**Ambient temperature affects mammalian predator-prey interactions in an African savanna**

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# Abstract

1. Climate warming may alter predator-prey dynamics by changing predator attack speed and prey escape speed, and by impacting the daily activity rhythms and habitat use of both predators and prey. As there is no direct link between metabolic rates and temperature in endotherms, it is widely assumed that climate warming will not affect interactions between endothermic predators and prey.
2. This assumption ignores evidence that many endotherm species change their habitat use and behaviour at high temperatures. Moreover, predator-prey chases generate metabolic heat, which larger-bodied endotherms may be less able to dissipate, potentially altering chase outcomes at high ambient temperatures.
3. We investigated how ambient temperature impacted predator-prey interactions in a three-species system comprising one predator species, the African wild dog (*Lycaon pictus*), and two prey species, dikdik (*Madoqua guentheri*) and impala (*Aepyceros melampus*).
4. We predicted that African wild dogs would kill more impala at high ambient temperatures via three mechanisms. Firstly, we predicted that African wild dog activity would be reduced in the day when temperatures were higher due to increased radiant heat. Secondly, we predicted that all three species would seek shade at high temperatures, using closed habitat where impala face higher predation rates. Third, we predicted that difficulties of dissipating metabolic heat during chases at high ambient temperatures would affect impala (40kg) more than dikdiks (5kg).
5. Although prey habitat selection and wild dog activity patterns changed with temperature as predicted, we found that fewer, not more, wild dog scats contained impala remains when ambient temperatures were high. Wild dogs spent less time hunting on hot days and, consistent with models of optimal foraging under time constraints, appeared to select abundant, lower-value dikdiks over rarer but higher-value impala.
6. Our findings show that weather can influence predator-prey interactions among endotherms, and suggest that studies assuming otherwise should be interpreted with caution.

**Keywords:** African wild dog;antipredator behaviour; climate change; dikdik; habitat selection; impala; predation; thermal tolerance

# Introduction

Climate change has far-reaching impacts on both species and ecosystems (Parmesan & Yohe 2003). Meta-analyses suggest that many climate impacts on individual species operate indirectly, through their effects on species interactions such as competition, herbivory, predation, and parasitism (Cahill *et al.* 2012; Ockendon *et al.* 2014). As weather patterns will shift under novel climate regimes, understanding how ambient temperature and other abiotic processes influence species interactions will become critical to wildlife conservation in the coming decades.

Climate is particularly critical for ectothermic species, which rely primarily on environmental temperatures to regulate their body temperature, meaning that high ambient temperatures directly lead to changes in physiology, movement and behaviour. These individual behavioural shifts can drive climate impacts on species interactions. For example, high ambient temperatures allow ectotherms to move more rapidly, potentially making them more efficient predators and more challenging prey, with cascading consequences for community structure (Dell, Pawar & Savage 2014). It is usually assumed that ambient temperature has no similar impacts on predation involving endotherms (e.g., Dell, Pawar & Savage 2014; Harfoot *et al.* 2014); however, birds and mammals may respond to high ambient temperatures by curtailing their foraging time (Ricklefs & Hainsworth 1968; Quaglietta, Mira & Boitani 2018), switching from diurnal to nocturnal foraging (Levy *et al.* 2018), selecting different habitats and seeking cooler microclimates (Austin 1976; Pigeon *et al.* 2016), choosing different foods (Doolan & Macdonald 1996; Garcia-Heras *et al.* 2017), and increasing their water intake (Veldhuis et al 2019), all of which are likely to influence their impacts on the species that they consume, or that consume them. It has been suggested that predator-prey interactions involving large-bodied endotherms might be especially sensitive to rising environmental temperatures, because the low surface-area-to-volume ratios of large animals may make it difficult to dissipate heat generated by pursuing or avoiding predation (Speakman & Krol 2010; Creel *et al.* 2016). Hence, with respect to the outcome of predator-prey interactions, high ambient temperatures might favour endothermic prey that are smaller than their endothermic predators, as the predators’ large body size would mean that they overheat faster than their smaller prey, leading to decreased predation rates on smaller prey species. Similarly, high ambient temperatures may also benefit endothermic predators that are smaller than their endothermic prey, as the large bodied prey would overheat faster than the smaller bodied predator, leading to shorter chase times and higher hunting success (Creel *et al.* 2016).

This theory, however, ignores the impact of evaporative cooling. Unlike small bodied species, such as rodents, which rely on dry heat loss due to their inability to store sufficient water, larger mammal species utilise evaporative cooling through both panting and sweating in order to dissipate heat load built up during exercise (Taylor 1977). In fact, it has been found that larger antelope species lose body heat from chases through sweating, whereas smaller antelope species store this heat (Taylor and Lyman 1972). Therefore this theory is likely to have limited applications outside of small mammal species, and it may be that larger species can more easily dissipate heat through evaporative cooling and as a result may be less likely to overheat during chases. Predation by and on large-bodied endotherms can have cascading effects on community structure (e.g. Hebblewhite et al 2005), hence any effect of temperature on endotherm predation might have broader impacts on ecological communities.

Using a three-species predator-prey system in an African savanna, we measured the impact of ambient temperature on predator-prey interactions. Specifically, we examined how ambient temperature affected the habitat use and activity patterns of a small-bodied prey species (the 5kg Guenther’s dikdik *Madoqua guentheri*), a larger-bodied prey species (the 40kg impala *Aepyceros melampus*), and their shared predator (the 23kg African wild dog *Lycaon pictus*). At our study site in Kenya, impala and dikdiks are the two most abundant ungulates, and their browsing shapes plant communities (Ford *et al.* 2014; Ford *et al.* 2015). Wild dogs are crepuscular, and hunt by running prey down (Creel & Creel 1995); dikdiks and impala together comprise 82% of the prey biomass that wild dogs consume at our study site (Woodroffe et al. 2007).

