rufus*—Litvaitis et al. 1986; lynx, *Lynx lynx*—Herfindal et al. 2005). However, for some carnivores, home-range sizes are independent of prey availability (e.g., grizzly bear, *U. a. horribilis*—Nagy and Haroldson 1990; Egyptian mongoose, *Herpestes ichneumon*—Palomares 1994) and are presumably influenced by other factors. The role of climatic and environmental variation, for example, is increasingly being recognized as another key driver of animal movements, with recent studies showing that climate affects home ranges (Rivrud et al. 2010) and often in a scale-dependent way (Börger et al. 2006). At short timescales, temperature and precipitation affect home-range size directly (e.g., red deer, *Cervus elaphus*—Kamler et al. 2007) by forcing individuals to regulate

movement due to thermal stress and energy constraints (Parker et al. 1984; Börger et al. 2006) while over longer timescales climate change has the potential to affect animal movement indirectly through its critical role in ecosystem processes.

In addition to extrinsic pressures, intrinsic factors such as sex and body size have also been shown to be important determinants of home-range size in ungulates (Kjellander et al. 2004) and of movement distance in some canids (e.g., maned wolf, *Chrysocyon brachyurus*—Lima Sabato et al. 2006). In some species, social factors may also affect home-range size: home-range size increases with pack size in Ethiopian wolves (*Canis simensis*—Ashenafi et al. 2005), while pack size accounts for 87% of variation in range size in coyotes (*Canis latrans*—Bowen 1981), though this relationship is not apparent in some canids (e.g., African wild dogs, *Lycaon pictus*—Mills and Gorman 1997; Creel and Creel 2002).

Understanding the drivers of ranging patterns is important for any species, but perhaps particularly so for endangered species with large home ranges, as such species may be endangered in large part due to their wide-ranging behavior (Woodroffe 2011). African wild dogs are endangered large carnivores (IUCN 2012) and have declined dramatically across their range over the past century, with highly fragmented populations remaining in Southern, Eastern, and possibly Central and Western Africa (Fanshawe et al. 1991; Croes et al. 2012). Studies of African wild dog home ranges have produced widely varying size estimates (Table 1), including significant variation (up to an order of magnitude) within populations. Some amount of variation in home-range size is to be expected since home ranges are the result of dynamic ecosystem processes and such variation occurs in all carnivores (Wang and Grimm 2007). However, variation in African wild dog ranging patterns is not well understood and has, for the most part, eluded clear description, despite the suggestion that their wide-ranging behavior is a key driver of population declines (Woodroffe 2011). Hinting at the effect of extrinsic factors such as prey availability on ranging behavior, home ranges are generally smaller where prey are relatively sedentary (e.g., Kruger National Park, South Africa—Fuller et al. 1992) while dogs living in areas with seasonal abundances of migratory prey (e.g., the Serengeti short-grass plains in Tanzania—Frame et al. 1979) have the largest known home ranges. In the Okavango Delta in northern Botswana, seasonal variation in forage quality and quantity related to annual flooding strongly influences prey distributions (Bonyongo 2005) and possibly contributes to comparatively complex patterns of resource availability for wild dogs, but such factors have not been considered in previous wild dog ranging studies (Pomilia 2012). Intrinsic factors such as pack size (but see Mills and Gorman 1997; Creel and Creel 2002) or pack composition may also influence ranging patterns, and while reproductive status may not affect ranging patterns in social groups to the extent that it does solitary animals, range contraction during denning is well documented in African wild dogs (Frame et al. 1979; Creel and Creel 2002). If variation in ranging patterns is, in fact, nonuniform among and within populations, better understanding the dynamics and drivers of this variation may be useful for African wild dog conservation management. It may, for example, help to predict whether small- or medium-sized reserves provide sufficient area to support a viable population and/or highlight how changing ecological/environmental conditions could affect African wild dog movement patterns.

Temporal scale is becoming an increasingly discussed point in home-range studies, since home ranges may respond to different factors at different timescales (Loveridge et al. 2009). It is important to consider ranging patterns (both in terms of area covered and step length) over various timescales, as this can reveal temporally specific drivers that would not be apparent over larger and more typical (i.e., annual) scales. Although a multiscale approach is, thus, critical for understanding patterns of spatiotemporal variation in species' ranging behavior, in most studies of African wild dogs, ranging has often only been described at one specific temporal scale (usually annual; e.g., Creel and Creel 2002). While it is clearly important to consider multiple factors describing variation in ranging, considering ranging patterns themselves over multiple timescales may also add to our understanding of these drivers. For example, while prey abundance is negatively associated with range size in a number of species (e.g., leopard, *Panthera pardus*—Marker and Dickman 2005; tiger, *Panthera tigris*—Simchareon 2014), concurrent measures of prey abundance and ranging may not always be available. For example, range expansion in periods of suspected low food abundance has been used to

Table 1.—Annual home-range estimates for African wild dogs, *Lycaon pictus*, from this study in and around Moremi Game Reserve, northern Botswana and other studies. KDE = kernel density estimation; MCP = minimum convex polygon; TAP = traversed area polygon.

Site	MCP (km²)			95% KDE (km²)			TAP (km²)			Reference
	$\bar{X}$	Range	n	$\bar{X}$	Range	n	$\bar{X}$	Range	n	
Moremi Game Reserve	1,043	412–1,608	7	739	367–999	7	748	340–975	7	This study
	617	375–1,050	9	513	176–762	7				Fuller et al. (1992)
Samburu-Laikipia	278	60–718	29	423	212–833	29				Woodroffe (2011)
Lower Zambezi NP	273	74–459	7							Leigh (2005)
Hwange NP	423	260–633	4							Fuller et al. (1992)
Savé Valley Conservancy	499	352–844	10							Pole (2000)
Kruger NP	555	150–1,110	16							Reich (1981); Mills and Gorman (1997)
Serengeti NP	665	620–710	2							Schaller (1972)
Selous Game Reserve				379	206–851	8				Creel and Creel (2002)

imply that food abundance is an important driver of ranging in some species (e.g., grey-sided vole, *Clethrionomys rufocanus*—Ims 1987). This highlights that drivers of ranging may be identified where direct data on the factor of interest were unavailable. While the selection of timescales corresponding approximately to ecological events of interest (e.g., flood season, impala calving dates, denning) may be appropriate in some contexts, it may be more relevant to select time frames that are more arbitrary (e.g., weekly, monthly, annual) and therefore provide more comparable and balanced data sets both in terms of number of fixes and duration of spread, variation in both of which has been shown to impact ranging estimates (Hansteen et al. 1997; Börger et al. 2008). In this paper, we use a detailed data set from 5 packs of African wild dogs spanning 4 years to assess the drivers of movement and space use; behaviors that have been strongly linked to extinction risk in this endangered species (Woodroffe 2001). We estimate home-range areas and average daily distances travelled on multiple temporal scales in order to resolve the effects of extrinsic and intrinsic factors.

