

Constraints on behavioural thermoregulation in a tropical mammal increase climate change vulnerability

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MRes Biodiversity, Evolution and Conservation
Research Project I: BIOSG094

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Selected Journal: Journal of Animal Ecology

Abstract

1. Climate change is one of the greatest threats to species globally. Temperatures in Africa are predicted to increase to a greater extent than the global average, making it critical to identify species most at risk. This depends on their ability to adapt in range, phenology or behaviour. Little is known about the effect of temperature on mammals or the potential for behavioural thermoregulation but the complexity of mammalian behaviour suggests there may be scope for it
2. Here we assess wild dogs' ability to adapt by shifting the timing of their activity periods and explore how activity is affected by variables, such as temperature and moonlight.
3. Data was collected over the course of five years from 19 different dogs fitted with GPS collars. Activity was broken down into bouts. The strength of the associations between predictor variables and bout components, such as duration, intensity, start and stop time, were tested.
4. On hotter days, morning and evening bouts are shorter and less intense. Nocturnal compensation following hot days is restricted by moonlight. Wild dogs are more active during the day when denning but less active at night. There is little potential for behavioural thermoregulation in African wild dogs.
5. Data on the effect of temperature on behaviour in mammals is lacking but this should be an integral part of all climate change vulnerability assessments. This will enable us to more accurately predict climate change impacts and plan conservation strategy effectively.

Key words

Climate change, adaptation, behaviour, thermoregulation, activity, African wild dog, GLM

Introduction

Climate change is one of the greatest threats to species worldwide. In the last 100 years, temperatures have increased by 0.74°C , with global mean temperatures predicted to increase by a further $4.3 \pm 0.7^{\circ}\text{C}$ by 2100 (Pacifiçi *et al.* 2015). Current rates of extinction are in some cases several hundred times higher than would be expected from the fossil record, with many agreeing a sixth mass extinction event is already underway (Stork 2010; Barnosky *et al.* 2011). Climate change has caused shifts in the distribution and abundance of many species in the last 30 years, and could soon become the leading cause of extinction (Thomas *et al.* 2004). Not only will we see loss of species, but also the extinction of ecological interactions that could lead to extensive trophic cascades and ultimately the destabilisation of ecosystem functioning (Estes *et al.* 2011).

The effects of climate change can operate at all levels of biodiversity, from organism to population, to species, all the way up to biome level (Parmesan 2006; Bellard *et al.* 2012). Often these effects lead to the expression of fitness decreases but some species are able to respond to the effects of climate change by altering their climatic niche (Bellard *et al.* 2012). These shifts may occur in space (range), time (phenology) or self (physiology). According to global meta-analyses, ranges are shifting on average 6.1km per decade towards the poles, and spring events are advancing 2.3 days per decade (Parmesan & Yohe 2003). Range-restricted species, such as those that inhabit mountainous regions, have shown severe range contractions, which will be fatal if they continue as these species are unable to migrate elsewhere (Parmesan 2006). This was the case in the extinction of the locally endemic golden toad (*Bufo periglenes*) in the highland forests of Costa Rica (Pounds, Fogden & Campbell 1999), while 400-550 landbirds are projected to go extinct due to elevational limits with an intermediate estimate of surface warming of 2.8°C (Sekerçioğlu *et al.* 2008). Variable responses in phenology to warming have disrupted many species interactions, including plant-insect pollinator and predator-prey relationships, which could lead to the extinction of both species involved with expected knock-on effects in the wider community (Yang & Rudolf 2010). Physiological responses are well documented, with many species already exhibiting smaller body sizes and more predicted to shrink, following fundamental ecological and metabolic rules (Sheridan & Bickford 2011).

Once again, trophic cascades and ecosystem function disruption are likely given the heterogeneous nature of physiological responses.

While some species may have been able to cope with climatic change thus far, temperatures are predicted to rise at an increasingly rapid rate (Root *et al.* 2003). The global mean climate change velocity is $0.42\text{km}\text{yr}^{-1}$ with only 8% of global protected areas having climates with residence times over 100 years (Loarie *et al.* 2009). Given the current rate of change, accurately assessing which species are most vulnerable is more important than ever. Vulnerability is the 'predisposition to be adversely affected' (Pacifi *et al.* 2015) and is commonly agreed to be dependent on the species' exposure and sensitivity to change, its resilience to perturbation and its potential to adapt to change (Huey *et al.* 2012; Foden *et al.* 2013; Pacifi *et al.* 2015). The most vulnerable species are those with high exposure and sensitivity, but low adaptive capacity. Assessments of these criteria draw on species' modelled exposure to projected climatic changes and their biological traits (Foden *et al.* 2013). Traits associated with increased sensitivity include habitat specialisation, narrow environmental tolerances and the potential for disruption of ecological interactions. Traits associated with low adaptive capacity include poor dispersal potential and poor micro-evolutionary potential conferred by low genetic diversity, long gestation or low reproductive output (Foden *et al.* 2013). There are a number of approaches used to estimate vulnerability, but the behavioural, physiological and genetic data needed to accurately assess species on these criteria are often not available (Huey *et al.* 2012).

Many vulnerability assessments have focused on predicting changes in physiology and range to identify conservation priorities and devise species-specific strategies. For example, thermal performance curves have been used to predict decreases in fitness as a direct result of environmental temperatures, highlighting that ectotherms, especially amphibians and reptiles, are most at risk (Foden *et al.* 2013; Sinclair *et al.* 2016). Similarly, studies have shown that these groups will be least capable of shifting their distributions making them more vulnerable to rapid environmental changes (Araújo & Pearson 2005). While such predictions of changes in physiology and range are commonplace in climate change vulnerability assessments, relatively little is known about how increasing temperatures will affect behaviour, especially in mammals. The potential buffering influence of behavioural thermoregulation could be

a key missing element from models of climate change impacts (Kearney, Shine & Porter 2009). Behavioural modifications such as the use of cool microclimates and nocturnal activity may be the key to buffering the consequences of climate change, however they often carry lost-opportunity costs and may increase maintenance energy costs (Kearney, Shine & Porter 2009; Fuller *et al.* 2010; Briscoe *et al.* 2014; Cunningham, Martin & Hockey 2015). *Sceloporus* lizards were observed utilising cool, forested habitats at high elevations and delaying the time at which they emerged from their shelters when ambient temperatures were higher, however these adjustments resulted in reduced opportunities for foraging and reproduction (López-Alcaide *et al.* in press). Similarly, Southern Fiscals in the Kalahari suffered compromised foraging intakes on hotter days when they preferred the use of shady perches (Cunningham, Martin & Hockey 2015).

Very little is known about whether mammals are capable of such thermoregulation, but given their behavioural complexity, it is likely a factor that should be incorporated into climate change vulnerability assessments (Huey *et al.* 2012; Pacifici *et al.* 2015). A recent study revealed that koala bears are capable of withstanding hot temperatures by seeking out and resting against tree trunks that were cooler than the ambient air temperature, a strategy which could be important for all tree-dwelling species (Briscoe *et al.* 2014). Assessments of mammalian species are typically limited to those living in temperate climates (Walther *et al.* 2002), despite the high level of biodiversity in the tropics. In this study we investigate the potential for behavioural thermoregulation in a tropical mammalian carnivore, the African wild dog (*Lycaon pictus*).

