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

# Abstract

In response to high ambient temperatures, individuals alter their resource use by curtailing foraging time, seeking cooler microclimates, choosing different foods, increasing water intake, and switching from diurnal to nocturnal activity. These shifts enable them to more effectively thermoregulate in the face of a high heat load. During hot weather, such behavioural shifts are likely to impact predator-prey interactions, with predation risk arising from the joint responses of predator and prey to weather conditions.

We investigated how ambient temperature impacted predator-prey interactions in a three-species system comprising one predator, the African wild dog (*Lycaon pictus*), and two prey species, ca. 5 kg dik-diks (*Madoqua guentheri*) and ca. 40 kg impala (*Aepyceros melampus*). We suggest predator-prey dynamics could change in three ways. Firstly, we predicted African wild dog activity would be reduced when daytime temperatures were higher, and that this would lead to increased predation on abundant dik-diks over less abundant impala. Secondly, we predicted that as impala in habit more open areas they would seek shade more than dik-diks, attracting impala to areas with reduced visibility - increasing their risk of predation. Thirdly, we investigated whether difficulties of dissipating metabolic heat during chases at high ambient temperatures would affect impala more than dik-diks.

Habitat use (by dik-diks and impala) and activity (of African wild dogs) changed with temperature as we predicted. However, in contrast to our predictions that increased habitat overlap would increase predation on impala, fewer wild dog scats contained impala remains when ambient temperatures were high. Consistent with our hypothesis of optimal foraging in the face of reduced hunting activity by wild dogs, wild dogs spent less time hunting on hot days and appeared to select abundant dik-diks over rarer impala. Ambient temperature can influence predator-prey interactions among endotherms, and studies assuming otherwise should be interpreted with caution.

**Keywords:** African wild dog;antipredator behaviour; climate change; dik-dik; habitat use; impala; predation; thermal tolerance

# Introduction

Climate change is having far-reaching impacts on both species and ecosystems (Parmesan & Yohe 2003 Pacifici et al 2017). Meta-analyses suggest that many climate impacts on species operate indirectly by influencing the outcomes of competition, herbivory, predation, and parasitism (Cahill *et al.* 2012; Ockendon *et al.* 2014). As weather patterns are expected to 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.

The effects of changing weather conditions on species interactions will be affected by traits, especially those traits linked to metabolism, thermoregulation and osmoregulation. Ectotherms rely primarily on external sources of heat to regulate their body temperature, meaning that high ambient temperatures directly lead to changes in their physiology, movement, and behaviour. These individual behavioural shifts of ectotherms can drive climate impacts on species interactions. For example, increasing speed of locomotion associated with increasing ambient temperatures may increase the efficiency of predators and the escape success of prey, with cascading consequences for community structure (Post et al 1999, Rall et al 2010, Dell, Pawar & Savage 2014). Because endotherms can regulate their body temperature independently of ambient temperature, it is often assumed that predator-prey interactions involving endotherms are relatively unaffected by high ambient temperatures (e.g., Dell, Pawar & Savage 2014; Harfoot *et al.* 2014). However, many birds and mammals 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 microclimates (Austin 1976; Pigeon *et al.* 2016), choosing different foods (Doolan & Macdonald 1996; Garcia-Heras *et al.* 2017), or increasing their water intake (Veldhuis et al 2019), all of which are likely to influence predator-prey interactions.

It has been suggested that predator-prey interactions involving large-bodied endotherms might be especially sensitive to increasing environmental temperatures, because the low surface-area-to-volume ratios of large animals makes it difficult for them to dissipate the heat load from the environment together with the metabolic heat generated by pursuing or escaping predation (Speakman & Krol 2010; Creel *et al.* 2016, Du Toit and Yemen 2005). If, during a chase, larger-bodied endotherms are prone to overheating more rapidly than smaller-bodied endotherms, higher ambient temperatures might favour the smaller-sized animal in a predator-prey interaction, i.e., prey that are smaller than their predators, and predators that are smaller than their prey (Creel *et al.* 2016). In this scenario, at high ambient temperatures, predation rates would be lower when prey are smaller than their predator, and higher when prey are larger than their predator (Creel *et al.* 2016).

