

Hot dogs: High ambient temperatures impact reproductive success in a tropical carnivore

Rosie Woodroffe¹  | Rosemary Groom^{1,2,3} | J. Weldon McNutt⁴

¹Institute of Zoology, Zoological Society of London, London, UK

²Department of Zoology, University of Johannesburg, Auckland Park, South Africa

³African Wildlife Conservation Fund, Chishakwe Ranch, Zimbabwe

⁴Botswana Predator Conservation Trust, Maun, Botswana

Correspondence

Rosie Woodroffe

Email: rosie.woodroffe@ioz.ac.uk

Handling Editor: Ken Wilson

Abstract

1. Climate change imposes an urgent need to recognise and conserve the species likely to be worst affected. However, while ecologists have mostly explored indirect effects of rising ambient temperatures on temperate and polar species, physiologists have predicted direct impacts on tropical species.
2. The African wild dog (*Lycaon pictus*), a tropical species, exhibits few of the traits typically used to predict climate change vulnerability. Nevertheless, we predicted that wild dog populations might be sensitive to weather conditions, because the species shows strongly seasonal reproduction across most of its geographical range.
3. We explored associations between weather conditions, reproductive costs, and reproductive success, drawing on long-term wild dog monitoring data from sites in Botswana (20°S, 24 years), Kenya (0°N, 12 years), and Zimbabwe (20°S, 6 years).
4. High ambient temperatures were associated with reduced foraging time, especially during the energetically costly pup-rearing period. Across all three sites, packs which reared pups at high ambient temperatures produced fewer recruits than did those rearing pups in cooler weather; at the non-seasonal Kenya site such packs also had longer inter-birth intervals. Over time, rising ambient temperatures at the (longest-monitored) Botswana site coincided with falling wild dog recruitment.
5. Our findings suggest a direct impact of high ambient temperatures on African wild dog demography, indicating that this species, which is already globally endangered, may be highly vulnerable to climate change. This vulnerability would have been missed by simplistic trait-based assessments, highlighting the limitations of such assessments. Seasonal reproduction, which is less common at low latitudes than at higher latitudes, might be a useful indicator of climate change vulnerability among tropical species.

KEYWORDS

African wild dog, climate change, conservation, global warming, inter-birth interval, *Lycaon*, population dynamics, reproductive success, tropics, wildlife

1 | INTRODUCTION

Weather conditions can profoundly affect organisms' reproductive success, through both direct abiotic effects such as heatwaves and

rainstorms (e.g. Fisher et al., 2015; Hansen, 2009), and indirect effects via biotic factors such as food availability (Ockendon et al., 2014) or abiotic factors such as the availability of sea ice habitat (Lunn et al., 2016). In many species, these impacts have imposed natural selection for

reproduction confined to seasons with favourable weather (Bronson, 1985; Visser, Caro, van Oers, Schaper, & Helm, 2010). Today, these same weather impacts help to influence how species are affected by climate change (Cahill et al., 2012; Ockendon et al., 2014).

The need to direct conservation effort towards the species most vulnerable to climate change places a new urgency on understanding how weather influences reproductive success (Ockendon et al., 2014; Pacifici et al., 2015). Such demographic effects are relatively well characterised at temperate latitudes, but less well understood in the tropics (Ockendon et al., 2014; Pacifici et al., 2015). Climate change impacts may vary across latitudes, through variation in both climate patterns (e.g. tropical environments may be less seasonal) and physiological responses (e.g. the high ambient temperatures prevalent in the tropics may constrain dissipation of body heat, Speakman & Krol, 2010). Understanding climate change impacts in the tropics, where most species occur, is therefore a conservation priority.

Assessments of climate change vulnerability often use limited data to identify species lacking traits assumed to confer an ability to persist under changing environmental conditions (Foden et al., 2013; Pacifici et al., 2015). Such trait-based assessments typically characterise the most vulnerable species as having restricted geographical ranges, specialised resource requirements, narrow physiological tolerance, slow reproductive rates, and poor dispersal abilities (Foden et al., 2013; Pacifici et al., 2015).

By these criteria, available data suggest that the African wild dog (*Lycaon pictus*), a largely tropical species, shows few of the traits typically linked to climate change vulnerability. Although the species is globally endangered through habitat loss and anthropogenic killing (Woodroffe & Sillero-Zubiri, 2013), it nevertheless inhabits over a million km² between 13°N and 25°S, occupying diverse habitats and hunting multiple prey species (Creel & Creel, 1995; Woodroffe, Lindsey, Romañach, & Ole Ranah, 2007; Woodroffe & Sillero-Zubiri, 2013). Available physiological data, while limited, suggest that wild dogs may be adapted to hunt at high ambient temperatures (Taylor, Schmidt-Nielsen, Dmi'el, & Fedak, 1971). Excellent dispersal abilities (Davies-Mostert et al., 2012; Masenga et al., 2016) and high reproductive rates (McNutt & Silk, 2008) can allow wild dogs to successfully (re)colonise suitable habitat where available (Woodroffe, 2011a). Trait-based assessments would therefore be expected to classify African wild dogs as relatively invulnerable to climate change.

However, wild dogs exhibit one trait which suggests a potentially important impact of climate. Unusually among African mammals (Skinner, Moss, & Skinner, 2002), wild dogs exhibit seasonal reproduction across much of their geographical range (McNutt, Groom, & Woodroffe, in review). Wild dogs typically raise pups during the cool dry season which, throughout southern Africa, coincides with the austral winter. If this phenology indicates that low ambient temperatures are optimal for reproduction, then climate change may harm wild dog populations, because the region's winters are projected to become hotter (IPCC, 2013). Alternatively, if low rainfall provides optimal conditions for wild dog reproduction (Buettner, Davies-Mostert, du Toit, & Mills, 2007), then climate change may prove beneficial, because winters are also projected to become drier (IPCC, 2013). Understanding the associations

between wild dog reproduction and weather patterns may therefore help to project climate change impacts on this endangered species.

African wild dogs face high reproductive costs, investing more in gestation and post-natal care than do most other social carnivores (Creel & Creel, 1991). Typically only one "alpha" female produces pups in each pack, but all pack members contribute to pup care and hence incur reproductive costs (Malcolm & Marten, 1982). During the 3-month period when pups are confined to a den, one or more adult "babysitters" usually stay with the pups while other pack members hunt (Malcolm & Marten, 1982). Pack members which have fed from a kill subsequently return to the den and regurgitate food to the pups and babysitter(s) (Malcolm & Marten, 1982). Hence, food intake for both adults and pups is constrained not only by prey availability and size, but also by the number of hunts per day, and the combined capacity of the hunters' stomachs. Larger packs' greater ability to meet these costs (Hubel et al., 2016) may help to explain their consistently higher reproductive success (Creel, Mills, & McNutt, 2004; Malcolm & Marten, 1982; McNutt & Silk, 2008; Woodroffe, 2011a).