All three species in the study are adapted to regulate body heat at high ambient temperatures: both wild dogs and impala have been found to engage in high intensity activity at temperatures of up to 41°C with little to no rise in body temperature (Maloiy and Hopcraft 1970, Taylor et al 1971), and dikdik have been found to maintain a constant body temperature at air temperatures of up to 44°C (Kamau 1988). African wild dogs, impala and dikdik have all been found to use evaporative cooling to dissipate heat during high intensity activity. African wild dogs (Taylor et al 1971) and dikdik (Kamau 1988) dissipate heat during exercise primarily using panting, however impala primarily use sweating as the mechanism through which they lose body heat during high intensity chases (Maloiy and Hopcraft 1970). We evaluated three hypotheses about the impacts of ambient temperature on predation by wild dogs on impala and dikdik (Table 1). First, we hypothesised that predator-prey interactions would be impacted by reduced predator activity on hot days (Table 1). Previously, we have shown that wild dog activity declines as ambient temperatures increase (Woodroffe et al 2017, Rabaiotti & Woodroffe 2019), which may reflect shorter hunting periods (Woodroffe 2011b). Optimal foraging theory suggests that, when foraging time is limited, individuals should accept lower-value prey, rather than continuing to search for higher-value prey (Lucas 1983). Therefore, we predicted that, if wild dogs had reduced foraging time, they would increase predation on dikdik (which are encountered more frequently but are too small to feed a whole pack) over impala, which are larger but encountered less frequently (Woodroffe *et al.* 2007). We term this, Hypothesis 1, the ‘reduced daytime foraging hypothesis’.

Second, we quantified whether habitat selection by both predators and prey might be affected by ambient temperatures, with consequences for predation. Many large mammals select shade in hotter weather (Mole *et al.* 2016; Pigeon *et al.* 2016), and we predicted that wild dogs, impala, and dikdik would do the same (Table 1). We would expect to see the greatest shift into denser woody cover by impala due to their body size, as it would be expected that larger animals which are more reliant on sweating would adjust their spatiotemporal patterns more in response to high temperatures (Veldhuis et al 2019). Further, we predicted that such a change would increase predation by wild dogs on impala, since impala face higher *per capita* predation rates in habitats characterised by higher woody cover (and thus shade; Ford *et al.* 2014). We term this, Hypothesis 2, the ‘shade-seeking hypothesis’.

Finally, we explored the potential consequences of both predators and prey overheating during chases. Creel *et al.* (2016) suggested that, during chases, wild dogs would overheat more slowly than their larger-bodied prey, leading to shorter and more successful chases at higher ambient temperatures. By extension, this would mean that wild dogs overheat less rapidly than impala but more rapidly than dikdiks, leading to increased predation on impala relative to dikdiks at higher ambient temperatures (Table 1). We termed this, Hypothesis 3, the ‘prey overheating hypothesis’.

These hypothesised behavioural responses to high ambient temperatures generated contrasting sets of predictions about trophic interactions between wild dogs, impala, and dikdik (summarised in Table 1). By testing these predictions, we explored the behavioural mechanisms underlying whether, and how, ambient temperature influenced interactions between predators and prey, in an attempt to evaluate how climate change might affect this ecosystem through predator-prey interactions.

# Methods

## Study area

The focal area for this study was the Mpala Conservancy, Kenya (0°17’ N, 36°53’ E), a 200 km2 area of semi-arid savanna managed jointly for livestock production and wildlife conservation. Mpala experiences little seasonal variation in ambient temperature; daily maximum temperature ranges from 20-37°C, and mean annual rainfall is 590mm, varying substantially both within and between years (Caylor, Gitonga & Martins 2017).

Mpala hosts 22 species of wild ungulate, of which dikdiks and impala are the two most abundant (Ford *et al.* 2015), at 139 individuals per km2 and 20.3 individuals per km2 respectively (Augustine et al 2004). Mpala also supports five species of large carnivore in addition to wild dogs: lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*), and striped hyaena (*Hyaena hyaena*), all of which have dietary overlap with wild dogs (Frank, Woodroffe & Ogada 2005).

## Data collection

We used Global Positioning System (GPS) collars to measure daytime and night-time activity, movement, and habitat use. GPS-collars (Savannah Tracking Ltd, Nairobi, Kenya) were fitted to 20 adult female impala (each from a different herd) between May and June 2011, as described in Ford *et al.* (2014). Each impala GPS-collar recorded a location every 20 minutes, for an average of 245 days. Likewise, GPS-collars (Savannah Tracking Ltd, Nairobi, Kenya) were fitted to 15 adult female dikdik between July 2010 and September 2011, as described in Ford & Goheen (2015). Each dikdik GPS-collar recorded a location every 10 minutes, for 18 days on average. Additionally, GPS collars (Vectronic Aerospace GmbH, Berlin, Germany) were fitted to 18 wild dogs in 13 packs between 2011 and 2016, using capture methods described in Woodroffe (2011a); all of these packs had home ranges overlapping Mpala, although none remained on Mpala year-round. Data were collected from one collar per pack at any one time. Each wild dog GPS-collar recorded locations at 01:00, 06:30, 07:00, 07:30, 08:00, 13:00, 18:00, 18:30, 19:30, and also recorded average acceleration in two planes (on a scale of 0 to 255 units) every five minutes, for 218 days on average.

We used faecal analysis to quantify the relative frequency of predation by wild dogs on impala and dikdik. Wild dog scats were collected during 2001-2004 across a 5,700km2 study area which included Mpala Conservancy, and analysed as described in Woodroffe *et al.* (2007). We avoided pseudoreplication by including only one randomly-selected scat collected from each pack on each occasion (Woodroffe *et al.* 2007). Because the GPS-collar data were collected ≥7 years after the scat samples, they came from the descendants of the individuals which deposited the scats. There were no major shifts in temperature and rainfall between the two time periods, however (Table S1).