Predictions that larger bodied mammals will be more impacted by high temperatures than smaller bodied mammals ignore the potential role of evaporative cooling in heat dissipation, however. Larger mammals rely more evaporative cooling to dissipate heat when ambient temperatures are high that smaller mammals, which are able to utilise microclimates such as burrows due to their small body size (Taylor 1977; Mitchell et al, 2018). Indeed, there is evidence that smaller species of antelope are more likely to store heat during exercise than larger bodied species (Taylor and Lyman 1972), and relatively large-bodied mammals such as cheetahs (*Acinonyx jubatus*) and impala (*Aepyceros melampus*) rapidly dissipate heat during exercise (Fuller et al., 2016). The variation in thermoregulatory mechanisms between different species means that simple relationships among body size, predation risk, and the risk of hyperthermia are unlikely for endotherms.

We measured the impact of ambient temperature on predator-prey interactions in a three-species system. Specifically, we examined how ambient temperature affected the habitat use and activity patterns of a small-bodied prey species (the ~5 kg Guenther’s dik-dik *Madoqua guentheri*), a larger-bodied prey species (the ~40 kg impala), and their shared predator (the ~23 kg African wild dog *Lycaon pictus*). At our study site in Kenya, impala and dik-diks are the most abundant ungulates, and their predation risk-averse habitat selection and browsing preferences shape tree cover across the landscape (Goheen *et al.* 2013; Ford *et al.* 2014; Ford *et al.* 2015; Otieno *et al.* 2019). Wild dogs are crepuscular, and hunt by running prey down (Creel & Creel 1995); dik-diks and impala together comprise 82% of the prey biomass that wild dogs consume at our study site (Woodroffe et al. 2007).

We evaluated three hypotheses concerning the impacts of ambient temperature on predation by wild dogs on impala and dik-diks (Table 1). First, we hypothesised that predator-prey interactions would be affected by reduced predator activity on hot days (Table 1). 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 exhibited reduced foraging time, they would increase predation on dik-diks (which are encountered more frequently) over impala, which are larger but encountered less frequently (Woodroffe *et al.* 2007, Augustine & McNaughton 2004). We term this, Hypothesis 1, the ‘reduced foraging hypothesis’.

Second, we quantified whether habitat use by both predator 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 dik-diks would do the same (Table 1). We would expect to see the greatest shift into denser woody cover at high ambient temperatures by impala, because they inhabit more open areas, and therefore are likely to be most exposed to solar radiation (Augustine 2004). Further, we predicted that such a change would increase predation on impala, which 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 dik-diks, leading to increased predation on impala relative to dik-diks at higher ambient temperatures (Table 1). We termed this, Hypothesis 3, the ‘prey overheating hypothesis’.

These hypothesised behavioural responses to increasing ambient temperatures generated contrasting sets of predictions about trophic interactions between wild dogs, impala, and dik-diks (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

Our study was conducted at the Mpala Conservancy, Kenya (0°17’ N, 36°53’ E), 200 km2 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 dik-diks and impala are the two most abundant (Ford *et al.* 2015), at 90-139 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). Because female impala form stable groups, collar data from individuals are indicative of herd-level movements. 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 dik-diks between July 2010 and September 2011, as described in Ford & Goheen (2015). Each dik-dik 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 dik-diks. 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 that deposited the scats. There were no major shifts in temperature or 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). A moonlight index was calculated by multiplying percentage illumination of the moon’s disc by the number of hours the moon was in the sky between sunset and sunrise. Finally, we used data from GPS-collars 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 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 >200m from the den site during the morning or evening – these days 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 using the following procedure. 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 energetically-demanding 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 were categorised into time periods as we anticipated that weather conditions, and in particular temperature, may have differing impacts on morning and evening hunts, given that morning hunts occur after a period of cold temperatures, when heat load on the animals is lower than that during evening hunts, which occur following a period of high midday temperatures. 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 GPS-collar location as falling inside or outside a hunting bout.

## Categorising activity periods of prey species

We categorised dik-diks and impala 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 dik-diks “evening” GPS-locations as those recorded between the first quartile of start times for hunting bouts (approximately 2h10min before sunset; Fig. S1) and sunset (which fell between 1841h and 1912h). We categorised impala and dik-diks GPS-locations as “midday” if they were recorded between the “morning” and “evening” periods, and “night” if they were recorded between sunset and sunrise. In order to establish movement patterns in each time period we calculated the total distance moved in this time by summing the displacement between each GPS point that fell in these periods.

