Ambient temperature provides an adaptive explanation for seasonal reproduction in a tropical mammal

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Running Head: Timing of reproduction in African wild dogs

Abstract

Understanding how reproductive timing has evolved to reflect climatic conditions is increasingly important as the climate changes, influencing species persistence and ecosystem dynamics. Among endotherms, seasonal reproduction is often linked to natural selection for reproducing when biotic conditions (e.g. food availability) are most favourable. In contrast, we present evidence that direct effects of an abiotic factor have selected for seasonal reproduction in a tropical mammal. We have shown previously that the African wild dog (*Lycaon pictus*), a diurnally-active coursing predator, has lower reproductive success at high ambient temperatures, when its hunting activity is constrained. We therefore hypothesised that natural selection would favour reproduction during cool weather conditions, in locations where such conditions occur predictably. We show that, as predicted, wild dogs reproduce seasonally at latitudes from 7-25°S, such that their pup-rearing periods coincide with the coolest (but not the driest) weeks of the year. Wild dog reproduction is aseasonal at latitudes ≤2°. As the climate warms, some temperate-zone species have tracked optimal conditions through altered phenology. However, in seasonally-breeding wild dog populations, any alteration in phenology would require breeding in hotter weather, probably reducing reproductive success. This endangered species may thus have a limited ability to adapt to climate change. Seasonal reproduction might be a trait indicating climate change vulnerability among tropical species.

Keywords: Climate change; *Lycaon*; phenology; seasonality.

Introduction

Many species reproduce seasonally, in synchrony with climatic seasons. At high latitudes, most vertebrates reproduce in spring and summer, a time when higher ambient temperatures increase food availability for both endotherms and ectotherms through increased primary production, and also provide ectotherms with conditions suitable for embryonic development (Bronson 1985, Wingfield *et al.* 1992, Brown & Shine 2006). At lower latitudes, weather conditions, and consequently food availability, tend to vary less predictably and seasonal reproduction is less common (Bronson 1985, Wingfield et al. 1992, Brown & Shine 2006, Stouffer, Johnson & Bierregaard 2013).

The factors which make reproduction more successful under certain environmental conditions (and thus select for reproducing at certain times of year), are also likely to influence species' responses to climate change. For example, red deer (*Cervus elaphus*) which give birth at the end of spring produce larger calves, with better survival prospects, than those which give birth earlier in the spring, when primary production is lower (Albon, Guinness & Clutton Brock 1983, Coulson *et al.* 2003). As climate change causes the annual springtime increase in primary production to occur earlier, births are also occurring earlier (Moyes *et al.* 2011), apparently reflecting an evolutionary response to natural selection for earlier parturition (Bonnet *et al.* 2019).

Importantly, the factors which drive natural selection for reproducing at certain times of year (ultimate causes) may differ from the cues which trigger reproduction (proximate causes, Tinbergen 1963). In the red deer example above, food availability provides an adaptive explanation for reproductive timing, but photoperiod plays an important role in triggering reproductive activity (Webster & Barrell 1985, Simpson, Suttie & Kay 1984), alongside nutrition (Pelaez *et al.* 2017). In red deer, as in most other temperate zone mammals (Bronson 1985), photoperiod acts as a cue which allows animals to predict likely future food availability in seasonal environments.

Studies of climate change impacts on populations of endotherms have tended to emphasise indirect impacts via biotic factors such as food availability (Ockendon *et al.* 2014), as in the red deer example above. In contrast, studies of ectotherms have emphasised direct (abiotic) effects of climate change on demography, for example through physiological sensitivity to high ambient temperatures (Huey *et al.* 2012). Nevertheless, ambient temperature appears to have direct impacts on reproductive timing (a proximate cue) and success (an ultimate cause) in some endotherms (Caro *et* *al.* 2013, Hart *et al.* 1961); hence climate change could potentially influence populations through both direct and indirect effects.

Seasonal reproduction has been reported from several populations of the African wild dog (*Lycaon pictus*), a social, diurnally-active, coursing predator with a mainly tropical distribution (Reich 1981, Creel & Creel 2002). Within each pack, reproduction is usually monopolised by a single dominant pair, although all pack members contribute to pup care (Malcolm & Marten 1982). Wild dogs' energetic demands are highest during the three-month period when they are rearing pups confined to a den (termed denning, Woodroffe, Groom & McNutt 2017), and hence temporarily become central-place foragers. Natural selection might be expected to favour denning at times of year when environmental conditions make it easiest to meet these energetic demands.

Seasonal reproduction in wild dogs has been anecdotally linked to food availability during the dry season (Reich 1981, Creel & Creel 2002). When rainfall is low, prey might be easily located close to water sources, and short grass might facilitate cursorial hunting (Reich 1981, Creel & Creel 2002, Mills 1995), potentially making prey more available to wild dogs (an indirect effect of rainfall on wild dog populations). However, food availability might also be highest at the start of the wet season, when wild dogs' main prey, impala (*Aepyceros melampus*) typically give birth (Moe, Rutina & du Toit 2007).

Alternatively, direct effects of weather conditions on wild dogs might influence natural selection on the timing of denning. We have shown previously that wild dogs experience lower reproductive success when denning coincides with periods of high ambient temperature, apparently because hotter days contain fewer daylight hours cool enough to hunt (Woodroffe, Groom & McNutt 2017, Courchamp & Macdonald 2001, Rabaiotti & Woodroffe 2019). Therefore, rather than reflecting seasonal food availability (an indirect effect of weather on wild dog populations), natural selection might favour wild dogs which raise pups during seasonally cooler periods, due to direct effects of weather on hunting opportunities.

As well as generating conflicting predictions about wild dogs' reproductive timing, these two hypothetical selective forces generate conflicting predictions about climate change impacts on this endangered species. Most wild dog populations remain in southern Africa (Woodroffe & Sillero-Zubiri 2013), a region projected to become both drier and hotter in future years (IPCC 2013). If natural selection has favoured pup-rearing during dry weather, then projected reductions in rainfall might improve wild dog reproductive success, increasing population growth. Conversely, if selection has favoured pup-rearing at low ambient temperatures, then climate warming could impact recruitment, lowering population density (Woodroffe, Groom & McNutt 2017) and increasing the risk of local extinction. We therefore tested these conflicting hypotheses, exploring whether the timing of pup-rearing in African wild dogs is most closely associated with rainfall (as a proxy for food availability) or ambient temperature.

Materials and Methods

We characterised wild dog reproductive timing using three datasets.

(i) We extracted exact birth-dates from long-term monitoring data collected at our own study sites in Kenya (0°N, Table S1), Zimbabwe (20°S, Table S2), and Botswana (20°S, Table S3). We also obtained records of daily maximum temperature and daily rainfall from weather stations within or near these three study sites (detailed in Supplementary Material). These weather variables were chosen because we have previously shown them to be associated with wild dog reproductive success (Woodroffe, Groom & McNutt 2017).