Materials and Methods

Study area.—The Okavango Delta and surrounding area of northern Botswana is home to one of the world's largest African wild dog populations (approximately 500 individuals—Woodroffe et al. 1997). The Botswana Predator Conservation Trust (BPCT) has been monitoring the African wild dog population (6–12 packs) in this area since 1989 and collecting detailed movement data since 2001. The study area (approximately 2,600 km^2; 19°31′S, 23°37′E; elevation: approximately 950 m) is situated just to the east of the Okavango Delta's main floodwaters and is bordered to the west and northwest by the Delta's permanent swamp, including a portion of the Moremi Game Reserve. The height of the Delta's annual flood pulse usually occurs between August and September, coinciding with the peak of the dry season. Further details can be found in McNutt (1996a).

GPS capture and data collection.—Between 2007 and 2010, 7 African wild dogs (6 males, 1 female; at least 1 individual from each of 5 packs) were immobilized using established techniques described elsewhere (Osofsky et al. 1996; McNutt 1996a). Individuals were fitted with GPS collars (Vectronic GmbH, Berlin, Germany) with very-high-frequency (VHF) transmitters to facilitate long-term monitoring and data retrieval. Three GPS fixes per day (0600, 1200, and 1800 h LMT) were stored within the collar and data were later downloaded via a coded ultrahigh frequency or VHF transmission from a nearby vehicle. Upon expiration of the collars (9–15 months), wild dogs were redarted and collars were replaced as part of the ongoing study.

Home-range and daily distance travelled estimation.—All GPS coordinates were projected in the Universal Transverse Mercator (UTM) coordinate system in the Geographic Information System ArcGIS 9.3.1 (ESRI 2009). We used our data set on African wild dogs to evaluate 4 home-range estimation techniques; 2 polygon (minimum convex polygon; traversed area polygon) and 2 kernel (fixed kernel, $h = 2,400$;

Benhamou's kernel, $h = 1, 250$). Their performance was evaluated on sensitivity to both sampling duration and hard boundaries (flood extent), because these criteria are among the most critical, yet most problematic in home-range estimation (Powell 2000; Benhamou 2011). In order to evaluate estimator sensitivity to this "hard" floodwater boundary, we calculated the extent to which annual home ranges erroneously included flooded areas. Overall, kernel methods were much more robust than polygon methods to short sampling duration and (unlike polygons) approached asymptotic values with longer sampling durations. Both kernel methods displayed similar sensitivity to sampling duration (i.e., similar shape and slope of curve), but Benhamou's kernels (estimated using the 95% isopleth) encompassed smaller flooded areas (mean 5.6%) than kernels (8.9%) and so was therefore used in this study. Recognizing that animal locations are serially autocorrelated and that important biological information on animal space use patterns resides within these patterns (Cushman et al. 2005), Benhamou's method assumes that the probability of finding an animal at some intermediate location between points should be distributed preferentially in the movement direction, rather than uniformly in any direction (Benhamou 2011). Home ranges were, therefore, estimated using Benhamou's fixed kernel density estimation (KDE) method (Benhamou 2011), as this method was the most conservative (in the sense of not overestimating home ranges), the least likely to include areas which African wild dogs rarely or never used, and most reliable at all timescales. Home ranges were estimated for each African wild dog at annual (i.e., the duration of the collar), seasonal, monthly, and weekly timescales. Daily distances travelled were estimated by converting locations to paths using Hawth's Tools extension (Beyer 2004) and measuring the length of the combined path between 4 consecutive locations over a 24-h period. Daily distance travelled is used here as a proxy for total distance travelled, which has significant biological consequences for mammals in terms of energy expenditure (Karasov 1992) and exposure to risk of predation or human-induced mortality (e.g., Norrdahl and Korpimäki 1998; Woodroffe 2001).