Both ambient temperature and rainfall could potentially influence wild dog reproduction. Wild dogs are cursorial hunters, engaging in frequent high-speed chases (Gorman, Mills, Raath, & Speakman, 1998; Hubel et al., 2016). Dissipating the heat generated by such activity is physiologically challenging (Speakman & Krol, 2010; Taylor et al., 1971), probably explaining wild dogs' tendency to hunt at dawn and dusk, when ambient temperatures are lower (Woodroffe, 2011b). High ambient temperatures may thus restrict the number of hours each day when wild dogs can hunt, potentially constraining food intake (Hubel et al., 2016). By contrast, high rainfall increases the abundance of wild dogs' ungulate prey (Ogutu, Piepho, Dublin, Bhola, & Reid, 2008; Owen-Smith & Mills, 2006). However, rainfall may also reduce prey catchability by improving prey body condition (Bourgarel, Fritz, Gaillard, De Garine-Wichatitsky, & Maudet, 2002; Davies-Mostert, Mills, & Macdonald, 2013) and by encouraging grass growth which can impede cursorial hunting (Mills, 1995). Hence, while high ambient temperatures are predicted to harm wild dog populations, the effects of high rainfall are harder to predict.

To better understand the likely impact of climate change on this species, we explored associations between weather conditions, reproductive costs, and reproductive success, across three African wild dog populations.

2 | MATERIALS AND METHODS

2.1 | Data collection

Most remaining wild dog populations reside in southern Africa (Woodroffe & Sillero-Zubiri, 2013), where both wild dog reproduction and weather conditions are seasonal (McNutt et al., in review). This seasonality could generate correlations between reproduction and weather, even if there were no causal link between the two. Therefore, to avoid interpreting possibly spurious correlations, we used data from an East African study site without seasonal reproduction (in Kenya, 37°2'E, 0°6'N) to help interpret evidence from two

consistently seasonal southern African sites (in Botswana (23°38'E, 19°30'S) and Zimbabwe (32°00'E, 20°05'S)). Details of the study areas are given in Supporting Information. Data on rainfall and temperature (measured with dry bulb thermometers) were taken from meteorological stations within the study areas (Kenya) or nearby (Botswana 30 km away, Zimbabwe 12 km away; see Supporting Information). Note that we did not seek to explain variation between sites; rather, we explored whether associations between wild dog reproduction and climatic variables were consistent across sites.

We monitored the reproductive status of individual wild dogs (recognisable from their unique pelage patterns, Maddock & Mills, 1994) during the years 2001–2012 in Kenya, 1989–2012 in Botswana, and 2008–2013 in Zimbabwe. The numbers of study packs each year varied from 2–10 in Kenya, 1–11 in Botswana, and 5–10 in Zimbabwe. At all three sites, at least one member of each study pack was fitted with a radiocollar, allowing us to locate packs to record their composition, and to identify periods when they were raising young pups in a den (termed “denning”).

In our Kenya study area, we also fitted GPS-collars (GPS-Plus, Vectronic Aerospace GmbH, Berlin, Germany) to 10 wild dogs in five packs in 2011–2015, monitoring each through denning and non-denning periods (Table S1). Collars were programmed to record locations at 01.00 hr, 06.30 hr, 07.00 hr, 07.30 hr, 08.00 hr, 13.00 hr, 18.00 hr, 18.30 hr, and 19.30 hr, to reflect a crepuscular activity pattern. As well as revealing movement behaviour, these locations facilitated precise estimates of the timing of denning and den shifts. In addition, every 5 min an inbuilt sensor recorded ambient temperature, and an accelerometer recorded activity (in two planes, maximum 255 in each plane). We summed activity records for the two planes, so the maximum raw activity score was 510. This frequency of data recording was too coarse-grained to allow us to measure hunting success (c.f. Hubel et al., 2016).

2.2 | Quantifying costs of reproduction

We assessed three short-term costs of reproduction by comparing, between denning and non-denning periods, (i) the wild dog biomass being supported by the hunting efforts of each individual; (ii) individuals' activity levels; and (iii) daily distance travelled. A fourth, longer-term, cost was the time elapsed from the birth of one litter to the birth of the next (the inter-birth interval). We assessed these costs only for our Kenya study area, since seasonal reproduction at our Botswana and Zimbabwe sites meant that the first three were potentially confounded by seasonal variation in environmental conditions (which might influence wild dog behaviour independent of denning), and there was little variation in the fourth.

To characterise the first cost we estimated total combined biomass, on a daily basis, for entire packs, and for those pack members who participated in hunting forays and thus had the opportunity to feed directly from kills. The ratio between these two biomass estimates was invariably 1 outside the denning period, when entire packs attended kills, but was higher when pups and a babysitter were confined to a den and reliant on food regurgitated by other pack members.

Biomass estimates were based upon demographical data from eight packs with frequent pack size estimates, contributing an average of 4.0 monitoring-years per pack. Details of biomass calculations are provided in Supporting Information.

To quantify the second cost, we used GPS-collars' integral accelerometers to calculate estimates of activity for 5-min and 24-hr periods. Wild dogs' activity pattern is strongly crepuscular (Figure 1); to estimate activity every 5 min independent of this pattern, we first calculated “expected” values as the smoothed average activity across all individuals and across five consecutive time points (e.g. the smoothed average for 07.30 hr covered 07.20–07.40 hr). We then calculated 5-min relative activity as the difference between each activity record (measured on a scale of 0–510), and the expected value for that time point. To calculate 24-hr activity, we summed raw activity records for all time intervals between sunrise on one day and sunrise the next (taking sunrise times from http://aa.usno.navy.mil/data/docs/RS_OneYear.php). We compared 5-min relative activity with temperature recorded simultaneously by the collars. We compared 24-hr activity with period (denning or not), daily maximum temperature at a nearby weather station (which was correlated with the number of daylight hours with low ambient temperatures, see Supporting Information), and daily rainfall. Within the denning period, we also compared 24-hr activity with litter size and pup age (two indices of litter energy requirements), time since occupying a particular den location (a possible index of prey depletion near the den), and adult pack size (an index of the number of animals potentially contributing to pup care).