Daily rainfall, daily maximum ambient temperature, and mean daily solar radiation; were collected from a weather station at Mpala Research Centre (Caylor, Gitonga & Martins 2017). Data on the timing of sunrise and sunset were taken from the *R* package *suncalc* (Agafonkin & Thieurmel 2017). Moonlight was calculated by multiplying percentage illumination by the number of hours the moon was in the sky between sunset and sunrise. Finally, we used GPS-collar data to identify periods when wild dog packs were denning (raising pups in a den, recognisable from the movement path which shows a “starburst” pattern of repeat visits to the same location, Woodroffe *et al* 2017) as activity levels have been shown to increase during this period (Woodroffe *et al* 2017). Mornings and evenings where individuals were babysitting (guarding the pups and therefore not hunting) were defined as days where the individual did not move from the den site during the morning or evening – these were removed from the analyses.

## Identifying hunting periods of wild dogs

To estimate the time that wild dogs spent hunting, and to compare prey and predator behaviour at times when predation risk was highest, we used accelerometry data collected by GPS-collars to identify wild dog hunting bouts. First, we summed the two accelerometer measurements for each 5-minute period, to give an overall measure of activity. We then defined hunting bouts based on three criteria: (i) activity >0 units for >20 minutes; (ii) total activity during the activity bout >500 units; (iii) followed by three or more consecutive records of 0 unit activity. These criteria excluded activity bouts which were too short to represent hunting, or which related to less energetic behaviours, such as socialising. Criteria were derived using visual inspection of activity plots and examining the characteristics of activity bouts in time periods during which wild dogs are typically observed hunting. For each hunting bout identified in this way, we recorded start time, end time, duration (in minutes), and intensity (total activity divided by duration). The distributions of start and stop times are shown in Fig. S1. We classified hunting bouts as “morning”, “evening”, “night” or “midday”, based on their start and stop times, as detailed in Table S2 and Fig. S1. Bouts that spanned multiple time periods were excluded from the analysis. After using accelerometry data to identify specific hunting bouts, we categorised each wild dog location as falling inside or outside a hunting bout.

## Categorising activity periods of prey species

We categorised dikdik and impala GPS collar locations into four time periods, reflecting diel variation in wild dog hunting activity and hence predation risk. We defined “morning” as the time period between sunrise (taken from the *R* package *suncalc*, Agafonkin & Thieurmel 2017) and the third quartile of end times for wild dog hunting bouts (approximately 3.5h after sunrise; Fig. S1). We classified impala and dikdik “evening” GPS-locations as those recorded between the first quartile of start times for hunting bouts (approximately 2hr10min before sunset; Fig. S1) and sunset (which fell between 1841h and 1912h). We categorised impala and dikdik GPS-locations as “midday” if they were recorded between the “morning” and “evening” periods, and “night” if they were recorded between sunset and sunrise.

## Habitat use

We analysed habitat use from a vegetation map of Mpala created from a 2011 Quickbird satellite image (Digital Globe, Longmont, CO, USA) by Ford *et al.* (2014). We estimated the woody cover (a measure of shadiness) associated with each impala, dikdik, and wild dog GPS-collar location as the proportion of woody cover within a circular area of radius 40m, centred on the collar location, calculated in *QGIS* (QGIS Development Team 2018).

## Statistical analyses

We used multi-model inference to evaluate associations between wild dog hunting outcome variables (duration, probability of occurrence, and intensity of morning, evening and night time hunts) and a range of explanatory variables (Table S3, Table S4). The reduced daytime foraging time hypothesis (Table 1, Hypothesis 1) predicted that wild dogs would spend less time hunting on hot days. To test this hypothesis, we split the activity data into morning, midday and evening. We analysed continuous outcome variables describing hunt duration, start time, stop time, and hunt intensity, as well as a binary outcome variable describing whether or not a hunt was recorded for each time period. Only 10% of hunting bouts occurred during the midday period (accounting for 2% of daily activity), so we considered these abnormal events and did not subject them to further statistical analyses. Morning and evening hunt periods were analysed separately as a number of the covariates (Table S3) were predicted to impact morning and evening hunts in different ways. For each outcome variable, we constructed Generalised Linear Mixed Models (GLMMs) using the package *nlme* (Pinheiro *et al.* 2015) in *R*, with Gaussian error distribution for the continuous outcome variables and binomial error distribution for the binary outcome variable. Each model included the identity of individual animals and the date as random effects. Although our hypotheses concerned the potential effects of ambient temperature, we included several other explanatory variables known to influence activity patterns of wild dogs, namely denning status, rainfall, moonlight and, in models of night-time activity, time of moonrise and moonset. Detailed justifications for including each explanatory variable are shown in Table S3.

For each outcome variable, we built a series of statistical models using explanatory variables and biologically-meaningful interactions between explanatory variables, with individual identity as a random variable. We then used Akaike’s Information Criterion (AIC) to compare models using the *R version 3.3.2* (version 3.3.2, R Core Team 2017) package *MuMIn* (Bartoń 2017). We considered all models with delta AIC scores within 2 units of the lowest AIC model (*i.e.,* ΔAIC< 2) to have a high level of support (Burnham et al. 2002), referring to this array of models as the “top set”. We used model averaging (Burnham et al. 2002) to estimate the effect on the outcome variable of each explanatory variable in the top set.

In the shade-seeking hypothesis (Table 1, Hypothesis 2) we predicted that wild dogs, impala, and dikdiks would increase their use of shaded habitat at high ambient temperatures. To test this hypothesis, we constructed a series of models with use of woody cover as the outcome variable. To avoid pseudoreplication, we averaged the woody cover values for each individual across each morning, midday, evening or night-time period. For wild dogs, we only included measurements of woody cover at locations taken during hunting bouts. We analysed these outcome variables using GLMMs with individual identity as a random effect, building a separate array of models for each time of day, and for all times of day together. Candidate explanatory variables were the same as for the analyses of wild dog activity (i.e., temperature, rainfall, moonlight, and, for wild dogs, denning), but also included a variable describing rainfall phase (Table S4), which was predicted to impact herbivore behaviour and location (Goheen et al 2013). Following Ford *et al.* (2014), we considered days to fall within “wet phases” if >50mm of rain had fallen in the previous four weeks, and classed all other days as falling in “dry phases”. In constructing the array of models for multi-model inference, this rainfall phase variable was never included in the same model as daily rainfall, because the two were correlated. Model selection was performed using model averaging in the same way as when investigating wild dog hunting (Hypothesis 1 and 2b).