The African wild dog is a social carnivore that lives in packs most commonly made up of five to 15 individuals (Creel & Creel 2002). Within each pack there are clear dominance hierarchies. Although the alpha pair monopolise reproduction, the pack cooperate to hunt, raise young and protect resources from kleptoparasitism (Fanshawe & Fitzgibbon 1993). Wild dogs were once distributed across most of Sub-Saharan Africa but have now disappeared from 25 of the 39 countries in which they were formerly recorded (Woodroffe, Ginsberg & Macdonald 1997). The species is listed as Endangered on The IUCN Red List because they are restricted to only 7% of their former distribution, with less than 7,000 individuals remaining (Woodroffe & Sillero-Zubiri 2012). Under standard trait-based climate change assessments, wild

dogs would appear to be at low risk of population decline or extinction. This is because they have excellent dispersal abilities, the ability to occupy diverse habitats and high reproductive rates (Creel & Creel 2002; Foden *et al.* 2013). Despite these traits, a recent study has shown that wild dogs suffer lower reproductive success through decreased recruitment at higher temperatures (Woodroffe, R., Groom, R. & McNutt, J.W. unpublished data). With temperatures predicted to increase throughout Africa more than the global average (Campbell *et al.* 2009), this could put the African wild dog at greater risk of extinction than previously expected.

Wild dogs show little capacity to adapt to climate change in either space or time. Although they range widely, with packs using an area of 650km² on average (Woodroffe & Ginsberg 1999), there is little potential for them to increase their geographic range size. This is because there is little suitable habitat left for them to move into as temperatures rise, and what habitat remains is severely fragmented by human populations, increasing the risk of persecution and disease transmission (Fanshawe, Frame & Ginsberg 2011). Likewise, wild dogs are unable to mitigate the decreased recruitment they experience at higher temperatures by shifting their breeding season. This is because they already breed in the coolest part of the year (Woodroffe, R., Groom, R. & McNutt, J.W. unpublished data). Given this inability to adapt in space or time, wild dogs are left with few options.

A recent study showed that wild dogs were less active on days when maximum daily temperatures were higher, and that they increased their night-time activity following hot days more on nights with higher moonlight levels (Rabaiotti, D. & Woodroffe, R. unpublished data). It seems the primary opportunity to cope with climate change is therefore to shift their daily activity periods to exploit lower morning and night-time temperatures. These main periods of activity are when the dogs hunt, and they typically occur at dawn and dusk, and occasionally at night-time, with little activity across the middle of the day (Fig. 1). Although this study showed a decrease in average daily activity on hotter days, it was unclear how the timings and duration of each of the individual periods of activity were affected by the environmental variables.

In this study, we explored the adaptive capacity of African wild dogs and their potential for behavioural thermoregulation by shifting morning activity periods earlier, evening

activity periods later, and becoming more nocturnal. We used Global Positioning System (GPS) collars with built-in accelerometers to regularly record a measure of activity. We then devised a method for categorising periods of activity into bouts. We predicted that on hot days, morning bouts would be earlier, evening bouts later and night-time bouts would be longer. We hypothesised that on more moonlit nights, wild dogs would be active for longer, but subsequently less active the following morning. Finally, we expected denning individuals to be active for longer in both the morning and evening to cope with the increased energetic demands of the pup-rearing period. Understanding the small-scale behavioural shifts that may occur in response to changes in temperature, and the factors that limit them, is integral to accurately assessing the climate change vulnerability of one of Africa's most endangered predators.

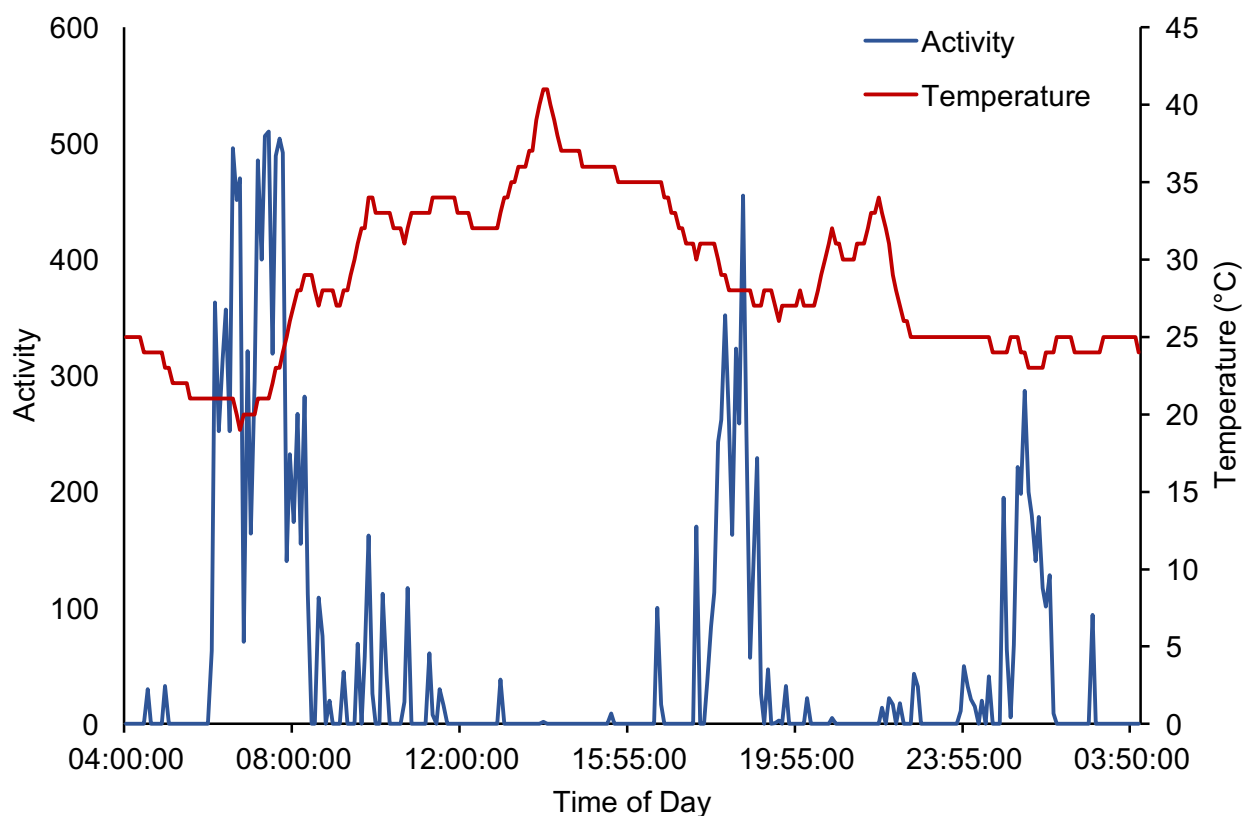


Figure 1: Graph showing how activity level varies with temperature across the course of a randomly selected day. Morning, evening and night-time peaks in activity coincide with times when temperature was lost.