To characterise the third cost, we used GPS-collar data to estimate daily distances travelled, and 10-day home range size. We calculated

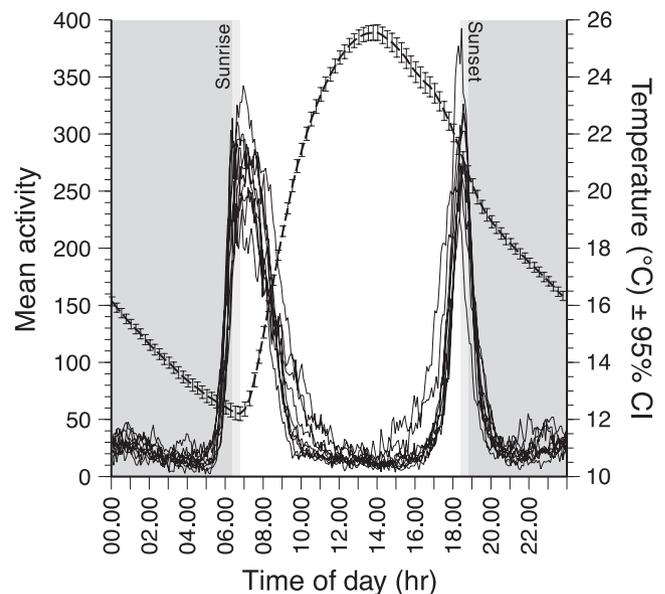


FIGURE 1 Daily activity patterns of African wild dogs in our Kenya study area. Solid lines show mean activity for each 5-min time interval, for 10 GPS-collared wild dogs tracked in 2011–2015; the dashed line shows mean temperature measured every 15 min at a weather station in the study area over 329 days in 2012. Activity can vary between 0 and 510. Shading denotes night-time; lighter shading indicates the annual range in sunrise and sunset times

daily distance travelled as the sum of the distances moved between successive GPS-locations during a 24-hr period, excluding days when not all GPS-locations were recorded. Sunrise times varied in the range 06.12–06.43 hr, and daily distance travelled was calculated from 06.30 hr on one day to 06.30 hr on the next. We estimated home range size by constructing minimum convex polygons (MCPs) enclosing all GPS-locations, for successive 10-day periods before and after pups' birth. The MCP approach was chosen because it is a simple, repeatable method, which gives reasonable estimates of the extent of animal movement from small numbers of locations (Downs & Horner, 2008) to facilitate comparison across time periods using a consistent method. We compared daily distance travelled with the same suite of independent variables used to explore 24-hr activity, and we compared home range size between denning and non-denning periods.

We estimated the fourth cost by using demographical data to calculate the lengths of 45 pack inter-birth intervals, excluding two litters born to beta females a few days after the alpha females' litters. Seven incomplete intervals (e.g. due to radiocollar failure) were censored, but included to avoid risking bias towards shorter complete intervals. We compared inter-birth intervals with mean daily maximum ambient temperature, and total daily rainfall, during the denning period, with litter size and adult pack size (both measured when pups were 3 months old), and with calendar year (to explore temporal trends).

2.3 | Quantifying reproductive success

In all three study areas, we measured packs' reproductive success as litter size (at 3 months), number of yearlings (at 12 months), and pup survival from 3 to 12 months. Because wild dog pups have not been recorded to disperse (McNutt, 1996), we assumed that pups had died if they were consistently not observed with their natal pack. We explored the demographic importance of these measures of reproductive success by comparing mean annual litter size and mean annual pup survival with estimated population density in the subsequent year (number of yearlings was not included as it was the product of litter size and pup survival).

We tested the hypothesis that weather conditions affected wild dog reproductive success by comparing, within each site, each of these measures with mean daily maximum ambient temperature, and total rainfall, during the 3 months following the pups' birth (approximating the denning period). We also included covariates describing adult pack size (measured when pups were 3 months old), mother's age, and litter type (alpha female as sole mother, alpha mother breeding in the same year as a beta female, beta mother). We investigated both linear and quadratic terms for pack size, since quadratic pack size effects have been reported elsewhere (Rasmussen, Gusset, Courchamp, & Macdonald, 2008). We included year as a linear covariate, because this was correlated with a number of ecological factors (e.g. prey density) which were not themselves measured consistently within or between sites (see Supporting Information). We also compared numbers of yearlings, and pup survival, with rainfall post-denning; for our Botswana and Zimbabwe sites we calculated total rainfall during the November–March wet season in the first year of life, and for our Kenya

site we calculated total rainfall over a 9-month period commencing the date pups were 3 months old. These analyses were restricted to breeding attempts with complete weather data, and concerned 254 pups in 35 litters from 16 packs in Kenya, 1,005 pups in 109 litters from 43 packs in Botswana, and 179 pups in 29 litters from 14 packs in Zimbabwe.

2.4 | Statistical analyses

We conducted all statistical analyses in R (R Core Team, 2013). We used random effects to account for repeated measures from the same individual or pack; all such analyses included ≥ 10 groups, and exploratory analyses of models involving 10 groups indicated that using random rather than fixed effects did not qualitatively affect the analysis outcomes. Most analyses used mixed effects models fitted using the package *NLME* (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2015). We used Poisson regression to analyse count data (e.g. litter size), and logistic regression to analyse binary outcome data (e.g. pup survival). Continuous and count independent variables were ln-transformed prior to inclusion in Poisson regressions. We analysed inter-birth intervals using Cox proportional hazards models with mixed effects, fitted using the package *COXME* (Therneau, 2014). We used linear regression models to explore inter-annual trends in ambient temperature, and associations between estimates of reproductive success and population density. We also used linear models to explore correlations between ambient temperature and rainfall. For each analysis, we dropped successive variables (and interactions between variables) from the full model until only statistically significant effects remained.

3 | RESULTS

3.1 | Costs of reproduction

Evidence from our Kenya study area suggested that reproduction was energetically costly for wild dogs. Outside the denning period, each animal met its own energy requirements by feeding directly from kills made by the pack; however, during the denning period pack members which fed from kills shared their stomach contents with the pups and babysitters, thus contributing to the energy requirements of 21.7% more wild dog biomass, on average (95% confidence interval [CI] 21.2%–22.1%), than at other times (Figure 2a). Coincident with this increased energy demand, during the denning period GPS-collared wild dogs' 24-hr activity levels (mean 20,521, CI 20,065–20,978) were significantly higher than those in the non-denning period (mean 17,700, CI 17,474–17,925; Figure 2b; Table 1). Despite these increased energy demands, returning repeatedly to the den led to 10-day home ranges during the denning period (mean area 37.1 km², CI 32.7–41.5 km²) that were significantly smaller than those in the non-denning period (mean area 144.2 km², CI 128.2–160.3 km²; linear mixed model of 10-day home range size including wild dog identity as a random effect, effect of period (denning): -1.03 , *SE* 0.094, $p < .001$, Figure 2c). Despite occupying smaller home ranges, packs did not travel shorter daily distances while denning (mean 10.6 km,