Climatic, ecological, and demographic data.—Climatic, ecological, and demographic variables were included as fixed effects in linear mixed-effects models. Temperature and rainfall data were obtained from the closest (Maun; 19°31′S, 23°37′E) weather station's historical records (Tutiempo Network, S.L. 2011). Daily recorded temperatures were averaged over the length of the analyzed period (i.e., weekly, monthly). Flood levels were determined using "flood maps," which are composite images of the yearly maximum flood extent during a given year (e.g., 2008, 2009, or 2010) reclassified using the Q1 band from the MODIS satellite images (Fig. 1). These are red and infrared band images which are 8-day composites of daily images and have a spatial resolution of 250 × 250 m. Reclassification of MODIS satellite imagery was restricted to the far eastern portion of the Okavango Delta, from the Khwai River in the north to the Santantadibe River in the south. Images containing cloud cover (during the rainy season) were identified by visual inspection and rejected from further analysis. Cloud-free images were reclassified using the bimodality of the histogram
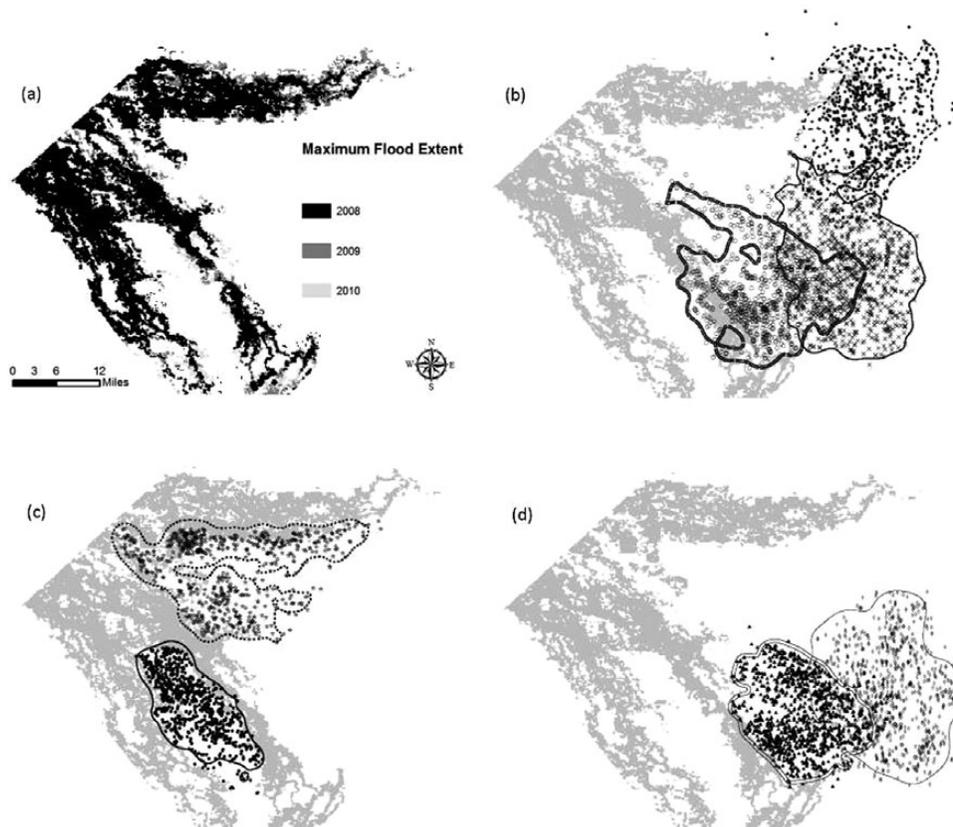
Fig. 1.—Maps displaying a) maximum annual flood extents in the eastern portion of the Okavango Delta from 2008 to 2010 as reclassified from MODIS satellite imagery; and annual home-range estimates for 5 African wild dog, *Lycaon pictus*, packs in and around Moremi Game Reserve, northern Botswana in b) 2008, c) 2009, and d) 2010 using Benhamou's kernel (*h* = 1,250).

of the red band. That histogram is characterized by 2 distinct peaks, one corresponding to the inundated areas (low reflectance) and the second corresponding to dry land and dry floodplain vegetation (higher reflectance). Fire scars, which have a spectrally similar signature to that of wet areas, were identified based on change of reflectance at a pixel in the weeks following reclassification, as fire scars tend to overgrow with vegetation, producing a sudden spike in reflectance. It was not possible to reclassify the entire Okavango Delta using the same set of parameters, because some vegetation types (i.e., submerged aquatic plants) which are more prevalent in the eastern section altered the appropriate binning thresholds for reflectance values of "inundated" and "dry" areas. Composite maximum flood extent maps were generated using the combined coverage of all reclassified images from a given year (2008, 2009, or 2010). Yearly flood maps were saved as .TIF files and imported into ArcGIS 9.3.1 (ESRI 2009), where they were converted to polygon shape files for analysis. Consistent with data from other parts of the Okavango Delta, the total inundated area increased each year, from 1,223 km² in 2008 to 1,336 km² in 2009 to 1,441 km² in 2010. Most of the increase from 2008 to 2009 occurred along the Khwai River and its tributaries in the north, while the increase from 2009 to 2010 was predominately along the Gomoti and Santantadibe Rivers in the south. For periods in which flood maps were not available, hydrographs from the Maun Bridge hydrological station

were substituted. Hydrographs were calibrated to flood maps using periods when both data sets were available and flood levels were subsequently estimated by assuming equivalent, proportional change over time.

Data were separated into seasons according to the dates during which a pack was denning ("denning season"; where the alpha female is restricted to a den site with pups, and the pack returns to provision them) or not ("nondenning season"), as determined by examination of GPS data and direct field observations. As denning is seasonal (June–September) in the study subpopulation, "season" was strongly correlated with several fixed effects (e.g., temperature, rainfall, and litter size). Therefore, seasonal data sets were analyzed separately and data from the radiocollar fitted to the breeding female were not used from the denning season. Data on pack size and litter size were obtained from BPCT's long-term records, which have been gathered continuously since 1989. For periods in which litter data were unavailable (where packs were not sighted on the ground), an exponential decay function was employed using pup counts on either side of the period in question. Although pup mortality may occur stepwise, primarily as a result of predation by lions, *Panthera leo* (Creel et al. 2001), we were unable to determine exact dates of pup mortality between observation visits. Overall, an exponential decay function was therefore deemed more appropriate and likely to introduce the least bias.

Statistical analyses.—To examine variation in African wild dog home-range size and daily distance travelled across temporal scales, we used linear mixed-effects models in the R library "nlme" (Pinheiro and Bates 2000). We employed the "dredge" command in the library "MuMIn" to evaluate all possible combinations of fixed effects and interactions and select the most parsimonious models based on AICc (Akaike Information Criterion adjusted for small sample size) values (Hurvich and Tsai 1989). Only interaction terms considered to be biologically relevant a priori were included in modeling, to avoid overparameterization (Grueber et al. 2011). We generated candidate model sets based on AICc values, listing competing models in cases where ΔAICc < 2.

Home-range size and daily distance travelled were log-transformed and fitted as response variables in all models. Depending on season and the temporal scale under consideration (seasonal, monthly, or weekly), combinations of the following fixed effects were included in mixed-effects models: temperature, flood level, pack size, and litter size (Table 2). "Dog ID" was fitted as a random effect in linear mixed-effects models to account for repeated measures by individuals (Krackow and Tkadlec 2001). Consistent with similar studies (van Beest et al. 2011; Di Stefano et al. 2011), "year" explained little variance in preliminary analyses and was not included as a random effect. Colinearity between covariates was checked using Pearson's correlation (all γ values were < 0.6). Data were only included for periods in which GPS collar fix rates (percentage of locations successfully captured and stored) were greater than 75%. Weekly models were restricted to periods during which reliable flood level data were available. Post hoc Shapiro–Wilk and Bartlett tests indicated that assumptions of normality and homogeneity of variances were met for all models.