The prey overheating hypothesis (Table 1, Hypothesis 3) could not be tested directly from our datasets, because our GPS-collar locations and accelerometer data were recorded too infrequently to estimate chase speeds, so our evaluation of this scenario relied on testing the prediction that wild dogs killed impala more frequently on hot days (Table 1). This outcome was also predicted under Hypotheses 2 and 3, however, and could not be used to specifically support Hypothesis 4. We tested this prediction by using a GLM with binomial error distribution to analyse whether or not wild dog scats contained impala remains. In this model, candidate explanatory variables were ambient temperature during the previous seven days (to account for delays between a scat being deposited and collected), and land use (as a previous study showed that impala were consumed far less frequently on community land, relative to private land, Woodroffe *et al.* 2007). Pack or individual identity were often unknown for wild dog scats, so these models did not include random effects. Model selection was performed using model averaging in the same way as when investigating wild dog hunting (Hypothesis 1 and 2b) and woody cover selection (Hypothesis 3).

# Results

## Daily movement patterns

African wild dogs showed a strongly crepuscular activity pattern, with hunts and daily activity concentrated in the morning and evening time periods (Fig. 1). Sixteen percent of wild dog hunting periods, and 17% of total daily activity, occurred at night (Fig. 2).

Impala had the highest levels of displacement between GPS locations at night (1.24km ±2.11(s.d.)) and lower displacement distances in the morning (0.90km ±1.4), daytime (0.97km ±1.7) and evening (0.89km ±1.3) time periods.

Dikdik had similar levels of displacement between GPS locations throughout the day, with the higher levels of displacement in the morning (0.27km ±0.3) and at night (0.26km ±0.27) and slightly lower displacement distances in the daytime (0.20km ±0.27) and evening (0.19km ±0.23) time periods.

## Associations between ambient temperature and wild dog hunting

Consistent with the reduced daytime foraging time hypothesis (Hypothesis 1), wild dogs’ daytime hunting periods were shorter in both the morning and evening time periods at high ambient temperatures (Table 2, Fig. 4). In addition to being shorter, both morning and evening hunts entailed less intense activity on hotter days (Table S5, Table S6). Evening hunts were less likely to occur at all on days with higher ambient temperatures (Table S6), though there was no such effect on morning hunts (Table S5). Temperature had a greater impact on the length, intensity and occurrence of evening compared to morning hunts, which is to be expected as wild dogs will experience a higher heat load in the evening following a hot day, when compared with the mornings following the cooler night-time period. Rainfall may have mitigated the effects of high ambient temperatures, with rainfall:temperature interactions included in some of the top models for hunt duration (Table S5, Table S6). Packs were consistently more active during daytime when they were denning (Table S5, Table S6).

## Habitat selection

The three species differed in their use of woody cover, with impala using the most open areas and wild dogs using the areas with the highest woody cover (Fig. 3). Impala use of open areas was most pronounced at night, and during the morning period, whereas wild dogs used the wooded areas to a greater extent at night (Fig. 3). The use of woody cover by dikdiks was relatively consistent throughout the day (Fig. 3).

As predicted under the shade-seeking hypothesis (Hypothesis 2), impala selected areas with denser woody cover on hotter days, during morning and midday periods, although not during the evening (Table 3). In contrast, there was no evidence for dikdiks selecting woody cover based on ambient temperature, and also no evidence of such selection by hunting wild dog packs (Table 3).

## Prey selection

Among 795 wild dog scats, 71 (9%) contained impala remains and 609 (77%) contained dikdik remains. As predicted under the restricted foraging time hypothesis (Hypothesis 1) but not the other three hypotheses, wild dog scats were less likely to contain impala remains when ambient temperatures had been higher in the previous seven days (Table 4, Fig. 3e).

# Discussion

Our analyses revealed clear associations between ambient temperature and the behaviour of both predator and prey species, which appeared to influence trophic interactions. Our findings were most consistent with the restricted foraging time hypothesis (Hypothesis 1), under which we predicted that, on hot days, wild dogs would spend less of the daylight period hunting, and therefore prefer abundant small prey over larger but less abundant prey. Consistent with these predictions, we found that wild dogs spent less time hunting during daytime hours (Fig. 4, Table S5, Table S6). Previously we posited that, on average, dikdik and impala would yield comparable returns, because the greater energy intake achievable by hunting impala was offset by the shorter travel distances associated with hunting dikdik (Woodroffe *et al.* 2007). However, optimal foraging theory predicts that a predator with limited time should select more abundant but lower-value prey (such as dikdiks) rather than waiting to locate rarer, higher value prey (such as impala, Lucas 1983). High ambient temperatures would therefore be expected to favour wild dogs eating dikdiks more than impala, and our observations were consistent with this prediction (Table 4).

Under the shade-seeking hypothesis (Hypothesis 2), we predicted that all three species would increase their daytime use of woody cover at high ambient temperatures. However, we found that only impala did so (Table 3). Of the three species, impala used the most open habitat (Fig. 3, b and c), which may have resulted in a greater need to seek shade at high ambient temperatures. Physiological studies suggest that dikdiks are dependent upon shade to thermoregulate (Kamau & Maloiy 1985) but, being small-bodied and less gregarious than impala, they may be able to use small patches of shade without moving into denser habitat. There was no evidence that wild dogs hunted in denser cover on hot days (Table 3), perhaps because hunting periods occurred before and after the hottest times of day (Fig. 3). The tendency of impala to move into denser cover at high ambient temperatures would be expected to increase their risk of being killed, since wild dogs typically occupied denser cover (Fig. 3), and impala are more likely to be killed in denser cover (Ford *et al.* 2014). Nevertheless, we found that impala remains were less likely to be found in wild dog scats following periods of high ambient temperature (Table 4). Hence, although impala behaviour changed in line with the predictions of the shade-seeking hypothesis (Hypothesis 2), this change did not generate the predicted impact on predation.