(ii) We drew upon published reports of specific birth-months in the Serengeti (2°S, Scott 1991, Schaller 1972, Frame *et al.* 1979) and Selous (7°S, Creel & Creel 2002) ecosystems, Tanzania, and narrative descriptions of birth timing in Zambia (16°S, Leigh 2005), and South Africa (25°S, Buettner *et al.* 2007). For these sites, we extracted data from published sources on total monthly rainfall and monthly mean daily maximum temperature (Table S4).

(iii) We compiled data on the exact timing of captive births using published studbooks (Rhodes, Quick & Long 2007, Verberkmoes & Verberkmoes 2007), recording the latitude of each captive facility. To illustrate the range of environmental conditions experienced by captive wild dogs across latitudes, we extracted data on total rainfall and mean maximum temperature from http://worldweather.wmo.int/en/home.html, and data on day length from https://aa.usno.navy.mil/data/docs/RS_OneYear.php, for five representative captive birth locations. We chose these representative locations by sorting the captive litters into bands of latitude (20-30°S, 20-30°N, 30-40°N, 40-50°N, and 50-60°N), and identifying the birth location of the litter with the median latitude within each band. These representative locations were De Wildt Cheetah and Wildlife

Centre, South Africa (26°S); Gladys Porter Zoo, Texas, USA (26°N); North Carolina Zoo, USA (36°N); Réserve Africaine de Sigean, France (43°N) and Wroclaw Zoo, Poland (51°N).

Following Colwell (1974) and Wingfield *et al.* (1992), we used data on birth dates from our three study sites (data source (i) above) to calculate three indices of reproductive seasonality, each taking a value between 1 and 0. The first, predictability (***P***), indicates whether the same pattern is observed consistently over multiple years (Colwell 1974). The second index, constancy (***C***), indicates similarity throughout the year; for example, complete constancy (***C***=1) would indicate births in each month of the year, every year. The third index, contingency (***M***) describes the consistency of variation within years; for example, complete contingency (***M***=1) might indicate that all births occurred in the month of May, every year. Constancy and contingency are components of predictability, such that ***P***=***C***+***M*** (Colwell 1974). In Table S5 we present a worked example of the calculation of ***P***, ***C***, and ***M***, and the procedure for testing the hypotheses that each differs from zero, based on Colwell (1974).

Where these analyses indicated that the reproduction of free-ranging wild dogs was seasonal, we conducted statistical analyses to characterise weather conditions associated with deviations from the median birth date. These analyses were intended to test competing hypotheses about the adaptive basis for seasonal reproduction, rather than to explain variation in birth date between packs or years. These analyses focused on weather conditions during the denning period, which are known to be associated with reproductive success at our three study sites (Woodroffe, Groom & McNutt 2017). Outcome variables were mean daily maximum temperature, and total rainfall, for the 90 days following the birth of each litter (approximating the denning period, Woodroffe, Groom & McNutt 2017). Birth date was included as an explanatory variable. Because our hypotheses predicted that both early and late births would be associated with suboptimal conditions for pup-rearing, we expressed birth date as the absolute number of days from the median for each site (e.g., a birth date 10 days before the median, and a date 10 days after the median, both took the value 10). This statistical approach allowed us to use linear statistics to test the hypotheses that denning periods starting both before and after the median would coincide with hotter or wetter conditions than those starting around the median birth date. These models were fitted using linear mixed-effect models (using the *R* package *nlme* (Pinheiro *et al.* 2015, *R* Core Team 2013)), and included pack identity as a random effect.

A set of secondary analyses is detailed in the Supplementary Material, exploring associations between pre-conception weather patterns and variation in birth date, which might indicate proximate cues for reproduction.

Results

Descriptive analyses showed that wild dog reproduction was strongly seasonal from 7°S southwards, but aseasonal at latitudes of 0-2° (Figure 1, Table S4). Wild dog litters at our Botswana study site had a median birth date of 3 June (interquartile range, 22 May-13 June), equivalent to a conception date of 23 March, while median birth date in Zimbabwe was 4 June (interquartile range, 18 May-8 July; equivalent to a conception date of 24 March). In contrast, there was no seasonal birth peak in Kenya (Figure 1).

At our Botswana and Zimbabwe study sites, wild dog births showed relatively high scores for predictability, attributable mainly to high contingency (Table 1). By contrast, at our Kenya study site (0°N), reproduction showed a low predictability score, not significantly different from zero (Table 1; Table S5). Within packs, 12 of 14 litters born to subdominant females were born after the dominant female's litter (Tables S1-S3). Excluding these subdominant litters reduced the proportion of late births in Botswana and Zimbabwe, but did not affect the aseasonal pattern of births in Kenya (Table S6).

In captivity, reproduction showed a seasonal pattern similar to that observed in wild populations, with a median birth date of 6 May (inter-quartile range 22 April-10 June) in the southern hemisphere (Figure 2). In the northern hemisphere, median birth date was 15 November (inter-quartile range 26 October -27 December), with little variation across a broad latitudinal range (Figure 2).

In the seasonally-breeding wild populations, few births occurred during the warm, wet season which falls between November and April in southern Africa (Figure 1). Births occurred during the cool, dry season, peaking just before the annual temperature nadir (Figure 1).

Statistical analyses showed that, at our Botswana and Zimbabwe study sites, litters born close to the median birth date experienced cooler denning periods than did those born earlier or later (Figure 3(a), Table 2). Associations between birth date and rainfall during denning were much weaker (Figure 3(b), Table 2).

Secondary analyses revealed no consistent associations between inter-annual variation in birth date and weather conditions in either the months prior to conception, or the previous denning period (Table S7).

Discussion

Despite their mainly tropical distribution (Woodroffe & Sillero-Zubiri 2013), African wild dogs reproduced seasonally across most of their remaining range. At 20°S, wild dogs' reproductive timing was as seasonally predictable as that of birds in temperate North America. For example, white-crowned sparrows (*Zonotrichia nuttalli*) living at 38°N in central California showed **P**=0.72, **C**=0.10 and **M**=0.62 (Wingfield et al. 1992), similar to the pattern shown by wild dogs in southern Africa (Table 1). By contrast, the low contingency shown by wild dogs at 0°N in Kenya (Table 1) is similar to that shown by sooty terns (*Sterna fuscata*) breeding at 8°S on Ascension Island (Wingfield et al. 1992). Wild dog reproduction was seasonal at latitudes as low as 7° (Figure 1).

Where births of free-ranging wild dogs were seasonal, they occurred in the cool, dry season (Figure 1). Birth timing caused denning periods to coincide more precisely with the coolest part of the year than with the driest at our Botswana and Zimbabwe sites (Figure 2). We have shown elsewhere that high ambient temperatures are associated with reduced hunting activity, especially during the energetically-costly denning period (Pomilia, McNutt & Jordan 2015, Woodroffe, Groom & McNutt 2017). Probably as a consequence, hotter denning periods yielded fewer surviving pups (Woodroffe, Groom & McNutt 2017). In contrast, associations between demography and denning-season rainfall were inconsistent across sites (Woodroffe, Groom & McNutt 2017). This evidence suggests that natural selection might have favoured reproduction during cool weather, where such weather occurs predictably, with no consistent selective advantage to dry-season denning. Such apparent selection for seasonal reproduction due to direct effects of weather on an endotherm may be less common than selection acting indirectly through factors such as food availability (Ockendon et al. 2014).