## 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, dik-dik, 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 and a range of explanatory variables (Table S3, Table S4). Under the reduced foraging hypothesis (Table 1, Hypothesis 1), we predicted that wild dogs would spend less time hunting on hot days. We analysed continuous outcome variables describing total hunt duration and mean hunt intensity across all of the hunts in a 24h period, as well as the number of hunts a wild dog participated in within that same 24h period. We then performed secondary analyses of hunt duration and intensity, as well as a binary outcome variable describing whether or not a hunt was recorded, for each time period (morning, midday and evening). As only 10% of hunting bouts occurred during the midday period, accounting for 2% of daily activity, we excluded these from our statistical analyses. 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, a Poisson error distribution for the number of hunts, and a binomial error distribution for the binary outcome variable. 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, 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 each outcome variable of each explanatory variable in the top set.

Under the shade-seeking hypothesis (Table 1, Hypothesis 2) we predicted that wild dogs, impala, and dik-diks 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, since we were interested in the effects of temperature on predation. 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, solar radiation, moonlight, and denning status), but excluded denning status for the impala and dik-dik models. We initially tested for differences in woody cover use between morning and evening periods by running a GLMM with time of day as an additional explanatory variable. If there was no significant difference, the morning and evening time periods were combined into a single analysis, representing the times at which wild dogs are most likely to be hunting. Model selection was performed using model averaging in the same way as when investigating wild dog hunting.

The prey overheating hypothesis (Table 1, Hypothesis 3) could not be tested directly from our telemetry datasets, because our GPS-collar locations and accelerometer data were recorded too infrequently to estimate chase speeds. Our evaluation of this hypothesis thus relied on testing the prediction that wild dogs would kill impala more frequently on hot days (Table 1). This outcome was also predicted under Hypothesis 2, however, and could not be used to distinguish Hypotheses 2 and 3. We tested this prediction by using a GLM with binomial error distribution to analyse whether or not wild dog scats contained impala remains (only 14% of scats contained neither impala nor dik-dik remains). In this model, candidate explanatory variables were ambient temperature during seven days prior to scat collection (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 land inhabited by communities than on 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 woody cover selection (Hypothesis 2).

# Results

## Daily movement patterns

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

Impala travelled the furthest at night (1.24km ± 2.11km (s.d.)), with lower displacement distances in the morning (0.90km ± 1.4), daytime (0.97km ± 1.7) and evening (0.89km ± 1.3) time periods.

Dik-diks travelled similar distances throughout the day, with little difference in displacement between the morning (0.27km ± 0.3km), midday (0.20km ±0.27), evening (0.19km ±0.23) and night (0.26km ± 0.27km) time periods.

## Associations between ambient temperature and wild dog hunting

Consistent with the reduced foraging hypothesis (Hypothesis 1), the total duration of wild dogs’ hunts in a 24h period was shorter at high ambient temperatures (Table 2, Fig. 4a), and the mean intensity of hunts was lower (Table 2). 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), although there was no such effect on morning hunts (Table S5). Night time hunts were longer and higher intensity following hot days (Table S7). Wild dogs undertook a greater number of hunts across a 24h period at higher temperatures (Table 2), due to the higher likelihood of occurrence of night-time hunts (Table S7). Rainfall may have mitigated the effects of high ambient temperatures, with an interaction between rainfall and temperature included in some of the top models for total hunt duration over 24h and evening hunt duration (Table S5, Table S6). Wild dogs engaged in longer, more intense hunts across all times of day when they were denning (Table 2, Table S5- S7).

## Habitat use

Relative to other species, impala used the most open areas, and wild dogs used areas characterized by dense woody cover (Fig. 3). Impala use of open areas was most pronounced at night and during the morning period, whereas wild dogs used woody cover most at night (Fig. 3). Use of woody cover by dik-diks was relatively consistent throughout the 24h cycle (Fig. 3).

As predicted under the shade-seeking hypothesis (Hypothesis 2), impala selected areas with denser woody cover on hotter days, and during morning and midday periods, but did not do so during the evening (Table 3). In contrast, there was no evidence that dik-diks, of hunting wild dog packs, selected woody cover in relation to ambient temperature (Table 3).

## Prey selection

Among 795 wild dog scats, 71 (9%) contained impala remains and 609 (77%) contained dik-diks remains. As predicted under the reduced foraging hypothesis (Hypothesis 1) but not the other two 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. 4b).