Materials and Methods

Study Area

The study area covers the Laikipia District, east of the Great Rift Valley in Northern Kenya ($0^{\circ}6'N$, $37^{\circ}2'E$, 1800m ASL), spanning the Equator and parts of the neighbouring counties. Due to its location on the Equator, the study area experiences daily maximum temperatures ranging from 20-37°C. Rainfall ranges between 400 and 1000mm and varies seasonally and spatially (Thenya 2001). The habitat is largely semi-arid bushy grassland and savanna. The primary land uses are subsistence pastoralism, commercial ranching and tourism, with lower wild dog densities on community lands than commercial ranches (Woodroffe 2011). The study area is home to the sixth largest wild dog population in the world (Woodroffe 2011b).

Data Collection

Data for this study were collected between January 2011 and January 2017 from 19 wild dogs from several different packs. The dogs were fitted with Global Positioning System (GPS) collars with built-in accelerometers (Fig.2). Details of capture and



Figure 2: Image displaying the GPS-collars fitted to the dogs. Photo:
Helen O'Neill.

handling methods are provided in Woodroffe 2011b. The collars recorded acceleration along two axes on a scale from zero to 255 every five minutes. The two acceleration measurements were summed to calculate the activity variable for each five-minutely time-point.

We obtained detailed weather information from the local weather station at Mpala Research Centre (0°20'N, 36°53'E). We selected daily maximum temperature and daily rainfall as weather variables that could potentially explain wild dog activity patterns. Sunrise, sunset, moonrise and moonset times, and data on the proportion of the moon illuminated were accessed via the US Naval Observatory (USNO). These variables were selected based on literature review (Woodroffe 2011b; Cozzi *et al.* 2012; Woodroffe, R., Groom, R. & McNutt, J.W. unpublished data). We first calculated the hours of overlap between “night-time” (the time between sunset and the following sunrise) and the time the moon was in the sky. This number was then multiplied by the percentage illumination of the moon to give a moonlight variable that combined both how long the moon was present per night and how bright it was.

We included the status of the pack the individual dog belonged to as a biological variable that could potentially explain activity patterns. There were three possible states – denning (caring for pups at the den site), dispersing (newly mature individuals in search of mates and territories) and resident (this is the ‘typical’ state, packs reside within their home range but are not confined to a den). The dates the dogs were resident, denning or dispersing were determined by monitoring packs both through visual observations from vehicles and using the GPS collars.

Definition of a “bout” of activity

Before analysing the data, we needed to define what a “bout” of activity is and more specifically decide how to determine the start and end points of a bout. Martin and Bateson 1997 defined bouts as “behaviour patterns occurring in temporal clusters” and in this case, we were interested in bouts of a single behavioural state, where “the same relatively prolonged behaviour pattern occurs continuously for a period”. The behaviour pattern we were interested in was activity. We graphically visualised several random days of data to establish what the typical daily activity profile looked like. This

led us to determine the start point of a bout as any time the individual's activity went from zero to a value greater than zero, and the stop point as any time the individual's activity went from greater than zero to three consecutive recordings of zero activity. From the start and stop points, we calculated bout duration and the total amount of activity occurring in the bout. We then calculated the intensity of the bout – the mean amount of activity per unit of time (the total activity occurring in the bout was divided by the bout duration). Given the prolonged nature of wild dog activity periods, we excluded bouts from our analyses that were shorter than 20 minutes in duration because these bouts would not have corresponded to the main peaks in activity in which we were interested.

Categorisation of bouts

To categorise bouts based on the time of day they took place, we needed to determine two time windows within which the start and stop points had to occur to qualify for each type of bout. First, we looked at histograms of the frequencies of start and stop times for bouts longer than 20 minutes, and compared these for bouts with different minimum total activity levels (Fig.3). In addition to the condition on duration, we decided to only include bouts with total activity over 500. Setting the minimum total activity to 500

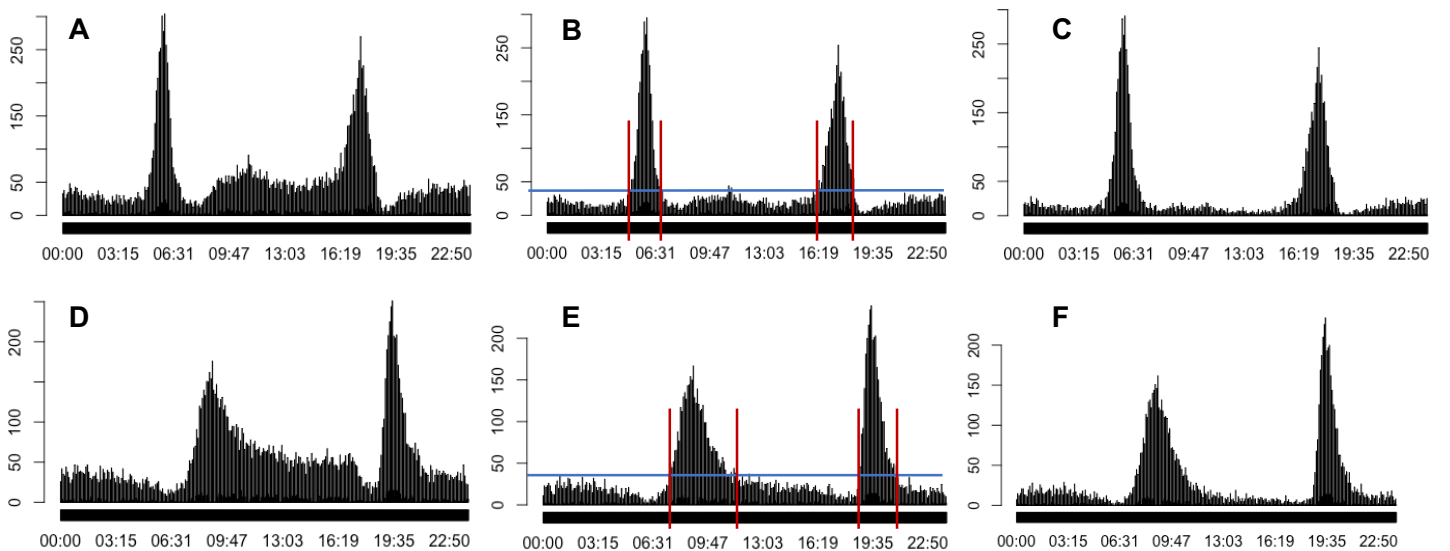


Figure 3: Frequencies of Start times (A-C) and Stop times (D-F) for bouts with minimum total activity of 200 (A and D), 500 (B and E) and 1000 (C and F). Blue lines at frequency of 30. Red lines demarcating where peaks in frequency begin and end.

allowed us to more clearly see the most frequent bout start and stop times. This eliminated the large tails before and after peaks present when 200 was the minimum total activity (which likely reflected socialising and greeting, not hunting) and ensured more bouts were captured than when 1000 was the minimum total activity while still isolating the peaks.

Second, we needed to determine at what times the peaks in frequency of Start and Stop times begin and end. From the histograms, we identified that the peaks begin when frequency became greater than 30 and end when frequency subsequently dropped below 30 (as shown by the blue and red lines on Fig. 3B and Fig. 3E). We made a vector of the frequency of each bin and then extracted the row numbers between which frequency was greater than 30. We then calculated the minute of the day that corresponded to these row numbers to get the beginning and end points for the peaks in Start and Stop time frequency.