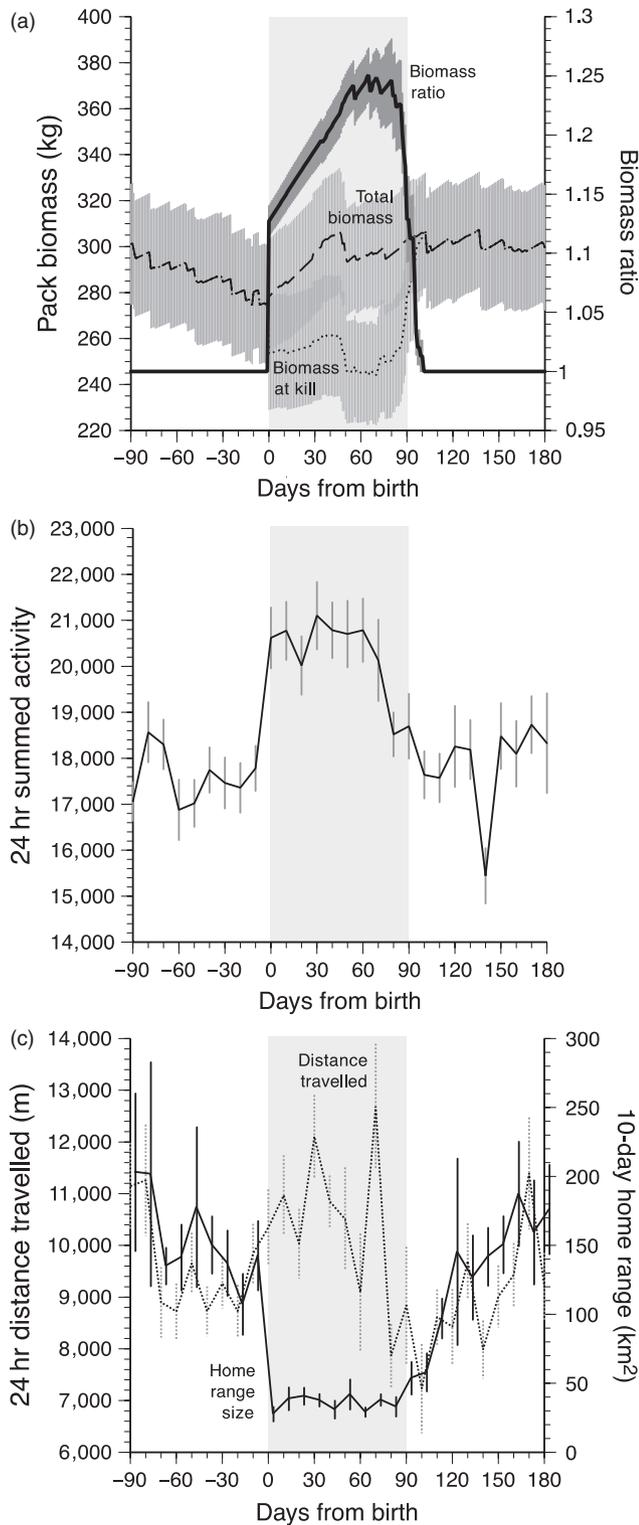


FIGURE 2 Short-term costs of reproduction for African wild dog packs in our Kenya study area. Shading shows the pups' first 90 days of life, approximating to the denning period. (a) Shows the total biomass of wild dogs to be fed in each pack (dashed line), the total biomass of pack members able to feed directly from kills (dotted line), and the ratio between the two (solid line). Values are $M \pm SE$ across 33 breeding attempts, involving eight packs. (b) Shows the total daily activity (from one sunrise to the next) for 10 GPS-collared wild dogs (10-day $M \pm SE$). (c) Shows the $M \pm SE$ home range area (solid line) and daily distance travelled (dashed line) for the same 10 animals

TABLE 1 Predictors of total 24-hr activity for 10 GPS-collared African wild dogs in our Kenya study area. These linear mixed models also included wild dog identity as a random effect

Variable	Estimated effect	SE	p
Denning and non-denning periods			
Period (non-denning)	-10,573.9	3,973.2	.008
Daily maximum temperature (°C)	-359.3	137.7	.009
Daily rainfall (mm)	43.9	18.3	.016
Period × maximum temperature	293.2	148.4	.048
Denning period only			
Days since occupying new den location	34.29	11.59	.003
Daily maximum temperature (°C)	-284.5	130.8	.030

CI 10.0–11.1) than during non-denning periods (mean 10.1 km, CI 9.8–10.4 km; linear mixed model of daily distance travelled including wild dog identity as a random effect, effect of period (denning): 0.30, SE 0.33, $p = .36$; Figure 2c).

The daily costs of reproduction increased as packs spent more time at a particular den location. In our Kenya study area, packs occupied their first den location for 46.4 days on average (CI 29.3–63.4 days) before moving to new locations successively over a denning period lasting 89 days on average (CI 83–95 days; Figures S1 and S2). The longer a pack had occupied a particular den location, the further its members travelled each day (linear mixed model of daily distance travelled (in metres), including individual identity as a random effect; effect of days since occupying den location: 55.67, SE 18.30, $p = .003$), and the higher their 24-hr activity (Table 1). By contrast, there were no significant effects of pup age on either daily distance travelled ($p = .16$) or 24-hr activity ($p = .18$).

These short-term costs of reproduction appeared to impact longer-term fecundity. Reproduction in our Kenya study population was aseasonal (McNutt et al., in review), with a mean inter-birth interval of 331 days (CI 238–424 days). Larger litters were followed by longer inter-birth intervals than were smaller litters (Cox proportional hazards model of inter-birth interval, including pack identity as a random effect, effect of litter size: exp (coefficient) 0.614, $p < .001$; Table S2).

3.2 | Associations between reproductive costs and weather

In our Kenya study area, wild dog activity was strongly crepuscular; low activity from mid-morning to late afternoon coincided with high ambient temperatures (Figure 1). After accounting for this crepuscular pattern (by measuring activity relative to the smoothed mean for each time point), during daylight hours wild dog activity was lower during 5-min periods with higher ambient temperatures (linear mixed model of 5-min relative activity, including individual identity as a random effect, effect of ambient temperature (in °C) measured by the

collar: -3.17 , SE 0.047, $p < .001$). Hence, as documented previously (Woodroffe, 2011b), wild dogs were active for less time on days with high maximum temperature, ceasing activity earlier in the morning, and starting activity later in the evening, than on days with low maximum temperature.

Total activity over each 24-hr period was lower on hot, dry days (Table 1). Daily maximum temperature was lower on days with rain (Table S3; Figure S3). The association between wild dog activity and ambient temperature was modified during the denning period: a significant period \times temperature interaction indicated that denning wild dogs showed greater activity disproportionately on cooler days (Table 1). However, there was no indication that packs shifted den more frequently in response to weather conditions (Poisson regression model of number of den shifts per denning period, effect of $\ln(\text{mean daily maximum temperature})$ 2.55, SE 7.00, $p = .72$; effect of $\ln(\text{total rainfall})$ -0.382 , SE 0.670, $p = .57$).