# 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 reduced foraging hypothesis (Hypothesis 1): on hot days, wild dogs spent less time hunting, and preferred smaller, more abundant prey (dikdiks) over larger, rarer prey (impala). Previously we posited that, on average, hunting dik-diks and impala would yield comparable energetic returns for wild dogs, because the greater energy intake achievable by hunting impala was offset by the shorter travel distances associated with hunting dik-diks (Woodroffe *et al.* 2007). However, optimal foraging theory predicts that a predator with limited time should select more abundant prey—even if they are of lower value (such as dik-diks)—rather than waiting to locate rarer, higher value prey (such as impala, Lucas 1983). High ambient temperatures would therefore be expected to result in wild dogs increasing the proportion of dik-diks that they consume, compared to 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, with impala showing the greatest shift into closed vegetation due to increased exposure to solar radiation resulting from their body size and greater use of open habitats. Somewhat in contrast to our prediction, we found that only impala moved into more closed habitat at high ambient temperatures (Table 3). Physiological studies suggest that dik-diks are dependent upon shade to maintain homeothermy (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. Similarly, as dik-diks reside in dense woody cover, any need to move into denser vegetation in hot weather may be reduced, relative to impala. Dik-diks maintain a constant body temperature at air temperatures of up to 44°C (Kamau 1988), far lower than maximum temperatures recorded at our study site (Caylor et al 2016). There was no evidence that wild dogs hunted in denser cover on hot days (Table 3), perhaps because the vast majority of hunts occur before and after the hottest times of day (Fig. 1). The tendency of impala to move into denser cover at high ambient temperatures would be expected to result in a greater risk of predation, since wild dogs typically occupied denser cover (Fig. 3), and since 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). In sum, although impala behaviour changed in line with the predictions of the shade-seeking hypothesis (Hypothesis 2), this change appears not to have increased the rate at which they were consumed by wild dogs.

Under the prey overheating hypothesis (Hypothesis 3), high ambient temperatures were predicted to reduce chase distances for impala and increase them for dik-diks, as larger-bodied animals would be slowed down by hyperthermia to a greater extent than smaller-bodied animals (Creel et al. 2016). We were not able to test this hypothesis directly using telemetry data on movement rates because our monitoring methods did not allow us to measure chase distance or speed. However, this hypothesis also generated a prediction that predation upon impala would increase, relative to predation on dik-diks, when ambient temperatures were higher. Our observations showed the opposite pattern (Table 4, Fig. 4b); hence, a key prediction of the prey overheating hypothesis was not upheld by our observations. This discrepancy between prediction and observation may reflect the fact that impala can effectively dissipate body heat through sweating even during periods of exertion, maintaining a constant body temperature at ambient temperatures as high as 44°C (Maloiy and Hopcraft 1970). Thus, whilst higher ambient temperatures than those at our study site may increase the risk of hyperthermia, this ability of impala to dissipate heat by sweating may outweigh any restrictions on dry heat loss related to body size.

Additional evidence also favours the reduced foraging hypothesis (Hypothesis 1) over the shade-seeking hypothesis (Hypothesis 2) and the prey overheating hypothesis (Hypothesis 3). Under the reduced foraging hypothesis, 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.* 2021). In contrast, under the other two hypotheses, food intake (and thus potentially survival and reproductive success), would be expected to improve at high ambient 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 vital rates cannot confirm the reduced foraging hypothesis (Hypothesis 1), 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 dik-dik numbers, and that dik-diks browsing influenced tree abundance (Ford *et al.* 2015). Although we found that wild dog predation on dik-diks did not trigger cascading effects on vegetation under current climatic conditions (Ford *et al.* 2015), rising ambient temperatures would be expected to intensify wild dog predation on dik-diks, which might generate wider impacts on community structure.

Second, our findings suggest that the resilience of wild dog populations to climate change might hinge on the abundance of small, abundant prey. Our study site is unusual both in the density of dik-diks it supports (Augustine 2010; Ford et al. 2015) and the degree to which wild dogs rely on dik-diks as prey (Woodroffe *et al.* 2007). Across much of the geographic range of wild dogs, dik-diks 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 elsewhere, where impala are wild dogs’ principal prey (Woodroffe, Groom & McNutt 2017; Rabaiotti *et al.* 2021).

Our results help to explain the negative impacts of high ambient temperatures on the survival and reproductive success of the African wild dog (Woodroffe, Groom & McNutt 2017, Rabaiotti et al 2021), 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 abundance and body size often are correlated (Brown 1995, White et al 2007), small-bodied, abundant prey can be a substitute for larger-bodied, rarer prey 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 that 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. Our findings contrast with ecosystem and community ecology models that assume predation rates will increase at higher temperatures (e.g., Dell, Pawar & Savage 2014 , Harfoot et al 2014). However, our findings also highlight the difficulty of accurately predicting how ambient temperature would be expected to influence predator-prey interactions involving endotherms: all three of the hypotheses that we investigated were plausible, but they generated conflicting predictions about how predation on impala and dik-diks 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 – mediated by habitat type - influence trophic interactions would help to build a more general picture of the relationships between ambient temperature and endotherm predation within ecological communities.