From Fig. 3B and Fig. 3E, we identified two time windows within which most Start times occurred and two time windows within which most Stop times occurred respectively. The first one in each figure is in the morning and the second in the evening. Hence, these four time windows were used to categorise morning and evening bouts. We then used these timings to generate another four time windows to categorise daytime and night-time bouts. Table 1 lists the exact timings used for categorisation.

Table 1: Start and stop time periods used to categorise bouts.

Type of Bout	Start Between			Stop Between	
Morning	04:55:39	06:56:04	AND	07:30:41	12:51:33
Daytime	06:56:05	16:01:54	AND	12:51:34	18:47:02
Evening	16:01:55	18:26:52	AND	18:47:03	21:06:56
Night-time	18:26:53	04:55:38	AND	21:06:57	07:30:40

A total of 11,992 bouts were recorded in the study, of which 9,570 fit into these four categories. Bouts that did not fit into one of these categories were assigned to one of 11 other categories, for example, Late Morning and Early Evening. These bouts were

subsequently excluded from the dataset because they are infrequent and unlikely to be informative to our study.

We subsequently removed all daytime bouts from our final analyses. Although they accounted for 10-15% of the total number of bouts, they only accounted for 2-4% of the total activity (Table 2, Fig. 4). This means it was unlikely that these activity bouts were hunts and hence were not of interest in our study.

Table 2: Total number of types of bout and total activity within those bouts split by dog status.

	Resident		Denning		Dispersing	
Type of Bout	Number of Bouts	Total Activity in Bouts	Number of Bouts	Total Activity in Bouts	Number of Bouts	Total Activity in Bouts
Morning	2365	15631651	603	6154964	134	1378546
Daytime	669	775242	264	433277	39	63373
Evening	2248	9025611	588	3667664	129	658732
Night-time	1387	4765514	340	1357525	100	610317
Total	6669	30198018	1795	11613430	402	710968

Models and Statistical Analysis

We used Generalised Linear Models (GLMs) to investigate the effects of maximum daily temperature, rainfall, moonlight and denning status on bout duration, intensity and start and stop time. We used binomial GLMs to investigate the effects of the predictor variables on the likelihood of occurrence of each type of bout. Models were created separately for morning, evening and night-time bouts. We examined the interaction between maximum daily temperature and rainfall. We dropped interactions and variables from the models in a stepwise fashion until only those with $P < 0.05$ were left. We tested normality assumptions of the models using the Q-Q diagnostic plot. Analyses were carried out in R Studio version 1.0.136 (RStudio Team 2016) using the packages ‘chron’ (James & Hornik 2015) and ‘lubridate’ (Grolemund & Wickham 2011) to handle dates and times.

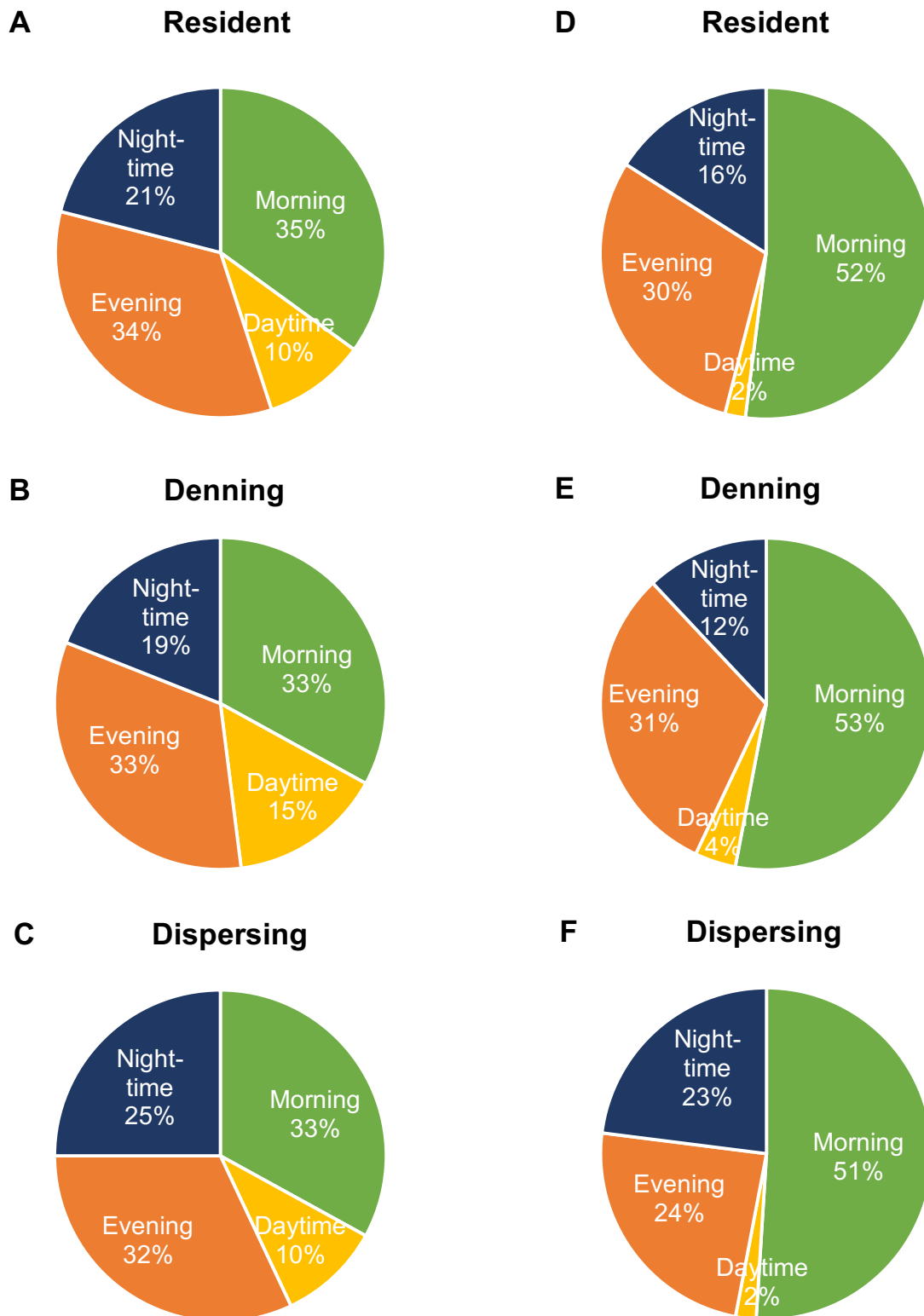


Figure 4: Comparison between the proportion of the total number of bouts per type (A-C) and the proportion of the total activity per type of bout (D-F) for each state.

Results

Table 3 summarises all directional effects of the predictor variables on bout duration, start time, stop time and intensity, and Table 4 summarises all directional effects of the predictor variables on the likelihood of bout occurrence. Estimated effects and significances of predictor variables can be found in Supplementary Information.

Effect of maximum daily temperature

On hotter days, morning bouts were shorter (Fig. 5) but this effect was reduced on days with higher rainfall. Morning bouts both started and ended earlier on hotter days, but their stop times were brought further forward than their start times. Morning bouts were also less intense but this effect was reduced on days when there was higher rainfall. On hotter days, evening bouts were shorter. This was because they started later but ended at the same time. They were also less intense on hotter days. Night-time bouts were longer and more intense following hot days, but there was no significant difference in start and stop times.