Under the prey overheating hypothesis (Hypothesis 3) it was predicted, in line with Creel et al 2016, that high ambient temperatures would reduce chase distances for impala and increase them for dikdiks, as larger-bodied animals would be slowed down by the heat to a greater extent than smaller-bodied animals. We were not able to test this hypothesis directly because our monitoring methods did not allow us to measure chase distance or speed. However, this scenario also predicted that predation upon impala would increase, relative to predation on dikdiks, when ambient temperatures were high. Our observations showed the opposite pattern (Table 4, Fig. 3e); hence, a key prediction of the prey overheating hypothesis was not upheld by our observations. Impala have previously been shown to be very good at dissipating body heat through sweating, maintaining a constant body temperature even when active at air temperatures as high as 44°C (Maloiy and Hopcraft 1970), significantly higher than any temperatures recorded in this study. On top of this, impala show very little rise in body temperature even during high intensity chases (Maloiy and Hopcraft 1970, Meyer et al 2008). Whilst at very high temperatures overheating during chases may pose a risk, it seems likely that those temperatures would be higher than those found at our study site, and impala’s ability to dissipate heat using sweating is also likely to give them an advantage that outweigh any body size related restrictions on heat dissipation.

Other evidence also favours the reduced foraging time hypothesis (Hypothesis 1) over the other hypotheses. Under Hypothesis 1, we would expect energy intake by wild dogs to be reduced at high ambient temperatures, due to constrained foraging time and a consequent acceptance of lower-energy prey. This prediction is consistent with our observations that this study population experiences higher mortality and lower reproductive success at high ambient temperatures (Woodroffe, Groom & McNutt 2017; Rabaiotti *et al.* in review). In contrast, under the other two scenarios, wild dogs’ food intake (and thus potentially their survival and reproductive success), would be expected to improve at high temperatures, because impala (higher-value prey) would be more accessible due to being in dense cover where they are vulnerable to predators (Hypothesis 2), or more easily captured due to their tendency to overheat during high speed chases (Hypothesis 3). Hence, while demographic patterns cannot confirm the reduced foraging time hypothesis (Hypothesis 1) as the most likely mechanism whereby ambient temperature influences predator-prey interactions in this system, they do contribute to refuting Hypotheses 2 and 3.

Our findings suggest that climate change might have two wider impacts through its effect on predation by wild dogs. First, we have shown previously that wild dogs suppressed dikdik numbers, and dikdik browsing influenced tree abundance (Ford *et al.* 2015). Although we found that wild dog predation on dikdiks did not trigger cascading effects on vegetation (Ford *et al.* 2015), rising environmental temperatures would be expected to intensify wild dog predation on dikdiks, which might generate wider impacts on community structure.

Second, our findings suggest that wild dog populations’ resilience in the face of climate change might be affected by the abundance of small, abundant prey. Our study site is unusual both in the density of dikdiks it supports (Augustine 2010; Ford et al. 2015) and the degree to which wild dogs rely on dikdiks as prey (Woodroffe *et al.* 2007). Across much of the geographic range of wild dogs, dikdiks are altogether absent (Kingdon & Hoffman 2013), and impala comprise the bulk of wild dog diets (Creel, Mills & McNutt 2004; Mbizah, Marino & Groom 2012). Without abundant small prey to hunt on hot days, we would expect wild dogs to more frequently make no kill at all, with potentially greater impacts on energy intake than may occur at our study site. Low reproductive success and high mortality at high ambient temperatures have been reported for wild dogs from two sites where impala are wild dogs’ principal prey (Woodroffe, Groom & McNutt 2017; Rabaiotti *et al.* In Review), although site-specific conditions complicate any comparison of the magnitude of temperature effects at the different sites.

Our results help to explain the negative impacts of high ambient temperatures on the survival and reproductive success of the African wild dog, an endangered species (Woodroffe & Sillero-Zubiri 2013). Our findings suggest that prey diversity may help to buffer wild dog populations against the effects of climate change, because abundant prey are readily located even when hunting time is constrained. Measures which maintain prey densities and diversity (such as limiting offtake by people) may help to conserve wild dogs in a warming climate. However, interventions which artificially raise prey densities (such as installation of waterholes) may risk increasing the densities of wild dogs’ predators (Creel & Creel 1996; Mills & Gorman 1997), and might have harmful consequences for wild dog conservation.

More generally, we have shown that ambient temperature can influence patterns of predation, even when both predator and prey are tropical endotherms. This finding contrasts with the assumptions of several general ecosystem and community ecology models (e.g., Dell, Pawar & Savage 2014 , Harfoot et al 2014), and suggests that such models may not accurately represent the responses of ecological communities in which endotherms play important roles. However, our findings also highlight the difficulty of accurately predicting exactly how environmental temperature would be expected to influence predation involving endotherms: all four of the hypotheses that we investigated were plausible, but they generated conflicting predictions about how predation on impala and dikdiks might vary in response to weather conditions, and only empirical testing indicated the true direction of the impact. Further investigations of how temperature-induced changes in the behaviour of predator and prey species together influence trophic interactions would help to build a more general picture of the relationship between ambient temperature and endotherm predation within ecological communities.

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# Author Contributions

D. Rabaiotti, Rosie Woodroffe and Adam Ford, designed the research questions. D. Rabaiotti organised the datasets, designed and carried out the final analyses and wrote the paper. Rosie Woodroffe oversaw data collection on wild dogs and contributed to the writing of the paper. Adam Ford and Jacob Goheen collected the dikdik and impala data and contributed to the writing of the paper. Ben Chapple helped design and carry out the analyses on the impala and dikdik data and African wild dog habitat use. Sophie Morrill assisted in designing and carrying out the analyses on wild dog hunt times.