While avoidance of high ambient temperatures may provide an ultimate adaptive explanation for seasonal reproduction in wild dogs, the proximate mechanism triggering reproductive activity remains unknown. In some tropical mammals, seasonal reproduction appears to be triggered by rainfall, through its influence on primary production and hence food availability (e.g., Ogutu *et al.* 2015, Bergallo & Magnusson 1999). In contrast, our analyses revealed no association between birth timing and inter-annual variation in preceding weather conditions (Table S7). The latitudinal pattern we describe would be consistent with timing maintained by some external annual cue, except at very low latitudes where the cue was undetectable. Photoperiod variation is a strong candidate for such a cue, as it influences reproductive timing in many mammal and bird species, yet is difficult to detect near the equator (Bronson 2009, Wingfield et al. 1992). A photoperiod trigger could also explain why the peak birth dates in captive wild dogs differ by approximately half a year between the southern and northern hemispheres (Figure 2). In Botswana and Zimbabwe, conception occurs around the March equinox, when a period of decreasing daylight reaches 12h light/12h dark. If these photoperiodic conditions trigger wild dog reproduction, it could explain why captive litters were born at similar times across nearly 40° of latitude in the northern hemisphere despite enormous variation in temperature, rainfall, day length amplitude and, presumably, husbandry (Figure 2), because the equinox occurs simultaneously across the globe. If photoperiod does indeed trigger wild dog reproduction, seasonal breeding at 7°S (Creel & Creel 2002) would be among the lowest latitudes where such patterns have been observed in free-ranging wildlife (Hau, Wikelski & Wingfield 1998). However, the role of photoperiod in wild dog reproduction has not been tested experimentally, and it is worth noting that, in a related species, the grey wolf (*Canis lupus*), removing photoperiod cues by excision of the pineal gland failed to halt seasonal reproductive cycling (Asa *et al.* 1987). The consistently later births of subordinate litters (Tables S1-S3) suggest that social factors can also play a role in wild dog reproductive timing within packs.

African wild dogs' reproductive seasonality contrasts with patterns in other large African carnivores such as leopards (*Panthera pardus*), lions (*P. leo*), cheetahs (*Acinonyx jubatus*) and spotted hyaenas (*Crocuta crocuta*), which reproduce year-round even at Africa's highest latitudes (Balme *et al.* 2013, Miller & Funston 2014, Crosier *et al.* 2007, Terio *et al.* 2003, Lindeque & Skinner 1982). In some populations of these species, births are skewed to certain times of year (e.g., Holekamp *et al.* 1999, Balme et al. 2013, Rudnai 1973), but nevertheless births occur in all months and reproductive seasonality is much less extreme than that described here. These other species may be less affected than wild dogs by high ambient temperatures because they hunt mainly at night (lions, leopards, hyaenas, Cozzi *et al.* 2012), or because their daytime hunts are relatively short bursts which rarely cause overheating (cheetahs, Wilson *et al.* 2013, Hetem *et al.* 2013).

Many temperate-zone species have responded to climate change by reproducing earlier in spring (Parmesan & Yohe 2003), in some cases tracking optimal weather conditions (Charmantier *et al.* 2008). Such adaptation is unlikely in wild dogs, however. Winter temperatures are rising in southern Africa (IPCC 2013) but, as wild dog denning already coincides with the coolest time of year (Figure 3A), they cannot track cooler temperatures by altered phenology. Additional responses to climate change shown by other species include shifting distribution to higher latitudes and altitudes (Parmesan & Yohe 2003), and shifting activity to take advantage of cooler conditions at night (Levy *et al.* 2018). Wild dogs have a limited ability to respond in these ways because their distribution is already highly restricted by habitat loss and fragmentation (Woodroffe & Sillero-Zubiri 2013), and their nocturnal activity is constrained by limited moonlight, nocturnal predators, and the need to guard pups (Rabaiotti & Woodroffe 2019). The demographic impacts of high ambient temperatures (Woodroffe, Groom & McNutt 2017) may thus intensify as the climate warms, increasing extinction risks.

Our findings suggest that seasonal reproduction, which is less common in the tropics than at higher latitudes, might signal sensitivity to climatic conditions. This trait might thus be a potential indicator of climate change vulnerability among tropical species.

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clearance within the three study countries; data collection in Kenya was also approved by the Ethics Committee of the Zoological Society of London.

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Figure Legends

Figure 1 Timing of African wild dog reproduction across the species' remaining range (shaded), indicating sites with (black triangles) and without (white triangles) seasonal reproduction. Numbers inside triangles indicate the locations of our Kenya (1), Botswana (2), and Zimbabwe (3) study sites. Letters inside triangles indicate the sites of published studies in Serengeti (a, Schaller 1972, Frame et al. 1979, Scott 1991, Caro 1994), Selous (b, Creel & Creel 2002), Lower Zambezi (c, Leigh 2005), and Kruger (d, Buettner et al. 2007). Graphs show, for the five sites for which monthly data are available, the proportions of litters born (solid bars), mean daily maximum ambient temperature (in °C; solid symbols), and mean daily rainfall (in mm; open symbols) in each month.