Temperature did not affect the likelihood of occurrence of morning bouts, but evening bouts were less likely to occur on hotter days. Night-time bouts were more likely to occur following hotter days but this effect was reduced on days with more rainfall.

Effect of daily rainfall

On days when there was more rainfall, the negative association between temperature and duration, and temperature and intensity in morning bouts was modulated. On days with more rainfall, morning bouts stopped later. Evening bouts were longer on rainy days because they started earlier but ended at the same time. They were also more intense on days with more rainfall. Following days with more rainfall, night-time bouts were shorter because they started at the same time but ended earlier. Night-time bouts were also less intense following days with more rainfall.

Rainfall did not have a significant effect on the likelihood of occurrence of either morning or evening bouts. However, there was a significant negative interaction

between temperature and rainfall for night-time bouts – rainfall modulated the positive association between temperature and likelihood of occurrence.

Effect of moonlight

On mornings following more moonlit nights, bouts were shorter (Fig. 6). This was because they both started later and ended earlier. Morning bouts were also less intense following more moonlit nights. Evening bouts were shorter preceding more moonlit nights. This was because they both started later and ended earlier. Evening bouts were also less intense before more moonlit nights. On more moonlit nights, night-time bouts were longer. This was because they both started and ended later, but there was a greater positive effect of moonlight on stop time than start time. Night-time bouts were also more intense on more moonlit nights.

Morning bouts were less likely to occur following more moonlit nights, and evening bouts were less likely to occur preceding more moonlit nights. Night-time bouts were more likely to occur on more moonlit nights.

Effect of pack status

Individuals from denning packs were active for longer in the morning than individuals from resident packs. This was because they both started earlier and ended later. Morning bouts were also more intense when denning than when resident. Dispersing individuals were active earlier in the morning than resident individuals but stopped at the same time. Morning bouts of dispersing individuals were more intense than those of resident individuals. Individuals from denning packs were active for longer in the evening than individuals from resident packs. This was because they both started earlier and ended later. Evening bouts were also more intense when denning than when resident. There were no significant differences between the evening bouts of individuals from resident packs and individuals that were dispersing. There were no significant differences between the night-time bouts of individuals from resident packs and individuals that were dispersing. Dispersing individuals were active for longer during the night than resident individuals. This was because they started earlier but

stopped at the same time. Night-time bouts were also more intense for dispersing individuals than for those belonging to resident packs.

There was no significant difference in the likelihood of occurrence of morning bouts between individuals from denning packs and those from resident packs. Dispersing individuals, however, were less likely to be active in the morning than resident individuals. Individuals from denning packs were less likely to be active in the evening than resident individuals, whereas, there was no significant difference in the likelihood of occurrence of morning bouts between dispersing individuals and those from resident packs. There was no significant difference in the likelihood of occurrence of night-time bouts between resident individuals and denning or dispersing individuals.

Table 3: Directions of relationships between components of activity bouts and predictor variables.

Asterisks indicate relationships where $P < 0.05$. + and – symbols refer to the directions of association in the statistical models which best fit the data.

Type of Bout	Bout Component	Daily Maximum Temperature	Daily Rainfall	Moonlight	Dog Status (compared to resident)	
					Denning	Dispersing
Morning	Duration	—*	—	—*	+*	+
		*Interaction: the more rainfall, the weaker the effect of increased temperature				
	Start Time	—*	+	+*	—*	—*
	Stop Time	—*	+*	—*	+*	—
	Intensity	—	+*	—*	+*	+*
		*Interaction: the more rainfall, the weaker the effect of increased temperature				
Evening	Duration	—*	+*	—*	+*	—
	Start Time	+*	—*	+*	—*	+
	Stop Time	—	+	—*	+*	+
	Intensity	—*	+*	—*	+*	—
Night-time	Duration	+*	—*	+*	—	+*
	Start Time	+	—	+*	—	—*
	Stop Time	+	—*	+*	—	—
	Intensity	+*	—*	+*	—	+*

Table 4: Directions of relationships between likelihood of types of bout and predictor variables. Asterisks indicate relationships where $P < 0.05$. + and – symbols refer to the directions of association in the statistical models which best fit the data.

Type of Bout	Daily Maximum Temperature	Daily Rainfall	Moonlight	Dog Status (compared to resident)	
				Denning	Dispersing
Morning	—	—	—*	—	—*
Evening	—*	—	—*	—*	+
Night-time	+	+	+	+	—
	*Interaction: the more rainfall, the weaker the effect of increased temperature				

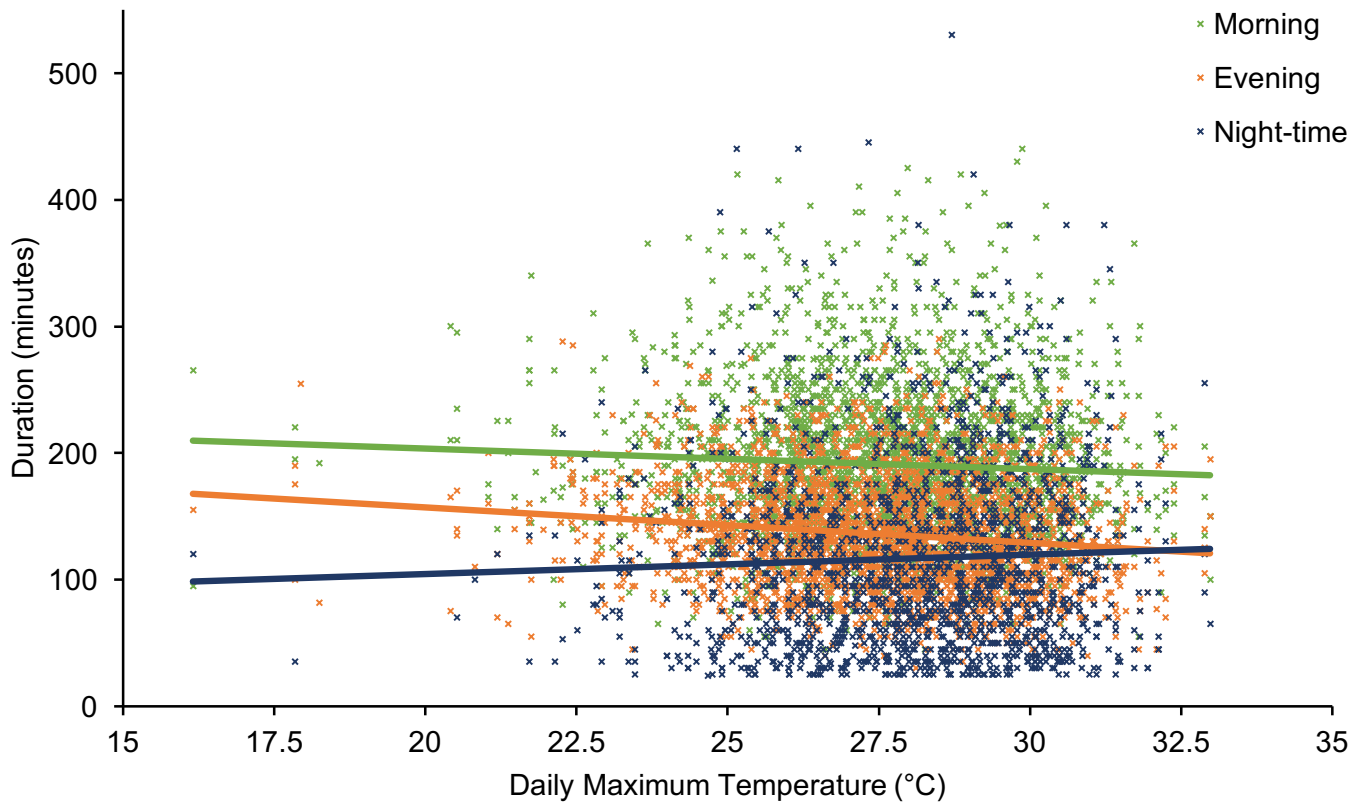


Figure 5: Graph of bout duration across a range of daily maximum temperature levels for each type of bout.