# Data Availability Statement

Should the article be accepted, the data will be deposited on Dryad and the DOI included at the end of the article

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| --- | --- | --- | --- | --- |
| **Table 1** Hypotheses describing how predator behaviour, prey behaviour, and predation risk might vary with ambient temperatures | | | | |
| **Hypothesis** | **Species** | **Explanation** | **Implication for predator** | **Expected dietary change at high temperatures** |
| Hypothesis 1: Restricted foraging time | Wild dogs | Wild dogs are expected to spend less time hunting in daytime when temperatures are high1. | Predators with limited foraging time are predicted to select more abundant prey even if it contains less energy2 (in this case dikdiks). | Increased ratio of dikdik to impala |
| Hypothesis 2: Shade seeking | All species | Wild dogs, impala and dikdik are all predicted to move into denser vegetation at high ambient temperatures to avoid overheating. | Wild dogs are able to hunt impala more successfully, as impala are more vulnerable to predation in denser vegetation4. | Decreased ratio of dikdik to impala |
| Hypothesis 3: Prey overheating | Impala | When running at high ambient temperatures, larger bodied animals overheat more quickly, and therefore impala slow down more than dikdiks. | Wild dogs are able to capture impala more easily because impala overheat more quickly when running than the smaller-bodied wild dogs5. | Decreased ratio of dikdik to impala. |
| 1(Rabaiotti 2019), 4(Lucas 1983), 3(Augustine 2004); 3 (Ford *et al.* 2014); 4(Ford *et al.* 2014),5(Creel *et al.* 2016). | | | | |

**Table 2** Variables associated with the **duration of hunting periods** of African wild dogs in the morning and evening. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 2) for the duration of hunting periods in the morning and evening (in minutes). The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Outcome variable | Explanatory variable | Estimate | Lower  95% CI | Upper  95% CI | Variable  Importance (n) |
| Morning hunt duration (minutes) | Intercept | 211.608 | 193.373 | 229.842 | — (2) |
| Denning (Yes) | 17.952 | 13.633 | 22.271 | 1.00 (2) |
| Moonlight night before | -2.126 | -2.461 | -1.790 | 1.00 (2) |
| Temperature (°C) | -0.793 | -1.481 | -0.167 | 0.72 (1) |
| Evening hunt duration (minutes) | Intercept | 206.230 | 191.461 | 220.999 | — (2) |
| Temperature (°C) | -2.275 | -2.794 | -1.757 | 1.00 (2) |
| Moonlight | -1.794 | -2.048 | -1.539 | 1.00 (2) |
| Denning (Yes) | 20.435 | -12.132 | 53.002 | 1.00 (2) |
| Rainfall | 2.619 | 0.058 | 5.180 | 0.34 (1) |
| Rainfall:Temperature | -0.083 | -0.179 | 0.013 | 0.34 (1) |
|  | Denning:Temperature | 0.434 | -1.592 | 2.429 | 0.34 (1) |

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| --- | --- | --- | --- | --- | --- |
| Outcome variable | Explanatory variable | Estimate | Lower  95% CI | Upper  95% CI | Variable  importance (n) |
| impala - morning | Intercept | 0.0465 | 0.0352 | 0.0578 | (1) |
| Temperature | 0.0019 | 0.0003 | 0.0022 | 1.00 (1) |
| impala - midday | Intercept | 0.0772 | 0.0650 | 0.0894 | (1) |
| Temperature | 0.0014 | 0.0011 | 0.0017 | 1.00 (1) |
| impala - evening | Intercept | 0.0948 | 0.0878 | 0.1018 | (1) |
| dikdik – morning and evening | Intercept | 0.1211 | 0.1011 | 0.1412 | (1) |
| dikdik - midday | Intercept | 0.1288 | 0.1102 | 0.1474 | (1) |
| wild dog – morning and evening | Intercept | 0.1666 | 0.1506 | 0.1827 | - (1) |

**Table 3** Variables associated with **selection of woody cover** by African wild dogs, impala, and dikdiks. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 2). The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n).

**Table 4** Variables associated with **African wild dog consumption of impala**. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc<2) for African wild dog consumption of impala. The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n).

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| --- | --- | --- | --- | --- |
| Explanatory variable | Estimate | Lower 95% CI | Upper 95% CI | Variable importance (n) |
| Intercept | 0.355 | 0.181 | 0.530 | — (1) |
| Daily maximum temperature | -0.007 | -0.013 | -0.001 | 1.00 (1) |