All research followed the American Society of Mammalogists' guidelines (Sikes et al. 2011) and was undertaken under permit from the Botswana Department of Wildlife and National Parks. No formal ethical review was conducted.

RESULTS

In total, 8,170 GPS locations were recorded ($\overline{X}$ = 1,167/collar). The mean fix rate (successful fixes/attempted fixes) was 92% (range: 83–96%) and fix rates above 90% were recorded for 5 of the 7 individuals, with 1 female's low fix rate (87%) occurring when she was below ground in a den. The average dilution of precision (DOP; a measure of the multiplicative effect of numerous satellites on positional precision) was 3.7 (range: 3.4–4.1). No points were excluded on the basis of poor DOP values, as we judged the potential bias of location estimate imprecision to be low relative to the size of African wild dog home ranges.

Home-range size.—A total of 383 home ranges (7 annual, 32 seasonal, 93 monthly, 251 weekly) were estimated using Benhamou's KDE (h = 1,250) method. Mean annual home-range size was 739 ± 81 km^2 (range: 367–999 km^2), with 6 of 7 African wild dogs using a home range of greater than 500 km^2 (Table 3). During the denning season, home ranges contracted to 160 ± 28 km^2 or about 27% the size of nondenning seasonal home ranges (582 ± 34 km^2). Even weekly home ranges were smaller during the denning season ($F_{1, 195} = 68.2$, $P < 0.001$). In terms of scale-dependent variation, home-range size increased significantly from weekly to monthly ($P < 0.001$) and monthly to seasonal ($P < 0.01$) scales (Fig. 2a). When including the denning season, there was also a significant increase in home-range size between seasonal and annual ($t_{8.84} = 2.60$, $P < 0.05$) scales.

Due to small sample size (n = 7 individuals), we did not develop models to predict annual home-range size. To ascertain the most important fixed effects determining home-range size at seasonal, monthly, and weekly scales, we employed linear

Table 2.—Description of covariates fitted as fixed effects in linear mixed-effects models explaining variation in African wild dog *Lycaon pictus* home-range size and daily distance travelled, in and around Moremi Game Reserve, northern Botswana.

Covariate	Description
Temperature	Mean temperature as recorded at Maun weather station.
Flood level	Proportion of study site under water as determined from reclassification of MODIS satellite images.
Pack size	For weekly and monthly models: the number of African wild dogs > 1 year of age; excluded at seasonal scale (correlated with litter size).
Litter size	For nondenning periods, all models: the number of African wild dogs < 1 year of age; excluded at seasonal scale (correlated with pack size).

Table 3.—Home-range sizes as estimated using Benhamou's fixed kernel density estimation (h = 1,250) and average daily distance travelled of 7 African wild dogs, *Lycaon pictus*, fitted with GPS collars in and around Moremi Game Reserve, northern Botswana (2007–2010).

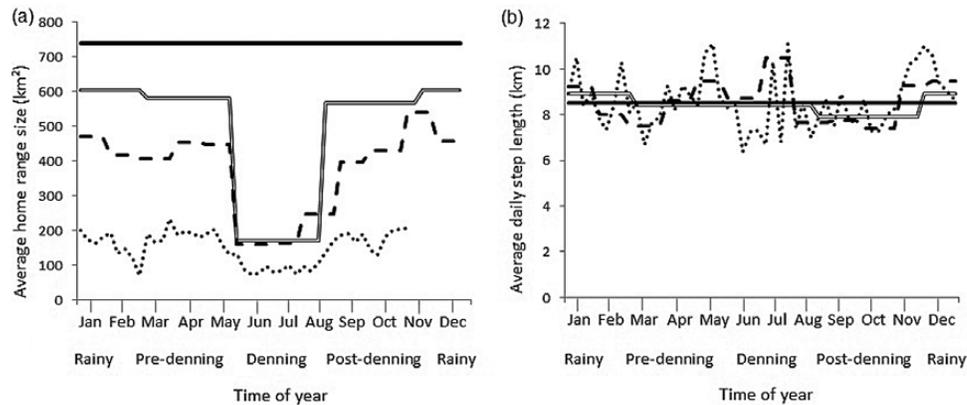| Pack	Individual	Primary year	Home-range size (km^2)	Step length (km)
Mankwe	Verreaux	2008	767	9.3
Matthew's	Beck	2008	894	7.9
Hawking	Hawking	2008	999	10.6
Xakanaxa	Sauza	2009	693	7.5
Chitabe	Jones	2009	367	6.6
Matthew's	Yolo	2010	580	8.0
Hawking	Pyles	2010	873	9.9
Population mean			739	8.5

Fig. 2.—African wild dog, *Lycaon pictus*, movement in and around Moremi Game Reserve, northern Botswana: a) 95% kernel density estimation home-range size and b) average daily distance travelled (distance between contiguous GPS locations over 24 h as observed at 4 temporal scales: solid line = annual; compound line = seasonal; dashed = monthly; and dotted = weekly).

mixed-effects models with "Dog ID" as a random term. For nondenning periods, fixed effects included temperature, flood level, pack size, and litter size.

Nondenning models revealed that litter size was the most important variable affecting home-range size, with large litters leading to the use of smaller home ranges at all temporal scales. Litter size was the lone fixed effect retained in monthly and seasonal home-range models (Table 4). Pack size was a poor predictor of home-range size and was not retained in the final weekly and monthly models. Pack size was excluded from seasonal models, as it was positively correlated with litter size (Pearson's ⅄ = 0.63) and was a much poorer predictor of home-range size. Higher daily temperatures did not affect home-range size at any scale and flood level was not an important predictor of home-range size in any mixed-effects model.

During the denning season, linear mixed-effects models were generated only at monthly and weekly scales (seasonal scale was excluded due to small sample size [$n = 5$]) and included flood level, temperature, and pack size as fixed effects. During the denning season, the most parsimonious models were basic, i.e., included only the random term, except for a weak negative effect of temperature on step length (Table 5).