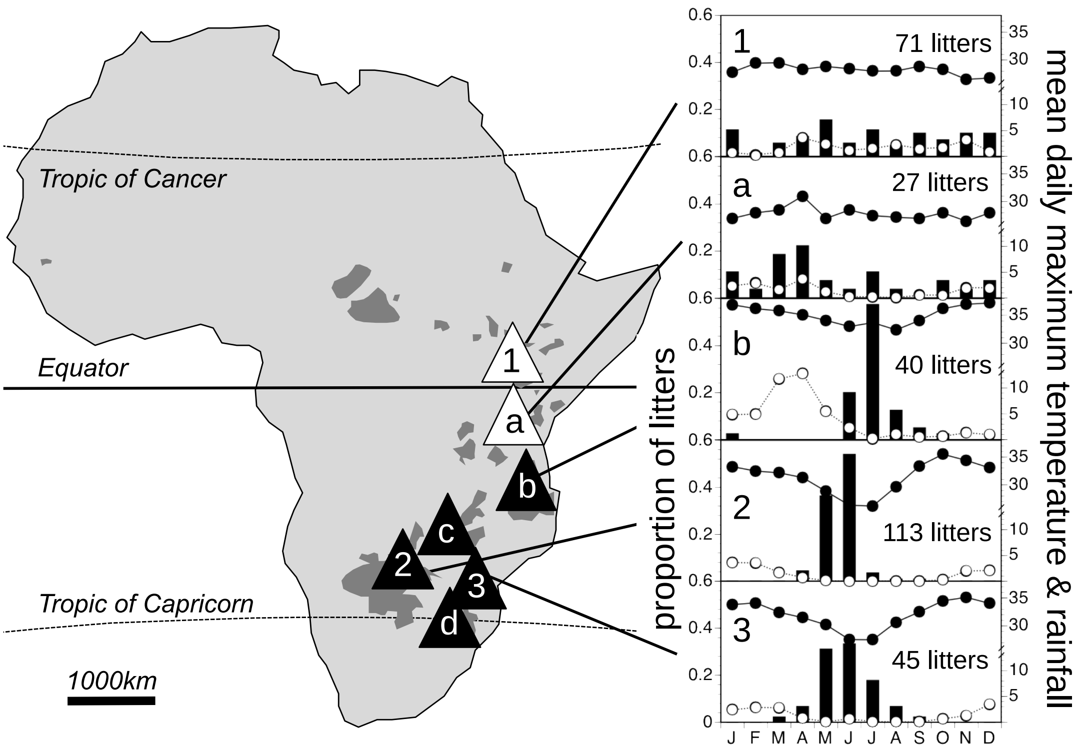

Figure 2 Timing of African wild dog births in captivity, at 50-60°N (A; 224 litters), 40-50°N (B; 120 litters), 30-40°N (C; 57 litters), 20-30°N (D; 16 litters) and 20-30°S (E; 37 litters). Data on birth timing cover the years 1984-2007, and were extracted from captive population studbooks (Rhodes, Quick & Long 2007, Verberkmoes & Verberkmoes 2007). Data on environmental conditions relate to the birth location of the litter with the median birth latitude within each 10° band, and are expressed as proportions of the maximum across all five locations. Vertical dashed lines denote the annual equinoctes.

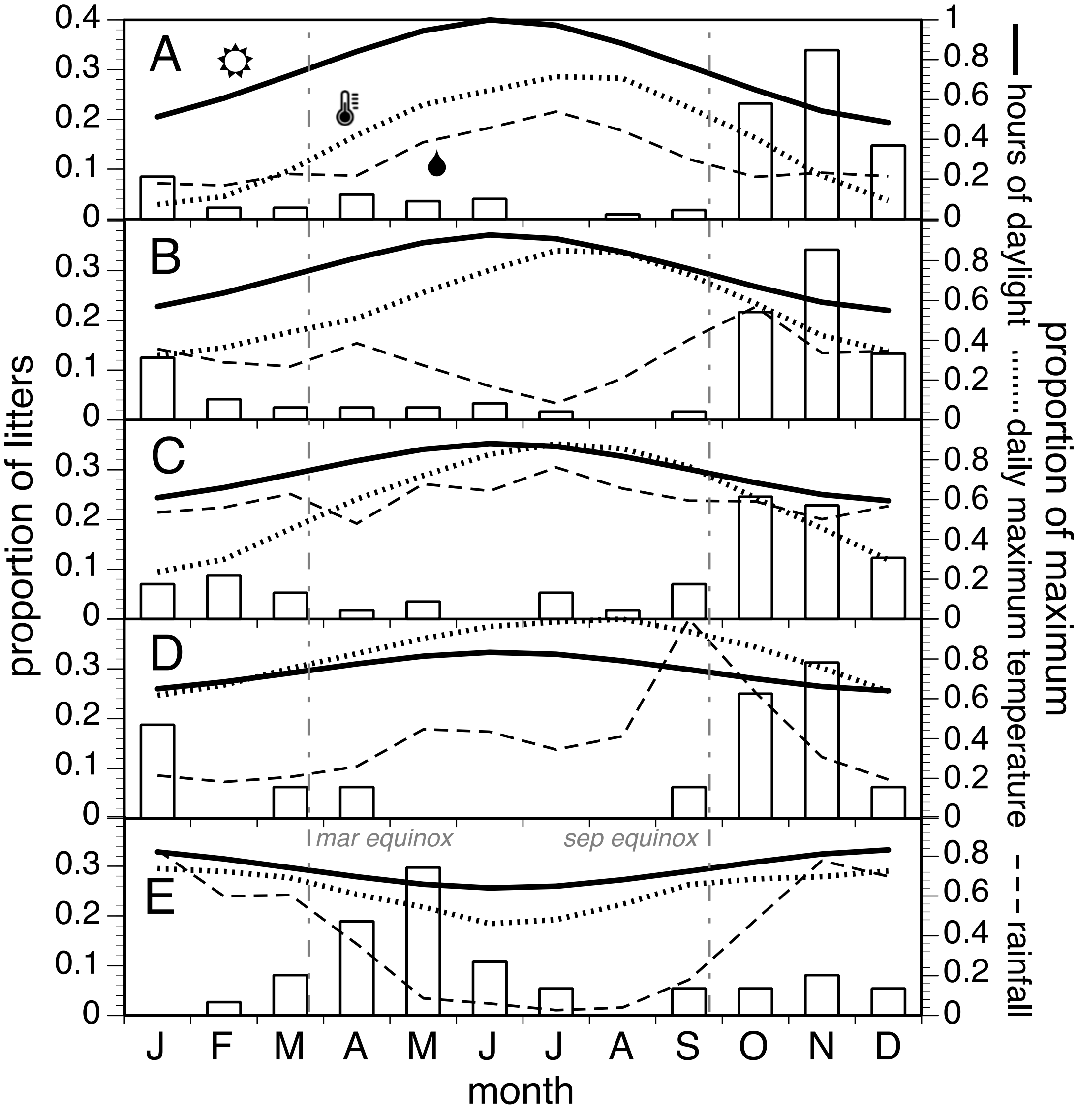

Figure 3 Weather conditions during the denning period for African wild dog litters with different birth dates. Deviations from the median birth date are plotted against (a) ambient temperature and (b) rainfall, during a 90-day period immediately following the birth date, representing the denning period. Sample sizes are lower than in Figure 1 because complete daily meteorological data were not available for all years. Statistical analyses are presented in Table 2.