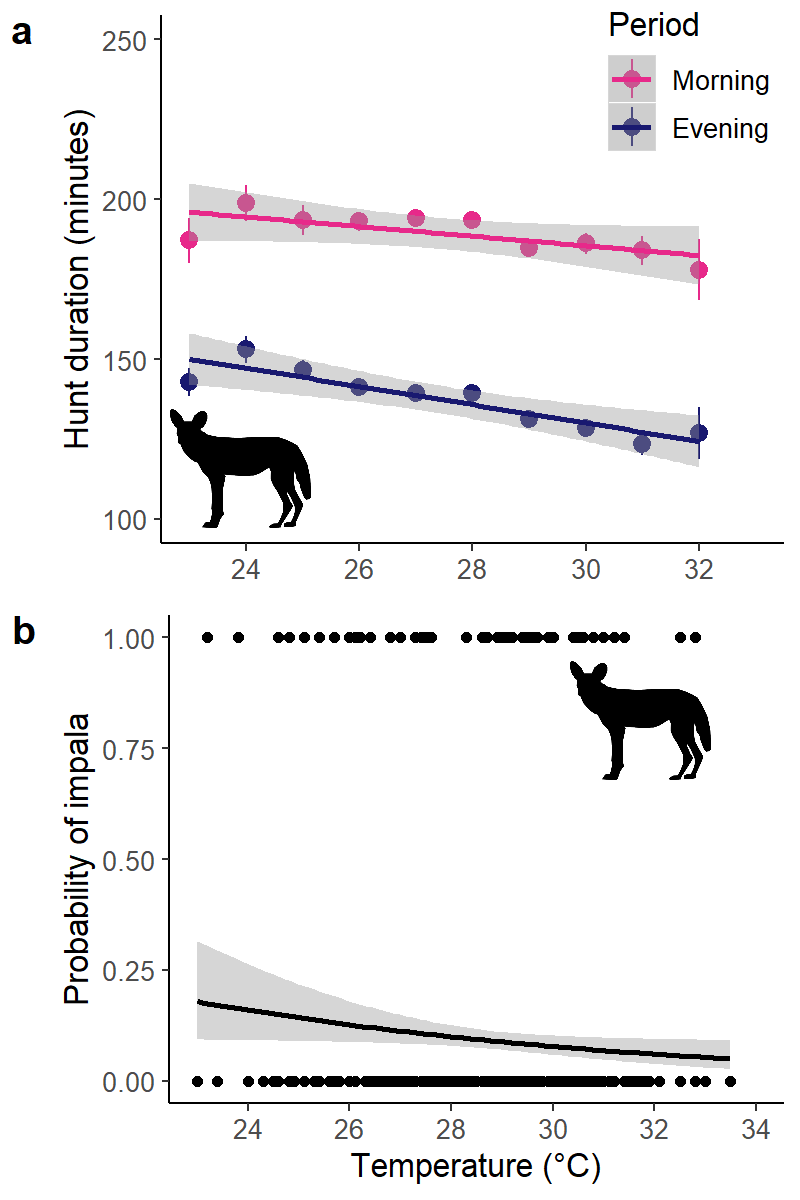
**Figure 1** Daily movement patterns of African wild dogs (A) activity measured by collar-mounted accelerometers fitted to 18 wild dogs; blue bands denote the start and stop times used to classify morning and evening hunts (B) Mean maximum temperature throughout the day at the study site

A screenshot of a cell phone

Description automatically generated**Figure 2** Percentage of hunts and total activity which fall in Morning, Midday, Evening and Night periods, and the percentage of bouts and total activity which spanned multiple time periods, and were therefore determined not to be hunts.

**Figure 3** Diel variation in woody cover use by impala, dikdiks and Africanwild dogs across time periods.



**Figure 4** Associations between ambient temperature and African wild dog hunting behaviour a) Duration of African wild dog morning and evening hunts at different daily maximum temperatures (°C). Points represent the means for each 1°C interval, vertical bars indicate the standard error b) Probability of the presence of impala in wild dog scat at different daily maximum temperatures (°C). Lines represent conditional mean, and shaded areas represent the 95% confidence interval.

**Temperature affects predator-prey interactions in an African savanna**

D. Rabaiotti1,2, Adam T. Ford3, Ben Chapple2, Sophie Morrill2,

Jacob Goheen4 and Rosie Woodroffe1

**Supplementary Material**

**Figure S1** Frequency distribution of (A) start times and (B) stop times of African wild dog hunting periods, identified using collar-mounted accelerometers.



A

B

Time

|  |  |  |  |  |  |  |
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| **Table S1** Annual temperature and rainfall values at Mpala Research Centre throughout the period of the study. | | | | | | |
|  | Temperature (°C) | | | | Rainfall (mm) | |
| Year | Minimum | Annual Mean | Maximum | | Total | Annual Mean |
| 2000 | 3.85 | 19.99 | 31.54 | | 280.17 | 0.78 |
| 2001 | 8.23 | 19.76 | 32.19 | | 670.56 | 1.84 |
| 2002 | 6.92 | 19.81 | 38.03 | | 483.62 | 1.32 |
| 2003 | 4.39 | 19.59 | 32.64 | | 684.21 | 1.77 |
| 2004 | 7.67 | 19.53 | 38.78 | | 718.05 | 1.97 |
| 2005 | 3.61 | 19.18 | 34.02 | | 508.00 | 1.40 |
| 2006 | 6.76 | 19.80 | 32.51 | | 543.81 | 1.49 |
| 2007 | 5.66 | 19.55 | 33.08 | | 505.99 | 1.39 |
| 2008 | 5.87 | 19.69 | 32.15 | | 410.96 | 1.19 |
| 2009 | 7.53 | 20.66 | 33.31 | | 244.09 | 0.67 |
| 2010 | Data not available due to the weather station being broken | | | | | |
| 2011 | 7.15 | 18.60 | 31.95 | 703.35 | | 2.87 |
| 2012 | 3.07 | 18.73 | 32.12 | 639.85 | | 1.76 |
| 2013 | 5.79 | 19.01 | 31.86 | 660.93 | | 1.90 |
| 2014 | 6.53 | 19.51 | 31.59 | 395.72 | | 1.19 |
| 2015 | 6.09 | 19.33 | 32.98 | 548.36 | | 1.61 |
| 2016 | 8.18 | 19.98 | 32.89 | 706.12 | | 1.94 |

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| **Table S2** Start and stop times of hunting periods allocated to each time period within the analysis. | | | | |
| Type of Bout | Earliest start time | Latest start time | Earliest stop time | Latest stop time |
| Morning | 04:55:39 | 06:56:04 | 07:30:41 | 12:51:33 |
| Midday | 06:56:05 | 16:01:54 | 12:51:34 | 18:47:02 |
| Evening | 16:01:55 | 18:26:52 | 18:47:03 | 21:06:56 |
| Night | 18:26:53 | 04:55:38 | 21:06:57 | 07:30:40 |

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| **Table S3** Explanatory variables, other than temperature, included in models of wild dog hunts, and justification for their inclusion. | | | |
| Explanatory variable | Included in models for which time of day  (Morning, Evening, Night) | Justification | Citation |
| Denning status (yes/no) | All | We have previously shown that wild dogs are more active during the denning period | Woodroffe, Groom and McNutt 2017, Rabaiotti and Woodroffe 2019 |
| Total 24h rainfall (mm) | All | We have previously shown that rainfall mitigates the impact of high temperatures on wild dog activity levels so we would expect a negative interaction with temperature during the day and a positive one at night. | Rabaiotti and Woodroffe 2019 |
| Moonlight (proportion illumination\*hours of moonlight) | All (Moonlight the previous night was used in morning models, and the following night in evening models) | We and others have previously shown that wild dogs are more active on moonlit nights and would therefore expect a positive relationship between moonlight and nocturnal activity, and potentially a positive relationship with morning and evening activity. | Cozzi et al. 2012, Rabaiotti and Woodroffe 2019 |
| Moonrise (time) | Night |
| Moonset (time) | Night |