Daily distance travelled.—Daily distance travelled was 8.5 ± 4.9 km ($\overline{X} \pm SD$; range: 0.1–42.0 km) for all individuals combined. If calculated per individual, daily distance travelled averaged 8.5 ± 0.5 km (range: 6.6–10.6 km). Single-day travel distances of greater than 40 km were observed twice, once from a dominant male and once from a nondominant male at different times of the year. Variation in daily distance travelled was most pronounced at the weekly scale (Fig. 2b), though between-month variation was also significant ($F_{11, 72} = 2.73$, $P < 0.01$). However, no strong seasonality was observed ($F_{3, 20} = 0.068$, $P = 0.346$). Daily distance travelled was largest and most variable in July (denning season; daily median: 10.2 km, $SD = 3.7$ km, range = 6.9–15.0 km, $n = 4$ collars) and smallest and least variable in March (end of rainy season; daily median: 8.0 km, $SD = 1.4$ km, range = 5.5–9.3 km, $n = 7$ collars; Fig. 2b).

Linear mixed-effects models at seasonal, monthly, and weekly scales (Table 4) showed that during nondenning periods,

Table 4.—Parameter and beta coefficient estimates from the top linear mixed-effects (nondenning seasonal, monthly, and weekly) models explaining African wild dog, *Lycaon pictus* home-range size and daily distance travelled in and around Moremi Game Reserve, northern Botswana. Variables retained in final models included litter size (PUPS), pack size (P_SIZE), temperature (TEMP), and flood level (FLOOD).

Scale	Parameter	β estimate	SE	P
		Home-range size		
Seasonal	Intercept	6.627	0.111	0.000
	PUPS	−0.054	0.017	0.005
Monthly	Intercept	6.301	0.111	0.000
	PUPS	−0.047	0.016	0.004
Weekly	Intercept	2.383	0.031	0.000
	PUPS	−0.008	−0.0038	0.0307
	P_SIZE	−0.023	0.0048	0.000
		Step length		
Seasonal	Intercept	8.554	0.203	0.000
	PUPS	−0.030	0.008	0.002
	FLOOD	−0.060	0.029	0.055
Monthly	Intercept	8.454	0.199	0.000
	PUPS	−0.047	0.009	0.000
	FLOOD	−0.043	0.028	0.123
Weekly	Intercept	8.733	0.187	0.000
	PUPS	−0.042	0.010	0.000
	TEMP	−0.024	0.007	0.000

Table 5.—Parameter and beta coefficient estimates from the top linear mixed-effects models in the denning season (monthly and weekly) explaining African wild dog, *Lycaon pictus* home-range size and daily distance travelled in and around Moremi Game Reserve, northern Botswana. Variables retained in final models included temperature (TEMP) only.

Scale	Parameter	β estimate	SE	P
		Home-range size		
Monthly	Intercept	2.165	0.082	0.000
Weekly	Intercept	1.916	0.031	0.000
		Step length		
Monthly	Intercept	6.931	1.862	0.0029
	TEMP	−0.228	0.098	0.039
Weekly	Intercept	2.697	0.302	0.000

litter size was the most influential variable determining daily distance travelled at all temporal scales, with large litters limiting packs' ranging distances. As in home-range models, litter size had a parameter weight of 1, appearing in all top models. Pack size, excluded at the seasonal scale (again due to its correlation with litter size), demonstrated no effect on daily distance travelled at monthly or weekly timescales.

Flood level was the most influential climatic variable at seasonal and monthly timescales and temperature was the most influential at the weekly timescale. Higher flood levels in the Okavango Delta corresponded to shorter ranging distances, with the effect being strongest at the seasonal scale ($F_{1, 16} = 4.68$, $P < 0.05$). Flood did not affect ranging distances at the weekly level. Higher weekly temperatures were correlated with significantly shorter weekly ranging distances ($F_{1, 123} = 12.53$, $P < 0.001$).

DISCUSSION

Annual home ranges reported in this study are among the largest on record for African wild dogs (Schaller 1972; Reich 1981; Fuller et al. 1992; Mills and Gorman 1997; Pole 2000; Creel and Creel 2002; Leigh 2005; Parker 2009; Woodroffe 2011). During the denning season, home ranges contracted to 27% of the area of nondenning home ranges, and none of the measure variables had an effect on their size. During nondenning periods, litter size was the most influential driver of ranging patterns, with large litters restricting pack movements at all temporal scales. Paradoxically, larger packs had smaller ranges when considered at the monthly timescale. Higher ambient daily temperatures resulted in reduced daily distance travelled at the weekly scale, while higher flood levels were linked to shorter ranging distances at monthly and seasonal scales.

The relatively large African wild dog home ranges described in this study could be the result of: 1) differences in ecological, climatic, or demographic drivers of movement between this and other populations or 2) methodological differences in data capture or home-range estimation from other studies. The former cannot be dismissed, as relatively little is yet known about the underlying drivers of African wild dog ranging patterns elsewhere. In contrast, methodological difference are likely because this study used more GPS locations (> 1,000) and, importantly, a longer sampling duration (~12 months) in annual home-range estimates than most previous studies. Consistent with the results from Börger et al. (2006), our results demonstrate that number of days sampled greatly and positively influenced home-range estimates.

Litter size was the most important variable explaining intra-annual African wild dog movement distances and was the only covariate included in all final linear mixed-effects models (Table 4). Packs with larger litters moved shorter daily distances and had smaller home ranges at all temporal scales. This suggests that they may have been more restricted by the presence of additional pups. Few studies have related litter size to ranging, but our data contrast markedly with data from bank voles (*Clethrionomys glareolus*) where home-range sizes correlated positively with initial litter sizes and, interestingly,

manipulations in litter size did not affect home-range size (Mappes et al. 1995). It is, thus, worth considering that while juvenile mortality itself may not be a critical factor influencing population persistence (Bach et al. 2010), it may indirectly affect adult survival by influencing pack movements, as increased movement has been linked to elevated mortality in carnivores (e.g., bobcat—Chamberlain et al. 1999). Large litters may, for example, decrease adult mortality resulting from ambush by other large carnivores, especially lions, through dilution, relative speeds, and detection (McNutt 1996b); meanwhile costs associated with large litters are few (McNutt 1996b) but may include increased energetic requirements to provision large litters.