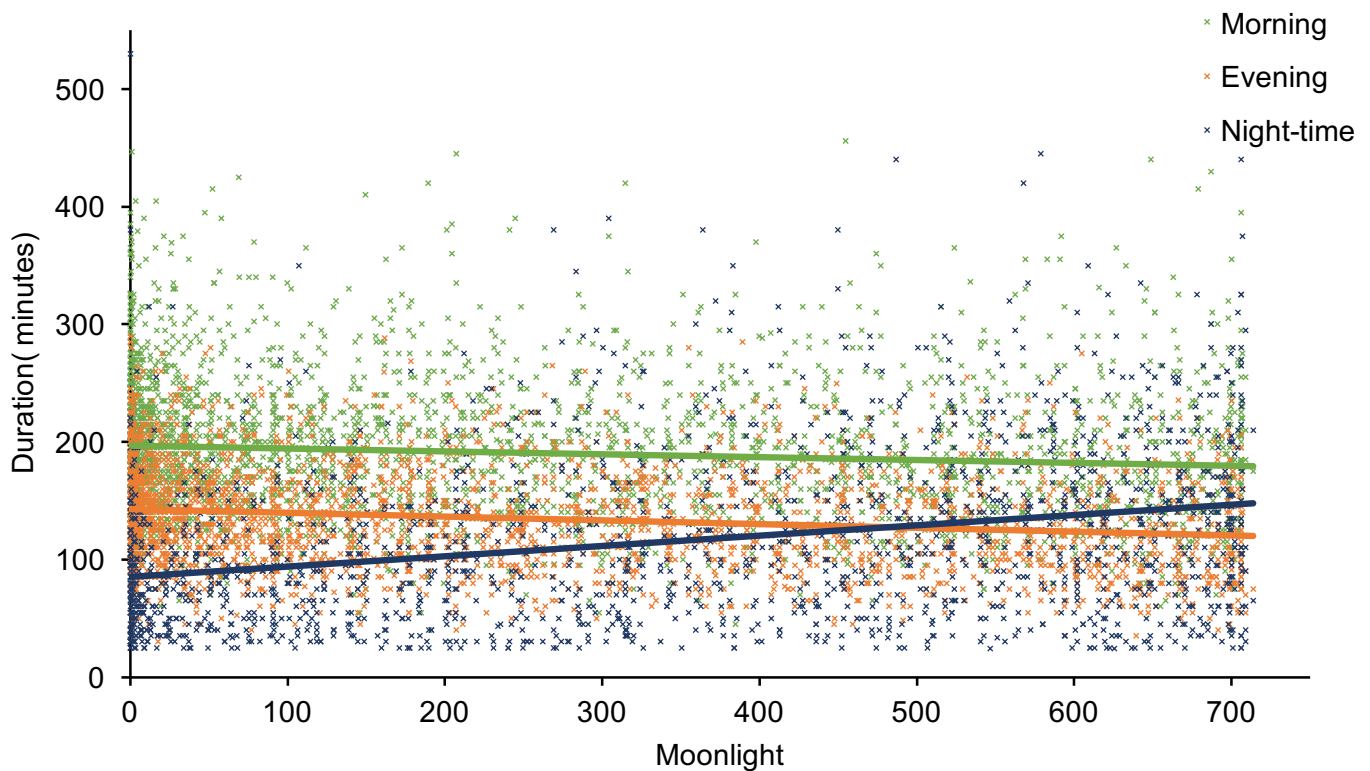


Figure 6: Graph of bout duration across a range of moonlight levels for each type of bout.

Discussion

On hotter days, wild dogs were active for less time and at lower intensities in both the morning and evening. In the morning, these effects were reduced on days when there was more rainfall. On hotter days evening bouts were less likely to occur, whereas night-time bouts were more likely. This effect was also reduced on days with more rainfall. We found that dogs compensate to a certain extent for the loss of activity on hotter days by being active for longer and at higher intensities at night. This compensatory nocturnal activity was, however, reduced when the pack was denning compared to when they were resident. Moonlight was a limiting factor of both duration and intensity of activity. Individuals from denning packs were active for longer and at higher intensities than resident individuals in both the morning and the evening. This was in contrast with dispersing individuals, who were active for longer and at higher intensities than resident individuals at night.

Overall, our data suggest that wild dogs are only able to minimally compensate for higher maximum daily temperatures. We showed that wild dogs are capable of making small-scale shifts in the timings of their periods of activity. In response to higher maximum daily temperatures, morning bouts shift earlier and evening bouts shift later to maximise the amount of time the dogs can spend hunting, by exploiting lower morning and evening temperatures. However, it seems that there are limits to the amount of time by which these bouts can vary. The standard deviations of the mean start and stop times for each type of bout (Table 5, Fig. 7) reveal that there are indeed differences in the possible variations in bout timings. Morning bouts have a small standard deviation in start time but larger standard deviation in stop time. This suggests that irrespective of the daily maximum temperature, wild dogs will only be able to vary their start time marginally, but they may be able to vary their stop time to a greater extent depending on temperature and rainfall. This is perhaps to do with always starting their activity while the temperature is lowest, as the sun is rising before it has time to warm the ground. Most evening bouts seem to both start and stop within narrow windows of time, suggesting there is little adaptive capacity in evening periods of activity. This could again be to do with fitting in their activity around when the temperature is lowest – after the sun has set but before terrestrial radiation increases surface temperature again. Night-time start and stop times are much more variable which could be explained by the more constant, lower temperatures experienced over-night while the surface of the Earth is in radiation debt. This would explain the way the peaks of activity fit with the lows in temperature in Fig.1. If this is the case, then there is very little potential for climate change adaptation by shifting periods of activity during the day, and notwithstanding the potential variation in timing of night-time bouts, the duration and intensity of these bouts would still be constrained by moonlight.

Table 5: Mean start and stop times and their standard deviations for each type of bout.