High ambient temperatures were also associated with longer-term impacts on fecundity. In our aseasonally breeding Kenya study population, litters raised during denning periods with higher ambient temperatures were followed by longer inter-birth intervals (Cox proportional hazards model including pack identity as a random effect and litter size as a fixed effect, effect of mean daily maximum ambient temperature during previous denning period: $\exp(\text{coefficient})$ 0.263, $p < .001$; Table S2), such that each 1°C rise in mean daily maximum temperature was associated with a 25-day increase in inter-birth interval. There was no significant effect of rainfall during denning on inter-birth interval ($p = .74$), though rainfall and temperature were negatively correlated (Table S4).

3.3 | Reproductive success

Both annual mean litter size at 3 months, and annual mean pup survival from 3 to 12 months, were significantly associated with estimated population density in the subsequent year, such that years with high reproductive success were followed by years of high population density (Table S5; Figure S4).

High ambient temperatures during the 3-month denning period were associated with fewer surviving yearlings in all three study areas

(Table 2). In Kenya and Botswana, pup survival from 3 to 12 months was lower following denning periods with high mean daily maximum temperatures (Table 3), with no earlier effect on pup numbers at 3 months (Table 4). By contrast, in Zimbabwe (the hottest site), high ambient temperatures were associated with smaller litters at 3 months (Table 4) but not with their subsequent survival (Table 3). Rainfall during denning was associated with pup survival at all three sites, but the direction of effects was inconsistent, being significantly negative in Zimbabwe and Kenya but significantly positive in Botswana (Table 3). Correlations between rainfall and ambient temperature during denning were also inconsistent across sites, being significantly negative in Kenya but (non-significantly) positive in Botswana and Zimbabwe (Table S4), suggesting that consistent associations between ambient temperature and reproductive success were not driven by rainfall.

In addition to these associations with weather conditions, there were consistent social effects on reproductive success. In all three study areas, larger packs raised more pups to 3 months (Table 4), and pups in larger litters experienced better survival to 12 months (Table 3). Other significant effects varied between sites (Tables 2–4).

3.4 | Temporal trends in climate and reproduction

In our Botswana study population (which was monitored for longer than the other two populations) the ambient temperatures experienced by denning packs increased over 24 years of study (linear mixed model of mean daily maximum ambient temperature during denning (in $^\circ\text{C}$), including pack identity as a random effect and litter type as a fixed effect, linear effect of year: 0.134, SE 0.028, $p < .001$; Figure S5, Table S6). This trend reflected a year-on-year increase in dry season ambient temperatures in the study area (linear regression, effect of year on mean daily maximum ambient temperature (in $^\circ\text{C}$) during the period 20 May–10 Sep: slope 0.035, $p = .049$), rather than any consistent change in birth timing (linear mixed model of birth date (expressed in days relative to the median), including pack identity as a random effect and litter type as a fixed effect, linear effect of year: 0.35, SE 0.35, $p = .32$; Table S7).

Over the same 24 years of monitoring, both the proportion and numbers of pups surviving to 1 year declined (see year effects in

Variable	Estimate	SE	<i>p</i>
Kenya			
\ln mean daily maximum temperature during denning ($^\circ\text{C}$)	-10.49	4.85	.031
Botswana			
\ln number of adults	0.508	0.115	<.001
\ln mean daily maximum temperature during denning ($^\circ\text{C}$)	-3.643	1.037	<.001
\ln total rainfall November-March (mm) after birth	0.543	0.174	.002
\ln year	-0.267	0.109	.014
\ln days from median birth date (absolute)	-0.126	0.062	.044
Zimbabwe			
\ln mean daily maximum temperature during denning ($^\circ\text{C}$)	-0.268	0.089	.003
\ln total rainfall during denning (mm)	-5.104	2.038	.012

TABLE 2 Predictors of numbers of yearlings recruited to African wild dog packs per breeding attempt, in three study areas. Each of these three Poisson regression models also includes pack identity as a random effect

TABLE 3 Predictors of African wild dog pup survival from 3 to 12 months of age, in three study areas. Each of these three logistic regression models also includes pack identity as a random effect

Variable	Estimate	SE	p
Kenya			
Number of pups at 3 months of age	0.280	0.084	<.001
Mean daily maximum temperature during denning (°C)	-1.289	0.424	.002
Total rainfall during denning (mm)	-0.603	0.285	.034
Botswana			
Number of pups at 3 months of age	0.094	0.037	.012
Mean daily maximum temperature during denning (°C)	-0.158	0.070	.024
Total rainfall during denning (mm)	0.025	0.008	.001
Total rainfall November-March after birth (mm)	0.0018	0.0008	.020
Days from median birth date (absolute)	-0.025	0.010	.010
Year	-0.077	0.028	.007
Zimbabwe			
Litter type			
Beta mother vs. alpha mother	2.262	0.809	.005
Sole breeder vs. alpha mother	1.678	0.593	.005
Number of pups at 3 months of age	0.262	0.098	.008
Total rainfall during denning (mm)	-0.039	0.012	.001

TABLE 4 Predictors of numbers of pups raised to 3 months of age within African wild dog packs in three study areas. Each of these three Poisson regression models also includes pack identity as a random effect

Variable	Estimate	SE	p
Kenya			
Ln number of adults	0.269	0.130	.038
Botswana			
Ln number of adults	0.222	0.060	<.001
Litter type			
Beta mother vs. alpha mother	-0.800	0.303	.008
Sole breeder vs. alpha mother	-0.017	0.146	.906
Zimbabwe			
Ln number of adults	0.616	0.248	.013
Ln mean daily maximum temperature during denning (°C)	-5.590	1.654	<.001

Tables 2 and 3). To illustrate, litters born in the first 12 years of monitoring (1989–2000, mean daily maximum ambient temperature during denning 26.8°C, SD 1.69°C) experienced 51.4% survival to 12 months (exact binomial CI 47.1%–55.7%), yielding 5.07 (SD 3.32) yearlings per litter, whereas those born in the second 12 years of monitoring (2001–2012, mean daily maximum ambient temperature during denning 27.9°C, SD 1.69°C) experienced 38.7% survival (exact binomial CI 32.9%–44.6%), yielding 3.30 (SD 3.04) yearlings per litter. Across the

same two periods, mean estimated population density declined from 2.84 adults and yearlings/100 km² (SD 0.62) in 1989–2000 to 2.16 (SD 0.58) in 2001–2012 ($t = 2.69, p = .014$).

Our Zimbabwe and Kenya study populations were monitored for shorter periods and we observed no significant temporal trends in either weather or reproductive success. The Kenya population was growing over part of the monitoring period, following natural recolonisation of the site (Woodroffe, 2011a), whereas the Zimbabwe population was relatively stable (Funston, Groom, & Lindsey, 2013).