Pack size was also a significant predictor of home-range size, but only at the weekly scale, with larger packs surprisingly utilizing smaller ranges. That pack size did not predict range size at longer timescales was consistent with data from packs in Selous, Tanzania, at either annual or multiyear timescales (Creel and Creel 2002), and contrasts with data from Kruger National Park, South Africa, which showed a nonsignificant positive relationship between pack size and home-range size measured over multiple years (Mills and Gorman 1997). There are a number of possible explanations for why pack size was inversely related to home-range size at short timescales. First, larger packs may be better able to defend areas of high prey abundance from smaller packs, particularly since pack size appears to affect interpack encounter outcomes in African wild dogs, with larger packs generally repelling smaller packs from encounter sites (e.g., Creel and Creel 1996). Small packs would therefore have to range more widely in search of food, or to avoid interpack aggression. Unfortunately, we have no measurement of home-range quality to evaluate this. As the wide ranging behavior of wild dogs is generally thought to relate to the avoidance of interspecific competition (Creel and Creel 2002) and the risk of predation by African lions in particular (Webster et al. 2012), smaller home ranges may expose residents to greater predation risk. However, this risk may be diluted in larger packs with more eyes on the ground. Additionally, due to juvenile recruitment in cooperative breeders (Creel et al. 2004) and the greater success of larger groups in gaining access to resources via territorial exclusion (Creel and Creel 2002), it may be that larger packs have been resident in their range for longer than smaller packs. Established packs may be better at utilizing their range more effectively, having accumulated knowledge of prey movements for example, and so are more likely to be in the right place at the right time than newly formed packs. Finally, it has been shown that larger packs may have higher hunting success (e.g., Creel and Creel 2002) and so larger packs may need to travel shorter distances in search of prey. This latter hypothesis would also predict that larger packs move shorter distances in search of prey, but we do not find this in our data set. Packs moved similar daily distances irrespective of pack size at all time frames. It is also worth emphasizing again that this weekly effect of pack size on home-range size does not translate to monthly differences at the monthly timescale, which suggests it may be relatively short lived. Though the 2 factors were not strongly correlated

in this study, an effect of pack size on daily ranging (measured at the weekly scale) could possibly be related to the fact that larger packs tend to produce and successfully raise larger litters (McNutt and Silk 2008), which may have a greater restricting effect on range utilization in the short term than pack size per se.

Higher ambient temperatures led to smaller weekly home ranges and shorter daily distances travelled (averaged at the weekly scale), but only during nondenning periods (i.e., excluding winter months, during which denning occurs in southern African wild dog populations). While the negative effect of increased temperatures on African wild dog movements has been reported elsewhere (Woodroffe 2011), results here demonstrate the timescale dependence and seasonal variability of climate as a driver of carnivore movements. Analysis of flood levels of the Okavango Delta also demonstrated a scale-dependent effect on pack movements: packs moved shorter distances during the Delta's annual peak flood season (July–August). This reduction in daily distance travelled may reflect an indirect response by African wild dogs to seasonal fluxes in productivity and water availability, which strongly influence prey distribution patterns (Loveridge et al. 2009). It is important to note too that flood levels peak during wild dog denning season and that ranges shrink to approximately one quarter of their estimated annual home-range area during this 3-month period (June–September). Measured daily distances within this period are also lower than at other times of year, which is slightly surprising given a pack's tendency to return to the den following each successful hunt (Frame et al. 1979). This may indicate that the larger distances travelled at other times of year are not wholly related to food acquisition and may, for example, be related to other activities such as patrolling and demarcating their territory. In the months immediately following denning, monthly home-range size returns to predenning levels, while actual daily movement distance appears slightly suppressed compared to the few months predenning. Our results of the effect of litter size on daily movements suggests that the presence of pups may limit pack movements, but the trend may also be driven by a spike in daily distance moved apparent at the weekly timescale which may be due to the pack covering greater distances in search of suitable den sites. In the few months post-denning wild dogs appear to utilize areas approximating the full extent of their annual home range, possibly exploiting prey further afield than their potentially depleted denning prey base and perhaps even reestablishing their annual territory boundaries.

Monthly home-range size had 2 peaks, 1 in April and May and a 2nd in November, and weekly home ranges also expanded during these periods. Intriguingly, these peaks correlate to the seasonal breeding cycle of wild dogs primary prey species, impala, which make up approximately 85% of their diet in this study population (Creel et al 2004). Paradoxically, wild dogs utilize greater areas at the monthly and weekly scale when impala were theoretically most vulnerable. In the Okavango Delta, impala breeding consists of a highly synchronized rut in April/May, with calves subsequently born in November. However, the proportion of observed wild dog kills (90% of 40) during these months combined was not significantly different from all other times of year (79.1% of 86; binomial test of proportions with continuity correction: $X^2_{(1)} = 1.5684$, $P = 0.2104$). This suggests that fluctuations in prey vulnerability are not the driving force behind range size variation, possibly because it may be too energetically costly for animals to adapt home ranges to short-term variations in resource availability (Carr and Macdonald 1986). It may be important to note here the difference between resource density (the amount of resources per unit area) and resource availability (how accessible those resources are), as higher resource density has consistently been shown to decrease home-range size (e.g., lynx—Herfindal et al. 2005) and movement distances (e.g., wolves—Jedrzejewski et al. 2001) in carnivores. Resource availability, on the other hand, is more difficult to quantify and research has shown that the hunting behavior of some predators is highly dependent on dynamic and interacting factors related to prey vulnerability (Quinn and Cresswell 2004). Examination of GPS data for these periods revealed a number of exploratory movements by African wild dog packs (i.e., outside of established home range) as well as border patrol activity (i.e., movement along the edge of territory). It may be that African wild dogs use the relative ease of hunting during these periods as an opportunity to reestablish territorial boundaries, though more data are required to validate this tentative hypothesis. Gaining a better understanding of the potential interaction between prey vulnerability and territoriality may therefore be a critical step in developing a better understanding of wild dog ranging behavior.