Type of Bout	Mean		Standard Deviation	
	Start	Stop	Start	Stop
Morning	05:54:48	09:06:04	± 00:24:15	± 00:55:56
Evening	17:25:49	19:41:39	± 00:31:00	± 00:30:03
Night-time	00:01:36	00:44:02	± 01:16:26	± 01:15:11

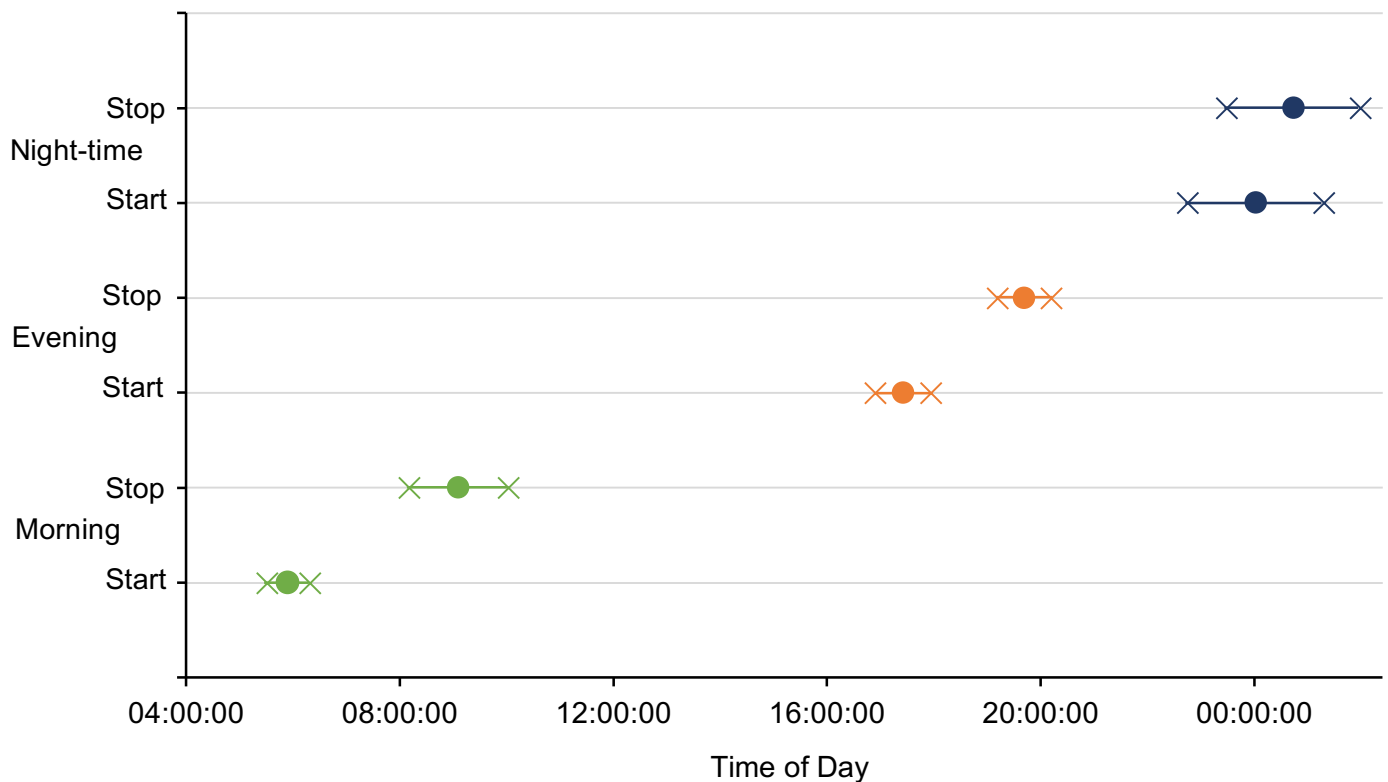


Figure 7: Graph of mean start and stop times (dots) and their standard deviations (crosses) for each type of bout.

Despite these small shifts in timings, bout durations were still shorter on hotter days. This means wild dogs are suffering from an overall decrease in the amount of time they can spend hunting, and hence a likely reduction in food intake on hotter days. The interaction between maximum daily temperature and rainfall suggests that higher rainfall may be able to mitigate the loss of activity on hotter days. However, this effect is likely due to an increase in cloud cover providing some respite from the sun, and not a direct effect of rainfall. Not only are temperatures predicted to increase across Africa, but rainfall is predicted to decrease (Campbell *et al.* 2009), meaning rainfall will provide even less of a buffer against increasing temperatures in the future.

The results of our study show that compensatory nocturnal activity following hot days is constrained by both moonlight and denning. This means it provides little opportunity for long-term climate change adaptation. We found that moonlight had a significant effect on both bout duration and intensity during the night. This was also found to be the case in a previous study on nocturnal activity in African wild dogs (Cozzi *et al.*

2012). While wild dog nocturnal activity varied with the lunar cycle, that of lions and hyenas remained constant. Despite wild dogs being labelled as crepuscular in nature, there was a large degree of temporal overlap between wild dogs, lions and hyenas. This suggests that wild dogs suffer may from poor vision, with which it is insufficient to hunt at night without moonlight. This poor vision may be problematic on nights with little moonlight available if wild dogs were to encounter other predators. Hence, not hunting when there is little moonlight available may be a form of pre-emptive competition avoidance to reduce the risk of mortality and kleptoparasitism.

Despite individuals belonging to denning packs being more active than residents in terms of duration and intensity both in the morning and in the evening, denning individuals were not more active at night. This is likely due to the increased need to protect the pups at night when most other predators are more active. If denning packs are unable to increase their nocturnal activity following hot days, they will have less opportunities to hunt and may be unable to meet the increased energy demands of feeding the pups as well as themselves. This is likely to lead to decreased recruitment and pup survival at higher temperatures (Woodroffe, R., Groom, R. & McNutt, J.W. unpublished data).

Potential Climate Change Adaptation in African Wild Dogs

Species' adaptive capacity can be conferred via three non-exclusive axes – space, time and self (Huey *et al.* 2012; Foden *et al.* 2013; Pacifici *et al.* 2015). Wild dogs are unable to adapt by shifting their geographic range as most suitable habitat has been destroyed or fragmented by human populations (Creel & Creel 2002). Likewise, wild dogs are unable to shift their phenology and breed earlier as they are already breeding in the coolest part of the year. This means the primary opportunity for climate change adaptation would be in self – either through changes in physiology or behaviour. Our study has shown that there is also very little potential for behavioural thermoregulation. This means the fate of the African wild dog is in far more danger than simple trait-based assessments would suggest (Foden *et al.* 2013). This leaves very few options for conservation practitioners, and it is likely that wild dogs will require conservation strategies targeted on areas predicted to experience less warming in the future. These strategies may include improving corridor connections between such areas that will

remain more stable in the coming years. This should help expand suitable habitat available to wild dogs so that they are able to utilise a larger range and hopefully prevent species decline and extinction.

Wider implications

Given the complexity of mammalian behaviour, one might assume this would confer high adaptive capacity. However, the effects of temperature on behaviour and behavioural responses to climate change are poorly understood and data on this topic is scarce. Our exploration of how temperature affects periods of activity in African wild dogs provides some much-needed information on the extent to which mammals can use behavioural thermoregulation to cope with the rapid rate of increasing temperatures. More studies of this kind into behavioural shifts and the fitness trade-offs they involve are critical. The findings need to be incorporated into climate change vulnerability assessments to more accurately predict climate change impacts, and subsequently plan conservation strategy more effectively.

Acknowledgements

I would like to thank my supervisor, Professor Rosie Woodroffe for her support throughout the project, and Daniella Rabaiotti for her invaluable advice and statistical help.