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| **Table S4** Explanatory variables, other than temperature, included in models of wild dog, impala and dikdik woody cover use and justification for their inclusion. | | | | |
| Explanatory variable | Included in models for which time of day  (Morning, Evening, Night) | Species | Justification | Citation |
| Denning status (yes/no) | All | Wild dogs | Wild dogs use more rugged areas with less vegetation during the denning period | Jackson et al 2014 |
| Total 24h rainfall (mm) | All | All | Rainfall mitigates the impact of high temperatures on activity levels and influences herbivore movement. | Rabaiotti and Woodroffe 2019, Ford et al 2014 |
| Rainfall phase | All | All | Rainfall phase impacts herbivore movement and assemblages | Goheen et al 2013 |
| Moonlight (proportion illumination\*hours of moonlight) | All (Moonlight the previous night was used in morning models, and the following night in evening models) | All | Wild dogs are more active on moonlit nights | Cozzi et al. 2012, Rabaiotti and Woodroffe 2019 |

**Table S5** Variables associated with the characteristics of African wild dog hunting periods in the **morning**. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 2) for each outcome variable. The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n).

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| --- | --- | --- | --- | --- | --- | --- | --- |
| Outcome variable | Explanatory variable | | Estimate | Lower  95% CI | Upper  95% CI | Variable  importance (n) | |
| Occurrence | Intercept | | 0.8005 | 0.7698 | 0.8312 | | — (1) |
| Moonlight before | | -0.0097 | -0.0115 | -0.0079 | | 1.00 (1) |
| Duration  (minutes) | Intercept | | 209.066 | 191.739 | 226.393 | | — (2) |
| Denning *vs* not | | 17.952 | 13.633 | 22.271 | | 1.00 (2) |
| Temperature (°C) | | -0.793 | -1.418 | -0.167 | | 0.72 (1) |
| Moonlight before | | -2.126 | -2.461 | -1.790 | | 1.00 (2) |
| Intensity | Intercept | | 50.9285 | 46.4112 | 55.4459 | | — (2) |
| Denning *vs* not | | 1.5610 | 0.7941 | 2.3279 | | 1.00 (1) |
| Temperature (°C) | | -0.2552 | -0.3743 | -0.1362 | | 0.52 (2) |
| Start time | Intercept | 05:52:31 | | 05:50:20 | 05:54:41 | | (1) |
| Moonlight before | -00:00:38 | | -00:00:30 | -00:00:46 | | 1(1) |
| Stop time | Intercept | | 09:09:40 | 09:06:44 | 09:12:36 | | (1) |
| Moonlight before | -00:01:30 | | -00:01:12 | -00:01:50 | | 1.00(2) |
| Denning *vs* not | 00:06:33 | | 00:02:29 | 00:10:37 | | 0.52(1) |

**Table S6** Variables associated with the characteristics of African wild dog hunting periods in the **evening**. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 2) for each outcome variable. The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Outcome variable | | Explanatory variable | | | Estimate | | Lower 95% CI | | Upper 95% CI | | Variable  importance (n) | | |
| Occurrence | | Intercept | | | 1.2315 | | 1.1211 | | 1.3419 | | | — (1) | |
| Moonlight | | | -0.0098 | | -0.0118 | | -0.0079 | | | 1.00 (1) | |
| Temperature (°C) | | | -0.0167 | | -0.0206 | | -0.0129 | | | 1.00 (1) | |
| Duration  (minutes) | | Intercept | | 206.230 | | | 191.461 | | 220.999 | | — (2) | | |
| Temperature (°C) | | -2.275 | | | -2.794 | | -1.757 | | 1.00 (2) | | |
| Moonlight | | -1.794 | | | -2.048 | | -1.539 | | 1.00 (2) | | |
| Denning (Yes) | | 20.435 | | | -12.132 | | 53.002 | | 1.00 (2) | | |
| Rainfall | | 2.619 | | | 0.058 | | 5.180 | | 0.34 (1) | | |
| Rainfall:Temperature | | -0.083 | | | -0.179 | | 0.013 | | 0.34 (1) | | |
|  | | Denning:Temperature | | 0.434 | | | -1.592 | | 2.429 | | 0.34 (1) | | |
| Intensity | | Intercept | | | 54.602 | | 58.198 | | 51.006 | | | — (1) | |
| Temperature (°C) | | | -0.335 | | -0.211 | | -0.459 | | | 1.00 (1) | |
| Denning *vs* not | | | 1.772 | | 2.634 | | 0.909 | | | 1.00 (1) | |
| Moonlight | | | -0.267 | | -0.201 | | -0.333 | | | 1.00 (1) | |
| Start time | | Intercept | | 15:56:05 | | | 15:46:08 | | 16:06:02 | | | (1) | |
| Temperature (°C) | | 00:03:30 | | | 00:02:43 | | 00:03:24 | | | 1.00 (1) | |
| Denning *vs* not | | -00:13:56 | | | -00:11:35 | | -00:16:17 | | | 1.00 (1) | |
| Moonlight | | 00:00:58 | | | 00:00:47 | | 00:01:09 | | | 1.00 (1) | |
| Stop time | | Intercept | | 19:44:47 | | | 19:43:40 | | 19:45:54 | | | (1) | |
| Denning *vs* not | | 00:13:25 | | | 00:07:44 | | 00:12:25 | | | 1.00(1) | |
| Moonlight | | 00:00:51 | | | 00:00:40 | | 00:01:02 | | | 1.00(1) | |