This study is the first to assess the effects of intrinsic and extrinsic factors on variation in home-range size and daily distance travelled in African wild dogs. Our results indicate that the effects of both extrinsic (e.g., temperature, flood level) and intrinsic (e.g., litter size) factors differed between temporal scales, supporting the suggestion that there is no single "best" or "most appropriate" scale at which to analyze carnivore movements. Considering the important role that wide-ranging movement plays in African wild dogs' risk of extinction (Woodroffe 2011), developing a more comprehensive approach to understanding their ranging behavior should be a key component of management strategies aimed at addressing their conservation.

Literature Cited

Ashenafi, Z. T., T. Coulson, C. Sillero-Zubiri, and N. Leader-Williams. 2005. Behaviour and ecology of the Ethiopian wolf (*Canis simensis*) in a human-dominated landscape outside protected areas. Animal Conservation 8:113–121.

BACH, L. A., R. B. F. PEDERSEN, M. W. HAYWARD, J. STAGEGAARD, V. LOESCHCKE, AND C. PERTOLDI. 2010. Assessing re-introductions of the African wild dog (*Lycaon pictus*) in the Limpopo Valley Conservancy, South Africa, using the stochastic simulation program VORTEX. Journal of Nature Conservation 18:237–246.

BENHAMOU, S. 2011. Dynamic approach to space and habitat use based on biased random bridges. PloS One 6:e14592.

BEYER, H. L. 2004. Hawth's analysis tools for ArcGIS. http://www.spatialecology.com/htools. Accessed 26 May 2011.

BONYONGO, C. M. 2005. Habitat utilization by impala (*Aepyceros melampus*) in the Okavango Delta. Botswana Notes and Records 37:227–235.

BÖRGER, L., B. D. DALZIEL, AND J. M. FRYXELL. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecology Letters 11:637–650.

BÖRGER, L., ET AL. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393–1405.

BOWEN, W. D. 1981. Variation in coyote social organization: the influence of prey size. Canadian Journal of Zoology 59:639–652.

BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

CARR, G. M., AND D. W. MACDONALD. 1986. The sociality of solitary foragers - a model based on resource dispersion. Animal Behaviour 34:1540–1549.

CHAMBERLAIN, M. J., B. D. LEOPOLD, L. W. BURGER, JR., B. W. PLOWMAN, AND L. M. CONNER. 1999. Survival and cause-specific mortality of adult bobcats in central Mississippi. Journal of Wildlife Management 63:613–620.

CREEL, S., AND N. M. CREEL. 1996. Limitation of African wild dogs by competition with larger carnivores. Conservation Biology 10:526–538.

CREEL, S., AND N. M. CREEL. 2002. The African wild dog: behavior, ecology and conservation. Princeton University Press, Princeton, New Jersey.

CREEL, S., J. W. MCNUTT, AND M. G. L. MILLS. 2004. Demography and population dynamics of African wild dogs in three critical populations. Pp. 337–350 in Biology and conservation of wild canids (D. W. Macdonald and C. Sillero-Zubiri, eds.). Oxford University Press, Oxford, United Kingdom.

CREEL, S., G. SPONG, AND N. M.CREEL. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pp. 35–60 in Carnivore conservation (J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, eds.). Cambridge University Press, Cambridge, United Kingdom.

CROES, B., G. RASMUSSEN, R. BUIJ, AND H. DE LONGH. 2012. Status of the African wild dog in the Bénoué Complex, North Cameroon. Canid News. http://www.canids.org/canidnews/15/African_wild_dogs_in_Cameroon.pdf. Accessed 25 June 2013.

CUSHMAN, S. A., M. CHASE, AND C. GRIFFIN. 2005. Elephants in space and time. Oikos 109:331–341.

DI STEFANO, J., G. COULSON, A. GREENFIELD, AND M. SWAN. 2011. Resource heterogeneity influences home range area in the swamp wallaby (*Wallabia bicolor*). Ecography 34:469–479.

ESRI. 2009. ArcGIS 9.3.1. Environmental Systems Research Institute, Redlands, California.

FANSHAWE, J. H., L. H. FRAME, AND J. R. GINSBERG. 1991. The wild dog - Africa's vanishing carnivore. Oryx 25:137–146.

FRAME, L. H., J. R. MALCOLM, G. W. FRAME, AND H. VAN LAWICK. 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti plains, Tanzania 1967–1978. Journal of Comparative Ethology 50:225–249.

FULLER, T. K., ET AL. 1992. Population dynamics of African wild dogs. Pp. 1125–1139 in Wildlife 2001: populations (D. R. McCullough and H. Barrett, eds.). Elsevier Science Publishers, London, United Kingdom.

GODSALL, B., T. COULSON, AND A. F. MALO. 2014. From physiology to space-use: energy reserves and androgenisation explain home-range size variation in a woodland rodent. Journal of Animal Ecology 83:126–135.

GRUEBER, C. E., S. NAKAGAWA, R. J. LAWS, AND I. G. JAMIESON. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

HANSTEEN, T. L., H. P. ANDREASSEN, AND R. A. IMS. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. Journal of Wildlife Management 61:280–290.

HERFINDAL, I., J. D. LINNELL, J. ODDEN, E. B. NILSEN, AND R. ANDERSEN. 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). Journal of Zoology (London) 265:63–71.

HURVICH, C. M., AND C. L. TSAI. 1989. Regression and time-series model selection in small samples. Biometrika 76:297–307.

IMS, R. A. 1987. Responses in spatial organization and behaviour to manipulation of the food resource in the vole *Clethrionomys rufocanus*. Journal of Animal Ecology 56:585–596.

IUCN. 2012. The IUCN Red List of threatened species. Version 2012.2. http://www.iucnredlist.org. Accessed 17 October 2012.

JEDRZEJEWSKI, W., K. SCHMIDT, J. THEUERKAUF, B. JEDRZEJEWSKA, AND H. OKARMA. 2001. Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. Canadian Journal of Zoology 79:1993–2004.

KAMLER, J. F., B. JĘDRZEJEWSKA, AND W. JEDRZEJEWSKI. 2007. Factors affecting daily ranges of red deer (*Cervus elaphus*) in Białowieża Primeval Forest, Poland. Acta Theriologica 52:113–118.