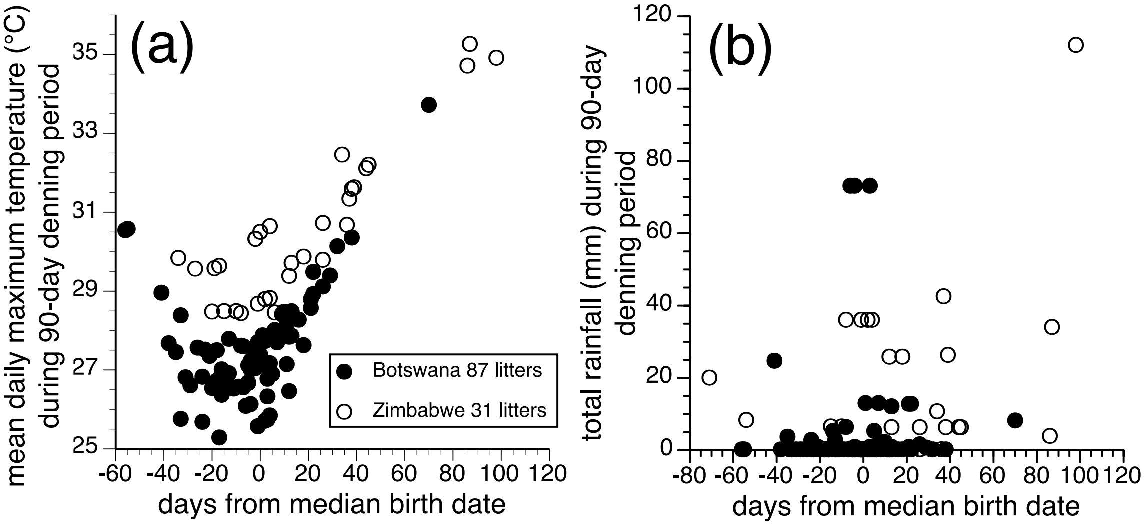

Table 1 Frequency matrices of breeding seasons for African wild dogs in three study areas. Figures show the numbers of monitoring-years with and without births during each month. Predictability, constancy, and contingency are calculated following Colwell (1974) and Wingfield *et al.* (1992).

	Number of monitoring-years											
month:	J	F	M	A	M	J	J	A	S	O	N	D
Botswana												
births	0	0	0	4	20	22	4	3	1	0	0	0
no births	24	24	24	20	4	2	20	21	23	24	24	24
	Predictability: 0.74				*Constancy: 0.30*				*Contingency: 0.43*			
	$G_P=294.2$, $p<0.001$				$G_C=121.3$, $p<0.001$				$G_M=172.9$, $p<0.001$			
Zimbabwe												
births	0	0	1	2	6	5	5	3	1	0	0	0
no births	6	6	5	4	0	1	1	3	5	6	6	6
	Predictability: 0.62				*Constancy: 0.10*				*Contingency: 0.53*			
	$G_P=62.2$, $p<0.001$				$G_C=9.60$, $p=0.002$				$G_M=52.6$, $p<0.001$			
Kenya												
births	6	1	3	5	7	4	6	3	6	5	3	6
no births	5	10	8	6	4	7	5	8	5	6	8	5
	Predictability: 0.10				*Constancy: 0.02*				*Contingency: 0.08*			
	$G_P=17.8$, $p=0.12$				$G_C=3.68$, $p=0.055$				$G_M=14.1$, $p=0.23$			

Table 2 Associations between deviation from the median birth date and weather conditions experienced during the denning period, in the two study areas with seasonal reproduction, Botswana (87 litters) and Zimbabwe (31 litters). All four models include pack identity as a random effect. Denning periods are assumed to last 90 days. Sample sizes are lower than in Figure 1 because complete daily meteorological data were not available for all years.

Effect of absolute days before or after median birth date on weather outcome variable	**Estimate**	**SE**	**P**
Mean daily maximum temperature (°C) during denning			
Botswana	0.074	0.007	<0.001
Zimbabwe	0.066	0.006	<0.001
Total rainfall (mm) during denning			
Botswana	0.152	0.101	0.139
Zimbabwe	0.331	0.139	0.028

Ambient temperature provides an adaptive explanation for seasonal reproduction in a tropical mammal

SUPPLEMENTARY MATERIAL

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1 Study sites

Our Kenya study site (Woodroffe 2011) centred on Laikipia County, and also encompassed parts of neighbouring Samburu, Isiolo, and Baringo Counties. Meteorological data were collected at Mpala Research Centre, in the middle of the study area. Although close to the equator (37° 2' E, 0° 6' N), the site's relatively high altitude (1800m ASL) means that ambient temperatures are relatively low (Main Text Figure 1). The site falls to the north of Mount Kenya, and in its rain shadow; mean annual rainfall at Mpala Research Centre is 590mm. Both temperature and rainfall show relatively little predictable seasonal variation (Main Text Figure 1). Wild dogs disappeared from the Kenya study area in the 1980s, but began to recolonise in the late 1990s; the first den in Laikipia was recorded in 2000 (Woodroffe 2011). The population grew rapidly, and by 2008 Laikipia alone was estimated to support 19 packs, totalling approximately 200 adult wild dogs (Woodroffe 2011). Wild dogs' two most important prey types in the Kenya study area are dikdiks (*Madoqua* spp) and impala (*Aepyceros melampus*, Woodroffe *et al.* 2007).

Our Botswana study site (23° 38' E, 19° 30' S, 960m ASL) lies on the eastern side of the Okavango delta, and includes parts of the Moremi Game Reserve as well as adjoining Wildlife Management Areas. Habitats include recent and dormant seasonal floodplains, savanna woodlands, and shrublands. Meteorological data were collected at a weather station at Maun airport, roughly 30km from the study area boundary and within the same ecosystem. This site experienced the lowest mean annual rainfall of the three sites (430mm), although primary production was also influenced by the annual flooding of the Okavango delta. At this site, most rain fell during a single annual rainy season between November and March, coinciding with the hottest part of the year (Main Text Figure 1). This study population forms part of the world's largest wild dog population, which extends from northern Botswana into western Zimbabwe, eastern Namibia, south-western Zambia, and south-eastern Angola (Woodroffe & Sillero-Zubiri 2013). Impala are the most important prey species, comprising 85% of kills (Creel, Mills & McNutt 2004).

Our Zimbabwe study site (32° 00' E, 20° 05' S, 550m ASL) falls within the Savé Valley Conservancy in the eastern lowveld. The habitat comprises woodland savanna, covering low hills with occasional rocky outcrops. Meteorological data were collected at Middle Sabi Research Station, 12km from the study area boundary. Like the Botswana site, the Zimbabwe site experienced a single warm, wet season each year, with most rain falling between November and March (Main Text Figure 1). Savé Valley Conservancy was founded in 1991 on land previously used for livestock farming. The area was initially re-stocked with native ungulates; wild dogs had recolonised naturally by 1996, and rapidly reached densities comparable with those observed inside protected areas (Pole 2000). Impala are wild dogs' principle prey at this site (Mbizah, Marino & Groom 2012).

2 Description of reproductive seasonality

We described the seasonality of reproduction at our three study sites following a method devised by Colwell (1974). The method is fully explained in Colwell's (1974) paper, but we provide a worked example in Table S5.

3 Birth timing of dominant and subdominant litters

Across our three study sites, 14 litters were born to subdominant females, in years when a dominant female also reproduced in the same pack (Tables S1-S3). Of these 14 subdominant litters (three (2.7%) in Botswana, nine (20%) in Zimbabwe, two (2.8%) in Kenya), 12 were born after the dominant's litter, one on the same day, and one before (Tables S1-S3). In Botswana and Zimbabwe, excluding these subdominant litters reduced the proportion of later litters, slightly increasing the predictability scores at both sites (Table S6). In contrast, excluding subdominant litters did not markedly alter measures of reproductive seasonality at our Kenya site (Table S6).