4 | DISCUSSION

Our findings suggest a consistent impact of high ambient temperatures on African wild dog behaviour and reproduction. High ambient temperatures were associated with reduced activity, longer inter-birth intervals, and poorer pup recruitment. These consistent associations between temperature and reproduction contrast with absent or inconsistent effects of rainfall. Impacts of high ambient temperatures on reproductive success were apparent in all three study areas, irrespective of whether or not reproduction was seasonal. Over two decades, our Botswana study area experienced both rising ambient temperatures and falling wild dog recruitment. Although correlation may not indicate causation, these findings are consistent with the view that climate warming is already impacting wild dog demography. They may also provide an adaptive explanation for seasonal reproduction in this species (McNutt et al., in review).

The energetic costs of reproduction were borne by both breeding and non-breeding pack members. Our GPS-collared animals were all non-breeders, but nonetheless all showed altered behaviour during the denning period. Although the energetic costs of reproduction are high in wild dogs (Creel & Creel, 1991), sharing them among pack members reduced per capita energy demands below those observed, for example, in small mammals (Speakman, 2008). Nevertheless, longer-term costs of reproduction were apparent at our Kenya site, where (aseasonally breeding) packs which raised larger litters took longer to produce their next litter.

Meeting these energy demands appears to have been constrained by den location. As each pack spent longer at a particular den, it travelled further each day, consistent with prey depletion in the vicinity of the den (as has been documented in our Kenya study area; Ford et al., 2015 [but see Mbizah, Joubert, Joubert, & Groom, 2014]). Such localised prey depletion (termed “Ashmole’s halo”) is widely reported among central place foragers (e.g. Elliott et al., 2009; Kuhn, Baker, Towell, & Ream, 2014).

We predicted that wild dogs would be less active at high ambient temperatures because of constraints on foraging time. Alternatively, the same association could be generated if high ambient temperatures improved hunting success (Creel, Creel, Creel, & Creel, 2016), reducing packs’ need for activity to supply their energy needs. However, under this alternative scenario, wild dogs would be expected to benefit from high ambient temperatures (because they could obtain the same energy intake with lower investment), in marked contrast

with the consistently detrimental demographic impacts that we documented.

Unlike activity, daily distance travelled was not associated with ambient temperature at our Kenya site. This difference may reflect the coarser-grained data on distance travelled (measured nine times a day), compared with activity (measured 288 times a day). At our Botswana site, Pomilia, McNutt, and Jordan (2015) found that packs did travel shorter distances at higher ambient temperatures.

Both activity and reproductive success were lower at high ambient temperatures, but the mechanistic link between the two is uncertain. Low activity might reduce reproductive success by constraining food intake; however, we could not test this hypothesis because we could not measure hunting outcomes. Pups which experience low food intake during their first 3 months might starve, or be less viable over subsequent months. Moreover, adults experiencing low food intake during denning might choose hunting over babysitting, increasing the risk of predation on pups (Courchamp, Rasmussen, & Macdonald, 2002). Additionally, packs with depleted energy reserves post-denning might take greater risks to obtain food, for example hunting more at night (Cozzi et al., 2012), or in prey-rich habitats also favoured by competing predators (Mills & Gorman, 1997), likewise increasing the risk of mortality through predation.

Another possible explanation for the link between high ambient temperatures and poor pup survival reflects the physiological challenge of lactation. Laboratory mice maintained at 30°C consume less food, produce less milk, and raise smaller offspring than do those maintained at 21°C, phenomena which have been linked to constraints on dissipating the heat generated by lactation when the gradient between body temperature and ambient temperature is shallow (Speakman & Krol, 2010; Zhao et al., 2016). The same mechanism could potentially explain wild dogs' low reproductive success at high ambient temperatures, independent of any effects on hunting behaviour, especially as lactating females spend less time hunting and more time babysitting than do other pack members (Malcolm & Marten, 1982). However, it is uncertain whether this mechanism alone would measurably reduce wild dog reproductive success at the ambient temperatures recorded in this study. For example, at our Kenya site mean daily maximum temperatures ranged up to 30°C, but lactating females experienced ambient temperatures below 20°C for the majority of each 24-hr period (Figure S6).

Long-term monitoring at our Botswana site revealed falling wild dog recruitment coinciding with rising ambient temperatures. However, we have previously documented temporal trends in prey density and wild dog body size at the same site (McNutt & Gusset, 2012). Prey decline could therefore provide an alternative explanation for declining pup survival. Equally, however, rising ambient temperatures could provide an alternative explanation for declining wild dog body size; similar effects have been documented repeatedly in other species (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011), potentially because smaller-bodied animals have greater capacity to dissipate heat (Speakman & Krol, 2010). Further study would be needed to disentangle the inter-relations between climate change, prey abundance, body size, and reproductive success (at our other sites, prey

densities declined over the monitoring period in Kenya (Ford et al., 2015) but increased in Zimbabwe (Groom, Lannas, & Jackson, 2016)). Nevertheless, this alternative explanation for the year-on-year trend in recruitment in Botswana does not undermine the clear link between high ambient temperatures and low reproductive success documented across all three sites.

The direct impacts of high ambient temperatures on wild dog vital rates that we infer contrast with meta-analyses which suggest that most effects of climate on demography occur indirectly through interspecific interactions (Cahill et al., 2012; Ockendon et al., 2014). Our results are, however, consistent with Huey et al.'s (2012) prediction that rising ambient temperatures could constrain the energy budgets of diurnal endotherms by restricting their activity times. Our findings also parallel those documented among *Sceloporus* lizards, which spent more time sheltering from the heat as climate change elevated daytime temperatures, and thus spent less time foraging, with consequently increased risks of population extinction (Sinervo et al., 2010).

These impacts of high ambient temperatures on wild dogs reflect their largely diurnal activity pattern, and probably their cursorial hunting habit. Other large African carnivores may be less affected because they are more nocturnal (lions, leopards, hyaenas, Cozzi et al., 2012) or engage in short daytime hunts which do not lead to over-heating (cheetahs, Hetem et al., 2013; Wilson et al., 2013).

Unfortunately, wild dogs may have a limited ability to adapt to climate change. Alterations in distribution (Parmesan & Yohe, 2003; Root et al., 2003), behaviour (Kearney, Shine, & Porter, 2009) or phenology (Bradshaw & Holzapfel, 2008) can potentially reduce the risks of species extinction due to climate change, but such adaptation may not be possible for wild dogs. Although wild dogs have remarkable dispersal abilities (Davies-Mostert et al., 2012; Masenga et al., 2016), geographical range shifts to higher latitudes or altitudes are unlikely, as they would require recolonising lands where the species has been previously extirpated through human impacts (Woodroffe & Sillero-Zubiri, 2013). Likewise, wild dogs are unlikely to adjust to rising ambient temperatures by becoming more nocturnal, because night-time hunting is constrained by moonlight (Cozzi et al., 2012). Moreover, it is unlikely that wild dogs (which reproduce during the cool season across most of their geographical range) could achieve cooler denning periods by altering their reproductive timing (McNutt et al., in review). As the impacts of ambient temperature on wild dogs appear to be widespread, the impacts of warming may already be evident, and opportunities for adaptation appear limited, it is possible that climate change will increase extinction risks for this already-endangered species.