KARASOV, W. H. 1992. Daily energy expenditure and the cost of activity in mammals. American Zoologist 32:238–248.

KJELLANDER, P., ET AL. 2004. Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies. Oecologia 139:478–485.

KRACKOW, S., AND E. TKADLEC. 2001. Analysis of brood sex ratios: implications of offspring clustering. Behavioural Ecology and Sociobiology 50:293–301.

LEIGH, K. A. 2005. The ecology and conservation biology of the endangered African wild dog (*Lycaon pictus*) in the Lower Zambezi, Zambia. Ph.D. dissertation, University of Sydney, Sydney, Australia.

LIMA SABATO, M. A., L. F. BANDEIRA DE MELO, E. M. VAZ MAGNI, R. J. YOUNG, AND C. M. COELHO. 2006. A note on the effect of the full moon on the activity of wild maned wolves (*Chrysocyon brachyurus*). Behavioural Processes 73:228–230.

LITVAITIS, J. A., J. A. SHERBURNE, AND J. A. BISSONETTE. 1986. Bobcat habitat use and home range size in relation to prey density. Journal of Wildlife Management 50:110–117.

LOVERIDGE, A. J., ET AL. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. Ecography 32:953–962.

MAPPES, T., E. KOSKELA, AND H. YLÖNEN. 1995. Reproductive costs and litter size in the bank vole. Proceedings of the Royal Society of London, B. Biological Sciences 261:19–24.

MARKER, L. L., AND A. J. DICKMAN. 2005. Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. South African Journal of Wildlife Research 35:105–111.

Massei, G., P. V. Genov, P. W. Staines, and M. L. Gorman. 1997. Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. Journal of Zoology 242:411–423.

McLoughlin, P. D., S. H. Ferguson, and F. O. Messier. 2000. Intraspecifc variation in home range overlap with habitat quality: a comparison among brown bear populations. Evolutionary Ecology 14:39–60.

McNutt, J. W. 1996a. Sex-biased dispersal in African wild dogs (*Lycaon pictus*). Animal Behaviour 52:1067–1077.

McNutt, J. W. 1996b. Adoption in African wild dogs (*Lycaon pictus*). Journal of Zoology (London) 240:163–173.

McNutt, J. W., and J. B. Silk. 2008. Pup production, sex ratios, and survivorship in African wild dogs, *Lycaon pictus*. Behavioural Ecology and Sociobiology 62:1061–1067.

Mills, M. G. L., and M. L. Gorman. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation Biology 11:1397–1406.

Nagy, J. A. S., and M. A. Haroldson. 1990. Comparisons of some home range and population parameters among four grizzly bear populations in Canada. Bears—Their Biology and Management 8:227–235.

Naidoo, R., et al. 2012. Factors affecting intraspecific variation in home range size of a large African herbivore. Landscape Ecology 27:1523–1534.

Norrdahl, K., and E. Korpimäki. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? Ecology 79:226–232.

Osofsky, S. A., J. W. McNutt, and K. J. Hirsch. 1996. Immobilization of free-ranging African wild dogs (*Lycaon pictus*) using a ketamine/xylazine/atropine combination. Journal of Zoo and Wildlife Medicine 27:528–532.

Palomares, F. 1994. Site fidelity and effects of body-mass on home range size of Egyptian mongooses. Canadian Journal of Zoology 72:465–469.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474–488.

Parker, M. N. 2009. Territoriality and scent marking behavior of African wild dogs in northern Botswana. Ph.D. disssertation, University of Montana, Missoula.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed effects models in S and S-PLUS. Springer-Verlag, New York.

Pole, A. 2000. The behaviour and ecology of African wild dogs (*Lycaon pictus*) in an environment with reduced competitor density. Ph.D. dissertation, University of Aberdeen, Aberdeen, United Kingdom.

Pomilia, M. A. 2012. Intraspecific variation in African wild dog (*Lycaon pictus*) ranging patterns in northern Botswana. M.Sc. thesis, University of Leeds, Leeds, United Kingdom.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65–110 in Research techniques in animal ecology; controversies and consequences (L. Boitani and T. K. Fuller, eds.). Columbia University Press, New York.

Quinn, J. L., and W. Cresswell. 2004. Predator hunting behaviour and prey vulnerability. Journal of Animal Ecology 73:143–154.

Reich, A. 1981. The behaviour and ecology of the African wild dog (*Lycaon pictus*) in the Kruger National Park. Ph.D. dissertation, Yale University, New Haven, Connecticut.

Rivrud, I. M., L. E. Loe, and A. Mysterud. 2010. How does local weather predict red deer home range size at different temporal scales? Journal of Animal Ecology 79:1280–1295.

Schaller, G. B. 1972. The Serengeti lion: a study of predator-prey relations. University of Chicago Press, Chicago, Illinois.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Simchareon, A. 2014. Female tiger *Panthera tigris* home range size and prey abundance: important metrics for management. Oryx 48:370–377.

Tufto, J., R. Andersen, and J. Linnell. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65:715–724.

Tutiempo Network, S.L. 2011. Maun historical records. http://www.tutiempo.net/maun.html?datos=calendario. Accessed 26 May 2011.

van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? Journal of Animal Ecology 80:771–785

Wang, M., and V. Grimm. 2007. Home range dynamics and population regulation: an individual-based model of the common shrew (*Sorex araneus*). Ecological Modeling 205:397–409.

Webster, H., J. W. McNutt, and K. McComb. 2012. African wild dogs as a fugitive species: playback experiments investigate how wild dogs respond to their major competitors. Ethology 118:147–156.

Woodroffe, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinction. Pp. 61–92 in Carnivore conservation (J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, eds.). Cambridge University Press, Cambridge, United Kingdom.

Woodroffe, R. 2011. Ranging behaviour of African wild dog packs in a human dominated landscape. Journal of Zoology (London) 283:88–97.

Woodroffe, R., J. R. Ginsberg, and D. W. Macdonald. 1997. The African wild dog: status survey and conservation action plan. International Union for the Conservation of Nature, Gland, Switzerland.