4 Comparisons of birth date with pre-conception conditions

Our primary statistical analyses (presented in the Main Text) tested hypotheses about the adaptive basis of average birth timing at the two seasonally-breeding sites (Botswana and Zimbabwe) by characterising the weather conditions associated with absolute deviations from the median birth date, across all years. Here, we present secondary analyses which explored associations between birth date and conditions prior to conception, which might provide a proximate trigger for reproduction. These secondary analyses considered only litters born to alpha females, since the birth dates of multiple litters born in the same pack in the same year were not statistically independent. For these analyses, birth date was the outcome variable, expressed as days before or after the median for the site (e.g., a birth date 10 days before the median took the value -10 and a date 10 days after the median took the value +10).

We used linear mixed effects models to compare these birth dates with several candidate explanatory variables, each fitted one-by-one along with pack identity as a random effect. These candidate variables were chosen to represent conditions prior to conception, assuming a median conception date of 23 Mar at the Botswana site and 24 Mar at the Zimbabwe site, estimated on the basis that wild dogs have a 72-day gestation (McNutt & Woodroffe 2013). These dates fall at the end of the warm wet season (see Figure 1 of the Main Text for graphs of annual temperature and rainfall patterns).

Among the candidate explanatory variables, two were included because Woodroffe et al. (2017) found them to be associated with inter-birth interval in the (non-seasonally breeding) Kenya study population. These variables were (i) mean daily maximum temperature during the previous 90-day pup-rearing period, and (ii) the number of pups raised to three months on the previous breeding attempt. A third variable [(iii) total rainfall during the previous 90-day pup-rearing period] was included to parallel the inclusion of temperature from the same period. While these variables describe conditions many months before conception, conditions at this time were associated with conception date (expressed as interbirth-interval) at our Kenya study site (Woodroffe, Groom & McNutt 2017), and could therefore potentially influence conception date (expressed as days relative to the median) at our Botswana and Zimbabwe sites.

Pack size was included as a candidate explanatory variable (iv), because it is associated with multiple behavioural and demographic traits in wild dogs (Creel & Creel 1995, Creel & Creel 2015, Courchamp & Macdonald 2001, Woodroffe, Groom & McNutt 2017).

Three candidate explanatory variables were included to characterise weather conditions during the warm, wet season preceding conception. These included (v) mean daily maximum temperature and (vi) total rainfall during the previous Nov-Feb, as well as (vii) the date of peak temperature (expressed in days from 1 Sep). Although most rainfall occurs during November-March at both sites (see Figure 1 in the Main Text), we used weather data from November-February because the median conception dates for both sites fell in March; hence, weather data from November-March would have included some data collected after the conception date for more than half the litters evaluated. We estimated the date of peak temperature by fitting a quadratic regression to daily maximum temperature between 1 Sep and 31 Mar, expressed as a function of the number of days since 1 Sep, and identifying the date corresponding to the highest point on the fitted curve. We included March data in calculating this variable because they helped to provide a more precise estimate of the timing of the temperature peak, which itself occurred well before March (and hence well before the median conception date).

Two additional candidate explanatory variables were selected to characterise the date of the start of the warm, wet season, which has been shown to correlate with the birth season for impala, wild dogs' main prey at the Botswana and Zimbabwe sites (Moe, Rutina & du Toit 2007). These variables were (viii) the number of days from the 1 Oct by which 40mm of rain had fallen, and (ix) the number of days after 1 Sep by which there had been three days with maximum temperature >37.5°C. Because most rain fell between November and March, October was an appropriate month to start counting days to describe the onset of the rains. However, temperatures start to rise before October (see Figure 1 in the Main Text). We chose to start counting days from 1 Sep to describe the onset of the hottest weather because denning typically ended in August, and females would not be expected to be influenced by weather conditions when they were potentially still lactating for the previous litter.

Finally, we included two candidate explanatory variables intended to characterise the end date of the warm, wet season which immediately preceded conception. These variables were designed to mirror the corresponding variables describing the start of the warm wet season, and were (x) the date when the last 40mm of the wet season (before 1 Mar) began to fall, and (xi) the last date before 1 Mar when maximum temperature exceeded 37.5°C. These variables were estimated relative to the 1 Mar because the median conception dates fell in late March.

Of the resulting 22 comparisons (11 variables at each of two sites), two indicated statistically significant associations (Table S7). As neither association was consistent across the two sites (Table S7), and random variation would be expected to generate an average of one significant association for every 20 tests, we concluded that none of the candidate explanatory variables was consistently associated with birth date.

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6 Supplementary Tables

Table S1 Timing of African wild dog births at our **Kenya** study site. Highlighting shows dual litters in the same pack. Weather variables were not analysed due to lack of seasonal reproduction at this site

Pack	Mother	Date
CF	dominant	06-Jul-01
CJ	dominant	08-May-01
CF	dominant	27-May-02
CJ	dominant	05-Apr-02
CV	dominant	24-Jul-02
DB	dominant	12-Jul-02
DB	subdominant	17-Jun-02
CC	dominant	28-Jul-03
CF	dominant	13-Apr-03
CF	subdominant	02-Jul-03
CK	dominant	22-Jun-03
CS	dominant	31-Dec-03
DB	dominant	27-May-03
DD	dominant	13-Aug-03
CF	dominant	04-Apr-04
CH	dominant	09-Apr-04
CP	dominant	21-Sep-04
CT	dominant	08-Jul-04
CX	dominant	17-Dec-04
CY	dominant	21-May-04
DB	dominant	27-Jan-04
DB	dominant	05-Dec-04
DD	dominant	24-Oct-04
CB	dominant	27-Sep-05
CE	dominant	25-May-05
CF	dominant	14-May-05
CP	dominant	15-Oct-05
CQ	dominant	15-Nov-05
CU	dominant	13-May-05
CX	dominant	27-Nov-05
CY	dominant	27-May-05
DB	dominant	24-Nov-05
DD	dominant	07-Aug-05
CB	dominant	10-May-06
CF	dominant	21-Jan-06
CI	dominant	29-Dec-06
CX	dominant	21-Jul-06
DB	dominant	26-Sep-06
CB	dominant	20-Mar-07
CD	dominant	18-Apr-07
CN	dominant	13-Dec-07
CZ	dominant	07-Jan-07
DA	dominant	12-Mar-07
DB	dominant	01-Jul-07
CB	dominant	04-Mar-08
CD	dominant	05-Apr-08
CF	dominant	09-Sep-08
CG	dominant	24-Nov-08
CI	dominant	07-Jan-08
CL	dominant	13-May-08
CM	dominant	15-Jun-08
CO	dominant	15-Dec-08
CR	dominant	15-Nov-08
CW	dominant	21-Sep-08
CZ	dominant	13-Jan-08
DB	dominant	26-May-08
DC	dominant	23-Oct-08
CA	dominant	23-Nov-09
CB	dominant	09-Feb-09
CF	dominant	12-Aug-09
CI	dominant	10-Jan-09
CI	dominant	23-Nov-09
CW	dominant	21-Jun-09
CZ	dominant	02-Mar-09
DC	dominant	26-Sep-09
CB	dominant	08-Jan-10
CF	dominant	10-Sep-10
CI	dominant	18-Oct-10
CZ	dominant	12-Jan-10
DE	dominant	25-Dec-10
CI	dominant	29-Oct-11

Table S2 Timing of African wild dog births at our **Zimbabwe** study site. "Rain" indicates total rainfall (in mm), and "Temp" mean daily maximum temperature (in °C) in the 90 days following the birth date. Highlighting shows dual litters in the same pack.