Wild dogs' sensitivity to high ambient temperatures represents narrow physiological tolerance, a trait predicted to increase climate change vulnerability (Foden et al., 2013). In this case, however, narrow physiological tolerance was a relatively cryptic trait, becoming apparent only after long-term study, and likely to have been overlooked by analyses which assess the climate change vulnerability of large numbers of species using limited data (Foden et al., 2013; Pacifici et al., 2015). The reliability of trait-based assessments might be improved by

seeking less cryptic proxies for narrow physiological tolerance. For example, in African wild dogs, seasonal reproduction (which is observed less frequently in tropical than temperate species, Bronson, 1985; O'Brien, 1993; Stouffer, Johnson, & Bierregaard, 2013) indicated sensitivity to weather conditions, and hence to climate change. This trait might potentially be a useful proxy for narrow physiological tolerance, which could be used to prioritise other tropical species for in-depth analyses of climate change vulnerability.

ACKNOWLEDGEMENTS

We thank the Kenya Wildlife Service, Kenya National Council for Science and Technology (permit NACOSTI/P/14/9920/1659), Botswana Department of Wildlife and National Parks (permit EWT 8/36/4XXXVIII), Zimbabwe Parks and Wildlife Management Authority, and the Research Council of Zimbabwe (permit 02598) for research permission. We also thank funders and research assistants too numerous to list individually. The authors declare no conflicts of interests.

AUTHORS' CONTRIBUTIONS

R.W. coordinated the study, contributed data, conducted the analyses, and drafted the manuscript. J.W.M. first suggested the role of temperature, contributed data, and helped with interpreting analyses and manuscript drafting. R.G. contributed data, and helped with interpreting analyses and manuscript drafting. All authors gave final approval for publication.

DATA ACCESSIBILITY

The data analysed for this study are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.779qv> (Woodroffe, Groom, & McNutt, 2017).

REFERENCES

- Bourgarel, M., Fritz, H., Gaillard, J. M., De Garine-Wichatitsky, M., & Maudet, F. (2002). Effects of annual rainfall and habitat types on the body mass of impala (*Aepyceros melampus*) in the Zambezi Valley, Zimbabwe. *African Journal of Ecology*, *40*, 186–193.
- Bradshaw, W. E., & Holzapfel, C. M. (2008). Genetic response to rapid climate change: It's seasonal timing that matters. *Molecular Ecology*, *17*, 157–166.
- Bronson, F. H. (1985). Mammalian reproduction – An ecological perspective. *Biology of Reproduction*, *32*, 1–26.
- Buettner, U. K., Davies-Mostert, H. T., du Toit, J. T., & Mills, M. G. L. (2007). Factors affecting juvenile survival in African wild dogs (*Lycaon pictus*) in Kruger National Park, South Africa. *Journal of Zoology*, *272*, 10–19.
- Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Ryu, H. Y., ... Wiens, J. J. (2012). How does climate change cause extinction? *Proceedings of the Royal Society B-Biological Sciences*, *280*, 20121890.
- Courchamp, F., Rasmussen, G. S. A., & Macdonald, D. W. (2002). Small pack size imposes a trade-off between hunting and pup guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology*, *13*, 20–27.
- Cozzi, G., Broekhuis, F., McNutt, J. W., Turnbull, L. A., Macdonald, D. W., & Schmid, B. (2012). Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, *93*, 2590–2599.
- Creel, S., & Creel, N. M. (1991). Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behavioural Ecology and Sociobiology*, *28*, 263–270.
- Creel, S., & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, *50*, 1325–1339.
- Creel, S., Creel, N. M., Creel, A. M., & Creel, B. M. (2016). Hunting on a hot day: Effects of temperature on interactions between African wild dogs and their prey. *Ecology*, *97*, 2910–2916.
- Creel, S., Mills, M. G. L., & McNutt, J. W. (2004). Demography and population dynamics of African wild dogs in three critical populations. In D. W. Macdonald, & C. Sillero-Zubiri (Eds.), *The biology & conservation of wild canids* (pp. 337–350). Oxford, UK: Oxford University Press.
- Davies-Mostert, H. T., Kamler, J. F., Mills, M. G. L., Jackson, C. R., Rasmussen, G. S. A., Groom, R. J., & Macdonald, D. W. (2012). Long-distance transboundary dispersal of African wild dogs among protected areas in southern Africa. *African Journal of Ecology*, *50*, 500–506.
- Davies-Mostert, H. T., Mills, M. G. L., & Macdonald, D. W. (2013). Hard boundaries influence African wild dogs' diet and prey selection. *Journal of Applied Ecology*, *50*, 1358–1366.
- Downs, J. A., & Horner, M. W. (2008). Effects of point pattern shape on home-range estimates. *Journal of Wildlife Management*, *72*, 1813–1818.
- Elliott, K. H., Woo, K. J., Gaston, A. J., Benvenuti, S., Dall'Antonia, L., & Davoren, G. K. (2009). Central-place foraging in an arctic seabird provides evidence for Storer-Ashmole's halo. *Auk*, *126*, 613–625.
- Fisher, R. J., Wellicome, T. I., Bayne, E. M., Poulin, R. G., Todd, L. D., & Ford, A. T. (2015). Extreme precipitation reduces reproductive output of an endangered raptor. *Journal of Applied Ecology*, *52*, 1500–1508.
- Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vie, J.-C., Akcakaya, H. R., Angulo, A., ... Mace, G. M. (2013). Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE*, *8*, e65427.
- Ford, A. T., Goheen, J. R., Augustine, D. J., Kinnaird, M. F., O'Brien, T. G., Palmer, T. M., ... Woodroffe, R. (2015). Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. *Ecology*, *96*, 2705–2714.
- Funston, P. J., Groom, R. J., & Lindsey, P. A. (2013). Insights into the management of large carnivores for profitable wildlife-based land uses in African savannas. *PLoS ONE*, *8*, e59044.
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology and Evolution*, *26*, 285–291.
- Gorman, M. L., Mills, M. G., Raath, J. P., & Speakman, J. R. (1998). High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, *391*, 479–481.
- Groom, R. J., Lannas, K., & Jackson, C. R. (2016). The impact of lions on the demography and ecology of endangered African wild dogs. *Animal Conservation*, <https://doi.org/10.1111/acv.12328>.
- Hansen, P. J. (2009). Effects of heat stress on mammalian reproduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 3341–3350.
- Hetem, R. S., Mitchell, D., de Witt, B. A., Fick, L. G., Meyer, L. C. R., Maloney, S. K., & Fuller, A. (2013). Cheetah do not abandon hunts because they overheat. *Biology Letters*, *9*, 20130472.
- Hubel, T. Y., Myatt, J. P., Jordan, N. R., Dewhurst, O. P., McNutt, J. W., & Wilson, A. M. (2016). Energy cost and return for hunting in African wild dogs and cheetahs. *Nature Communications*, *7*, 11034.
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *367*, 1665–1679.
- IPCC. (2013). Climate Change 2013: The physical science base. Retrieved from <http://www.ipcc.ch/report/ar5/wg1/>

- Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 3835–3840.
- Kuhn, C. E., Baker, J. D., Towell, R. G., & Ream, R. R. (2014). Evidence of localized resource depletion following a natural colonization event by a large marine predator. *Journal of Animal Ecology*, 83, 1169–1177.
- Lunn, N. J., Servanty, S., Regehr, E. V., Converse, S. J., Richardson, E., & Stirling, I. (2016). Demography of an apex predator at the edge of its range: Impacts of changing sea ice on polar bears in Hudson Bay. *Ecological Applications*, 26, 1302–1320.
- Maddock, A. H., & Mills, M. G. L. (1994). Population characteristics of the African wild dogs *Lycaon pictus* in the eastern Transvaal lowveld, South Africa, as revealed through photographic records. *Biological Conservation*, 67, 57–62.
- Malcolm, J. R., & Marten, K. (1982). Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behavioural Ecology and Sociobiology*, 10, 1–13.
- Masenga, E. H., Jackson, C. R., Mjingo, E. E., Jacobson, A., Riggio, J., Lyamuya, R. D., ... Roskaft, E. (2016). Insights into long-distance dispersal by African wild dogs in East Africa. *African Journal of Ecology*, 54, 95–98.
- Mbizah, M. M., Joubert, C. J., Joubert, L., & Groom, R. J. (2014). Implications of African wild dog (*Lycaon pictus*) denning on the density and distribution of a key prey species: Addressing myths and misperceptions. *Biodiversity and Conservation*, 23, 1441–1451.
- McNutt, J. W. (1996). Sex-biased dispersal in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, 52, 1067–1077.
- McNutt, J. W., Groom, R., & Woodroffe, R. (in review). *High ambient temperatures explain seasonal reproduction in a tropical mammal*.
- McNutt, J. W., & Gusset, M. (2012). Declining body size in an endangered large mammal. *Biological Journal of the Linnean Society*, 105, 8–12.
- McNutt, J. W., & Silk, J. B. (2008). Pup production, sex ratios, and survivorship in African wild dogs, *Lycaon pictus*. *Behavioural Ecology and Sociobiology*, 62, 1061–1067.
- Mills, M. G. L. (1995). Notes on wild dog *Lycaon pictus* and lion *Panthera leo* population trends during a drought in the Kruger National Park. *Koedoe*, 38, 95–99.
- Mills, M. G. L., & Gorman, M. L. (1997). Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology*, 11, 1397–1406.
- O'Brien, G. M. (1993). Seasonal reproduction in flying foxes, reviewed in the context of other tropical mammals. *Reproduction Fertility and Development*, 5, 499–521.
- Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., ... Pearce-Higgins, J. W. (2014). Mechanisms underpinning climatic impacts on natural populations: Altered species interactions are more important than direct effects. *Global Change Biology*, 20, 2221–2229.
- Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., & Reid, R. S. (2008). Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *Journal of Animal Ecology*, 77, 814–829.
- Owen-Smith, N., & Mills, M. G. L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs*, 76, 73–92.
- Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., ... Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, 5, 215–225.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2015). nlme: Linear and nonlinear mixed effects models. R package version 3.1-119. Retrieved from <http://CRAN.R-project.org/package=nlme>
- Pomilia, M. A., McNutt, J. W., & Jordan, N. R. (2015). Ecological predictors of African wild dog ranging patterns in northern Botswana. *Journal of Mammalogy*, 96, 1214–1223.
- R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org>
- Rasmussen, G. S. A., Gusset, M., Courchamp, F., & Macdonald, D. W. (2008). Achilles' heel of sociality revealed by energetic poverty trap in cursorial hunters. *American Naturalist*, 172, 508–518.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57–60.
- Sinervo, B., Mendez de la Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Cruz, M. V. S., ... Sites, J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328, 894–899.
- Skinner, J. D., Moss, D. G., & Skinner, D. C. (2002). Inherent seasonality in the breeding seasons of African mammals: Evidence from captive breeding. *Transactions of the Royal Society of South Africa*, 57, 25–34.
- Speakman, J. R. (2008). The physiological costs of reproduction in small mammals. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 363, 375–398.
- Speakman, J. R., & Krol, E. (2010). Maximal heat dissipation capacity and hyperthermia risk: Neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, 79, 726–746.
- Stouffer, P. C., Johnson, E. I., & Bierregaard, R. O. Jr (2013). Breeding seasonality in Central Amazonian rainforest birds. *Auk*, 130, 529–540.
- Taylor, C. R., Schmidt-Nielsen, K., Dmi'el, R., & Fedak, M. (1971). Effect of hypothermia on heat balance during running in the African hunting dog. *American Journal of Physiology*, 220, 823–827.
- Therneau, T. (2014). Mixed effects Cox models. Retrieved from <http://cran.r-project.org/web/packages/coxme/coxme.pdf>
- Visser, M. E., Caro, S. P., van Oers, K., Schaper, S. V., & Helm, B. (2010). Phenology, seasonal timing and circannual rhythms: Towards a unified framework. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365, 3113–3127.
- Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A., & McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature*, 498, 185–189.
- Woodroffe, R. (2011a). Demography of a recovering African wild dog (*Lycaon pictus*) population. *Journal of Mammalogy*, 92, 305–315.
- Woodroffe, R. (2011b). Ranging behaviour of African wild dog packs in a human-dominated landscape. *Journal of Zoology*, 283, 88–97.
- Woodroffe, R., Groom, R., & McNutt, J. W. (2017). Data from: Hot dogs: High ambient temperatures impact reproductive success in a tropical carnivore. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.779qv>.
- Woodroffe, R., Lindsey, P. A., Romañach, S. S., & Ole Ranah, S. M. K. (2007). African wild dogs (*Lycaon pictus*) can subsist on small prey: Implications for conservation. *Journal of Mammalogy*, 88, 181–193.
- Woodroffe, R., & Sillero-Zubiri, C. (2013). *African wild dog Red List Assessment*. Gland, Switzerland: IUCN.
- Zhao, Z.-J., Li, L., Yang, D.-B., Chi, Q.-S., Hambly, C., & Speakman, J. R. (2016). Limits to sustained energy intake XXV: Milk energy output and thermogenesis in Swiss mice lactating at thermoneutrality. *Scientific Reports*, 6, 31626.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Woodroffe R, Groom R, McNutt JW. Hot dogs: High ambient temperatures impact reproductive success in a tropical carnivore. *J Anim Ecol*. 2017;00:1–10. <https://doi.org/10.1111/1365-2656.12719>