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Supplementary Information

GLM outputs of the final models, with only significant terms remaining, for each bout component split by type of bout can be found below.

Morning Bouts

Duration:

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	242.972028	17.845442	13.615	< 2e-16	***
mornings\$MaxTemp	-1.871630	0.634527	-2.950	0.00321	**
mornings\$Rainfall	-6.581089	3.621051	-1.817	0.06927	.
mornings\$Moonlight_NB	-0.022636	0.005022	-4.508	6.87e-06	***
mornings\$StatusDenning	16.348709	2.784597	5.871	4.93e-09	***
mornings\$StatusDispersing	5.843680	5.707758	1.024	0.30603	
mornings\$MaxTemp:mornings\$Rainfall	0.269692	0.135544	1.990	0.04674	*

Intensity:

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	50.012932	3.858417	12.962	< 2e-16	***
mornings\$MaxTemp	-0.124660	0.137193	-0.909	0.363629	
mornings\$Rainfall	1.649493	0.782918	2.107	0.035234	*
mornings\$Moonlight_NB	-0.002445	0.001086	-2.252	0.024423	*
mornings\$StatusDenning	3.228200	0.602066	5.362	9.02e-08	***
mornings\$StatusDispersing	4.270047	1.234092	3.460	0.000549	***
mornings\$MaxTemp:mornings\$Rainfall	-0.059166	0.029306	-2.019	0.043610	*

Start Time

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	41.587505	6.610490	6.291	3.73e-10	***
mornings\$MaxTemp	-2.617007	0.235130	-11.130	< 2e-16	***
mornings\$Moonlight_NB	0.006911	0.002013	3.433	0.000608	***
mornings\$StatusDenning	-4.423750	1.115198	-3.967	7.50e-05	***
mornings\$StatusDispersing	-11.501385	2.287727	-5.027	5.34e-07	***

Stop Time

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	270.137462	15.840177	17.054	< 2e-16	***
mornings\$MaxTemp	-3.974932	0.561512	-7.079	1.90e-12	***
mornings\$Rainfall	0.789181	0.240420	3.283	0.00104	**
mornings\$Moonlight_NB	-0.015618	0.004749	-3.288	0.00102	**
mornings\$StatusDenning	11.704471	2.630643	4.449	9.01e-06	***
mornings\$StatusDispersing	-5.995843	5.395735	-1.111	0.26659	

Evening Bouts

Duration

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	210.50734	12.25312	17.180	< 2e-16	***
evenings\$MaxTemp	-2.47204	0.43545	-5.677	1.54e-08	***
evenings\$Rainfall	0.50250	0.18268	2.751	0.00599	**
evenings\$Moonlight	-0.03524	0.00371	-9.499	< 2e-16	***
evenings\$StatusDenning	8.07627	2.03750	3.964	7.60e-05	***
evenings\$StatusDispersing	-2.55249	4.03274	-0.633	0.52683	

Intensity

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	70.021278	3.956845	17.696	< 2e-16	***
evenings\$MaxTemp	-1.089928	0.140617	-7.751	1.35e-14	***
evenings\$Rainfall	0.208518	0.058993	3.535	0.000416	***
evenings\$Moonlight	-0.004977	0.001198	-4.155	3.38e-05	***
evenings\$StatusDenning	2.075285	0.657960	3.154	0.001630	**
evenings\$StatusDispersing	-0.534999	1.302273	-0.411	0.681243	

Start Time

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	-1.313e+02	8.373e+00	-15.685	< 2e-16	***
evenings\$MaxTemp	2.168e+00	2.975e-01	7.287	4.32e-13	***
evenings\$Rainfall	-3.938e-01	1.248e-01	-3.155	0.00163	**
evenings\$Moonlight	1.740e-02	2.535e-03	6.863	8.64e-12	***
evenings\$StatusDenning	-4.155e+00	1.392e+00	-2.984	0.00287	**
evenings\$StatusDispersing	2.646e+00	2.756e+00	0.960	0.33699	

Stop Time

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	70.849404	0.947677	74.761	< 2e-16	***
evenings\$Moonlight	-0.016730	0.002542	-6.582	5.66e-11	***
evenings\$StatusDenning	4.034293	1.400627	2.880	0.00401	**
evenings\$StatusDispersing	0.830040	2.674747	0.310	0.75634	

Night-time Bouts

Duration

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	18.85177	26.59233	0.709	0.47850	
nights\$MaxTemp	2.39431	0.92255	2.595	0.00955	**
nights\$Rainfall	-1.05128	0.47159	-2.229	0.02596	*
nights\$Moonlight	0.09012	0.00772	11.673	< 2e-16	***
nights\$StatusDenning	-6.71142	4.38584	-1.530	0.12619	
nights\$StatusDispersing	19.69599	8.54739	2.304	0.02136	*

Intensity

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	8.314351	6.069516	1.370	0.170960	
nights\$MaxTemp	0.632435	0.210566	3.003	0.002718	**
nights\$Rainfall	-0.370217	0.107637	-3.439	0.000601	***
nights\$Moonlight	0.022097	0.001762	12.541	< 2e-16	***
nights\$StatusDenning	-1.839218	1.001038	-1.837	0.066384	.
nights\$StatusDispersing	5.875102	1.950882	3.012	0.002648	**

Start Time

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	298.64997	6.58708	45.339	< 2e-16	***
nights\$Moonlight	0.06485	0.01462	4.436	9.85e-06	***
nights\$StatusDenning	-5.37517	8.47832	-0.634	0.5262	
nights\$StatusDispersing	-34.46161	15.55837	-2.215	0.0269	*

Stop Time

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	-336.1586	5.9395	-56.597	<2e-16	***
nights\$Rainfall	-1.7953	0.7713	-2.328	0.02	*
nights\$Moonlight	0.1603	0.0135	11.879	<2e-16	***

Binomial GLM outputs of the final models, with only significant terms remaining, for the likelihood of occurrence for each type of bout can be found below.

Morning Bouts

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	1.7627649	0.0796311	22.137	< 2e-16	***
occs\$Moonlight_NB	-0.0009681	0.0001955	-4.953	7.3e-07	***
occs\$StatusDenning	-0.2171319	0.1137754	-1.908	0.056336	.
occs\$StatusDispersing	-0.7839375	0.2276286	-3.444	0.000573	***

Evening Bouts

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	3.6837755	0.6609649	5.573	2.5e-08	***
occs\$MaxTemp	-0.0795973	0.0234211	-3.399	0.000677	***
occs\$Moonlight	-0.0007313	0.0001909	-3.830	0.000128	***
occs\$StatusDenning	-0.2647026	0.1091595	-2.425	0.015312	*
occs\$StatusDispersing	0.1008930	0.2802292	0.360	0.718819	

Night-time Bouts

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-6.6286274	0.6091478	-10.882	<2e-16	***
occs\$MaxTemp	0.1948307	0.0215337	9.048	<2e-16	***
occs\$Rainfall	0.2297444	0.1203425	1.909	0.0563	.
occs\$Moonlight	0.0029474	0.0001668	17.670	<2e-16	***
occs\$MaxTemp:occs\$Rainfall	-0.0089844	0.0044926	-2.000	0.0455	*