Pack	Mother	Date	Rain	Temp
BB	dominant	15-May-08	0	28.46
BB	subdominant	19-Jul-08	6.1	32.18
BE	dominant	17-Jun-08	6.1	29.69
BE	subdominant	12-Jul-08	6.1	31.57
BI	dominant	30-Jun-08	6.1	30.70
BI	subdominant	29-Aug-08	3.7	34.69
BM	dominant	18-Jul-08	6.1	32.09
BB	dominant	25-May-09	6.3	28.47
BB	subdominant	10-Jul-09	0	30.66
BE	dominant	20-May-09	6.3	28.47
BM	dominant	10-Jun-09	0	28.43
BN	dominant	30-Jun-09	0	29.77
BB	dominant	24-Apr-10	NA	NA
BE	dominant	21-May-10	NA	NA
BF	dominant	27-Jul-10	NA	NA
BH	dominant	01-Jun-10	NA	NA
BL	dominant	10-Sep-10	111.8	34.89
BM	dominant	06-Jun-10	NA	NA
BA	dominant	03-Jun-11	35.8	28.65
BC	dominant	27-May-11	35.8	28.42
BD	dominant	16-Jun-11	25.6	29.36
BF	dominant	22-Jun-11	25.6	29.85
BG	dominant	13-Jul-11	26.1	31.60
BI	dominant	06-Jun-11	35.8	28.77
BI	subdominant	11-Jul-11	42.3	31.32
BL	dominant	08-Jun-11	35.8	28.80
BA	dominant	02-Jun-12	0	30.30
BC	dominant	16-May-12	0	29.55
BD	dominant	08-Jun-12	0	30.62
BF	dominant	18-May-12	0	29.62
BG	dominant	04-Jun-12	0	30.48
BG	subdominant	08-Jul-12	10.5	32.43
BI	dominant	01-May-12	0	29.82
BK	dominant	08-May-12	0	29.54
BL	dominant	02-Jun-12	0	30.30
BL	subdominant	30-Aug-12	33.8	35.24
BA	dominant	16-May-13	NA	NA
BC	dominant	20-May-13	NA	NA
BG	dominant	17-May-13	NA	NA
BG	subdominant	22-Aug-13	NA	NA
BI	dominant	24-Apr-13	NA	NA
BJ	dominant	11-Apr-13	8.1	NA
BJ	subdominant	16-May-13	NA	NA
BK	dominant	25-Mar-13	19.8	NA
BL	dominant	22-May-13	NA	NA

Table S3 Timing of African wild dog births at our **Botswana** study site. “Rain” indicates total rainfall (in mm), and “Temp” mean daily maximum temperature (in °C) in the 90 days following the birth date. Highlighting shows dual litters in the same pack.

Pack	Mother	Date	Rain	Temp
Y	dominant	01-May-89	NA	NA
AI	dominant	21-May-90	0	27.77
T	dominant	01-May-90	0	28.36
Y	dominant	23-Apr-90	24.5	28.94
AB	dominant	25-Jun-91	0	29.46
AI	dominant	25-May-91	0	26.56
AN	dominant	22-May-91	0	26.53
AP	dominant	11-Jun-91	0	27.96
D	dominant	14-May-91	0	26.52
I	dominant	29-May-91	0	26.66
Y	dominant	18-May-91	0	26.46
AB	dominant	16-May-92	0	26.52
AH	dominant	10-May-92	0	26.81
AI	dominant	29-Apr-92	3.5	27.43
AN	dominant	06-Jun-92	0	26.76
AN	subdominant	01-Aug-92	8	32.47
B	dominant	19-Jun-92	0	28.25
I	dominant	29-Jun-92	1.4	29.09
J	dominant	15-Jun-92	0	27.82
M	dominant	27-May-92	0	26.54
U	dominant	29-May-92	0	26.65
Y	dominant	23-May-92	0	26.51
AB	dominant	07-Jun-93	0.7	27.15
AF	dominant	16-Jun-93	0.7	27.85
AI	dominant	18-May-93	0.7	27.00
AN	dominant	06-Jun-93	0.7	27.11
J	dominant	24-Jun-93	0.7	28.55
Y	dominant	13-May-93	0.7	27.33
AB	dominant	07-Jun-94	0	25.83
AF	dominant	05-Jun-94	0	25.69
AN	dominant	06-Jun-94	0	25.72
F	dominant	02-Jun-94	0	25.55
J	dominant	17-May-94	0	25.27
R	dominant	15-Jun-94	0	26.44
S	dominant	01-May-94	0	25.74
AB	dominant	09-Jun-95	0	27.97
AC	dominant	16-Jun-95	0	28.47
AF	dominant	03-May-95	0	26.79
AN	dominant	01-Jun-95	0	27.37
F	dominant	30-May-95	0	27.21
O	dominant	16-May-95	0	26.71
AJ	dominant	01-Jun-96	0	27.03
F	dominant	30-May-96	0	26.99
N	dominant	21-May-96	2.6	26.58
X	dominant	02-Jul-96	0.5	29.37
AJ	dominant	16-Jun-97	11.9	28.46
AK	dominant	20-May-97	5.1	26.89
B	dominant	25-Jun-97	12.6	28.90
F	dominant	21-May-97	5.1	26.90
H	dominant	24-Jun-97	12.6	28.77
N	dominant	13-Jun-97	2	28.45
X	dominant	12-Jun-97	2	28.39
AE	dominant	05-Jul-98	0	30.12
AJ	dominant	09-Jun-98	0	27.99
AK	dominant	27-May-98	0	27.58
B	dominant	05-Jun-98	0	27.71
F	dominant	02-Jun-98	0	27.57
H	dominant	12-Aug-98	20.6	33.70
N	dominant	08-Jun-98	0	27.90
X	dominant	09-Jun-98	0	27.99
AB	dominant	30-May-99	0	27.17
B	dominant	03-Jun-99	0	27.37
AB	dominant	10-May-00	2.6	25.66
F	dominant	14-Jun-00	0	27.13
AA	dominant	10-Jun-01	0	27.68
AA	subdominant	20-Aug-01	61.4	33.83
AO	dominant	18-May-01	0	26.35
B	dominant	02-Jun-01	0	27.08
G	dominant	14-Jun-01	0	28.13
AA	dominant	02-Jun-02	12.8	27.68
AL	dominant	16-May-02	0	27.48
AO	dominant	08-May-02	0	27.55
AQ	dominant	11-May-02	0	27.50
AR	dominant	04-Jun-02	12.8	27.86
Q	dominant	26-Apr-02	0	27.66
Z	dominant	26-May-02	6.2	27.60
AR	dominant	08-Jun-03	0	26.88
AA	dominant	11-Jun-04	0	NA
AQ	dominant	09-Jun-04	0	NA
AR	dominant	04-Jun-04	0	NA
A	dominant	10-Jun-05	0	NA
AD	dominant	09-Apr-05	0	30.56
AG	dominant	20-Jun-05	0	NA
AQ	dominant	23-May-05	0	NA
AR	dominant	17-May-05	0	NA
L	dominant	08-Apr-05	0	30.52
AR	dominant	29-May-06	0	27.10
AR	subdominant	29-May-06	0	27.10
V	dominant	02-Jun-06	0	27.24
W	dominant	02-Jun-07	0	27.26
AQ	dominant	11-Jul-08	0	30.34
V	dominant	15-Jun-08	0	28.44
W	dominant	02-Jun-08	0	27.50
AQ	dominant	21-Jun-09	0	27.61
C	dominant	06-Jun-09	72.9	26.31
K	dominant	28-May-09	72.9	26.07
W	dominant	30-May-09	72.9	26.11
AQ	dominant	09-Jun-10	0	NA
C	dominant	20-Jun-10	0	NA
K	dominant	07-Jun-10	0	NA
V	dominant	07-Jun-10	0	NA
W	dominant	25-May-10	0	NA
AM	dominant	09-Jun-11	NA	NA
C	dominant	11-Jun-11	NA	NA
E	dominant	24-Jun-11	NA	NA
K	dominant	27-May-11	NA	NA
V	dominant	14-Jun-11	NA	NA
W	dominant	03-Jun-11	NA	NA
AM	dominant	18-Jun-12	NA	NA
C	dominant	19-Sep-12	NA	NA
E	dominant	16-Jul-12	NA	NA
K	dominant	16-Jun-12	NA	NA
P	dominant	31-May-12	NA	NA
V	dominant	07-Jun-12	NA	NA
W	dominant	01-Jun-12	NA	NA

Table S4 – Birth seasons reported from seven free-ranging populations of African wild dogs at varying latitudes. Data sources: [1]This study [2]Scott (1991); [3]Schaller (1972); [4]Frame *et al.* (1979); [5]Caro (1994); [6]Creel & Creel (2002); [7]Leigh (2005); [8]Dunham (1989) [9]Buettner *et al.* (2007); [10]Kruger *et al.* (2002).

Site	**Latitude**	**Annual variation in day length**	**Annual range in mean monthly temperature °C**		**Coolest months**	**Driest months**	**Wild dog birth months**	**Source**
			min	*max*				
Samburu-Laikipia, Kenya	0° N	0 hrs	11-14	28-30	nov-dec	jan-feb	all months	1
Serengeti-Mara, Kenya-Tanzania	2° S	0.3 hrs	13-18	26-31	nov-jan	jun-oct	11/12 months	2-5
Selous Game Reserve, Tanzania	7° S	0.9 hrs	19-25	32-37	jun-aug	jul-dec	jun-aug	6
Lower Zambezi National Park, Zambia	16° S	1.9 hrs	9-22	29-39	may-aug	may-nov	may-jul	7-8
Okavango Delta, Botswana	20° S	2.5 hrs	8-21	26-35	jun-aug	jun-oct	may-jul	1
Savé Valley Conservancy, Zimbabwe	20° S	2.5 hrs	9-22	27-35	jun-aug	may-sep	may-jun	1
Kruger National Park, South Africa	25° S	3.2 hrs	6-21	26-32	jun-aug	may-aug	jun	9-10

Table S5 is provided as a separate file.

Table S6 Frequency matrices of breeding seasons for African wild dogs in three study areas, restricted to **dominant litters** only. Figures show the numbers of monitoring-years with and without births during each month. Predictability, constancy, and contingency were calculated following Colwell (1974) and Wingfield *et al.* (1992).

	Number of monitoring-years											
month:	J	F	M	A	M	J	J	A	S	O	N	D
Botswana												
births	0	0	0	4	20	22	4	1	1	0	0	0
no births	24	24	24	20	4	2	20	23	23	24	24	24
	Predictability: 0.76				*Constancy: 0.32*				*Contingency: 0.44*			
	$G_P=304.0$, $p<0.001$				$G_C=127.2$, $p<0.001$				$G_M=176.7$, $p<0.001$			
Zimbabwe												
births	0	0	1	2	6	5	3	1	0	0	0	0
no births	6	6	5	4	0	1	3	5	6	6	6	6
	Predictability: 0.68				*Constancy: 0.19*				*Contingency: 0.49*			
	$G_P=67.6$, $p<0.001$				$G_C=18.8$, $p<0.001$				$G_M=48.8$, $p<0.001$			
Kenya												
births	6	1	3	5	7	3	6	3	6	5	3	6
no births	5	10	8	6	4	8	5	8	5	6	8	5
	Predictability: 0.11				*Constancy: 0.02*				*Contingency: 0.08*			
	$G_P=19.4$, $p=0.08$				$G_C=4.39$, $p=0.036$				$G_M=15.0$, $p=0.18$			

Table S7 Comparisons of birth date with conditions prior to conception. Each candidate explanatory variable was added to a linear mixed-effects model of birth date (measured in days relative to the site median), including pack identity as a random effect.

Candidate explanatory variable		**Botswana**		**Zimbabwe**	
		estimate	*p*	*estimate*	*p*
(i)	Mean daily maximum temperature (°C) during previous denning period	1.454	0.438	1.685	0.418
(ii)	Litter size at 3mo for previous denning period	-0.217	0.851	-0.516	0.642
(iii)	Total rainfall (mm) during previous denning period	-0.031	0.869	0.186	0.109
(iv)	Pack size	-0.297	0.454	-0.976	0.371
(v)	Mean daily maximum temperature (°C) during previous Nov-Feb	-3.311	0.153	-8.774	0.173
(vi)	Total rainfall (mm) during previous Nov-Feb	0.007	0.579	-0.100	0.168
(vii)	Date of peak maximum temperature (in days from 1 Sep)	-0.037	0.693	0.147	0.479
(viii)	Days from 1 Oct by which 40mm rain had fallen	-0.006	0.975	0.378	0.332
(ix)	Days from 1 Sep by which three days had exceeded 37.5°C	0.008	0.838	2.904	0.024
(x)	Days counting backwards from 1 Mar by which 40mm rain had fallen	0.026	0.842	0.081	0.799
(xi)	Days from 1 Sep when maximum temperature last exceeded 37.5°C before 1 Mar	-0.061	0.227	-0.410	0.037