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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 hunting activity** | **Expected dietary change at high temperatures** |
| Hypothesis 1: Reduced foraging | Wild dogs | Wild dogs are expected to spend less time hunting in when temperatures are high1. | Wild dogs with limited foraging time are predicted to select more abundant prey, even if it contains less energy2 (in this case dik-diks). | Increased ratio of dik-diks to impala |
| Hypothesis 2:  Shade-seeking | All species | Wild dogs, impala and dik-diks are all predicted to move into denser vegetation at high ambient temperatures to avoid overheating, with impala showing the greatest shift due to greater exposure to solar radiation. | Wild dogs are able to hunt impala more successfully, as impala are more vulnerable to predation in denser vegetation3. | Decreased ratio of dik-diks 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 dik-diks. | Wild dogs are able to hunt impala more successfully, because impala overheat more quickly than wild dogs4. | Decreased ratio of dik-diks to impala. |
| 1(Rabaiotti 2019), 2(Lucas 1983), 3(Augustine 2004); 3 (Ford *et al.* 2014); 4(Creel *et al.* 2016). | | | | |

**Table 2** Variables associated with the **number, intensity and duration of African wild dog hunts over a 24h period**. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 2) for the total duration (in minutes) of morning, evening, daytime and night time hunts combined; the mean intensity of the hunts; and the number of hunts. The sum of weights for 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 | Sum of weights (n) |
| Number of hunts | Intercept | 0.6464 | 0.4558 | 0.8369 | — (3) |
| Moonlight (moonlit hours) | 0.0084 | 0.0013 | 0.0155 | 1.00 (3) |
| Denning | -0.0045 | -0.1276 | 0.0868 | 0.22 (1) |
| Temperature (°C) | 0.0004 | -0.0030 | 0.0038 | 0.21 (1) |
| Total duration of hunts (minutes) | Intercept | 321.7457 | 254.2567 | 389.2346 | — (3) |
| Temperature (°C) | -0.2510 | -3.0739 | 2.5719 | 1.00 (3) |
| Moonlight | 1.3351 | 0.0190 | 2.6512 | 1.00 (3) |
| Denning (Yes) | 21.6363 | 1.3947 | 41.7694 | 1.00 (3) |
| Rainfall | -4.2384 | -18.2746 | 9.7977 | 0.32 (1) |
| Rainfall:Temperature | 0.1627 | -0.3610 | 0.6863 | 0.32 (1) |
|  | Denning:Temperature | -0.0081 | -12.0277 | 12.0116 | 0.32 (1) |
| Mean Intensity of hunts | Intercept | 42.2066 | 34.9384 | 49.4748 | * (2) |
| Denning | 2.3456 | 0.2765 | 4.4147 | 1.00 (2) |
| Temperature (°C) | -0.2231 | -0.3651 | -0.0810 | 0.32 (1) |

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| 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) |
| midday | Intercept | 0.0772 | 0.0650 | 0.0894 | (1) |
| Temperature | 0.0014 | 0.0011 | 0.0017 | 1.00 (1) |
| evening | Intercept | 0.0948 | 0.0878 | 0.1018 | (1) |
| night | Intercept | 0.0583 | 0.0625 | 0.0541 | (1) |
| **Dik-diks** |  |  |  |  |  |
| morning and evening | Intercept | 0.1211 | 0.1011 | 0.1412 | (1) |
| midday | Intercept | 0.1288 | 0.1102 | 0.1474 | (1) |
| night | Intercept | 0.1005 | 0.0712 | 0.1296 | (1) |
| **Wild dogs** |  |  |  |  |  |
| morning and evening | Intercept | 0.1179 | 0.0976 | 0.1384 | (1) |
| Denning | -0.0504 | -0.0391 | -0.0616 | 1.00 (1) |
| night | Intercept | 0.1610 | 0.1243 | 0.1976 |  |
|  | Denning | -0.1694 | -0.1861 | -0.1526 | 1.00 (1) |

**Table 3** Variables associated with **selection of woody cover** by African wild dogs, impala, and dik-diks. 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, the only model with ΔAICc<2, for African wild dog consumption of impala.

|  |  |  |  |
| --- | --- | --- | --- |
| Explanatory variable | Estimate | Lower 95% CI | Upper 95% CI |
| Intercept | 0.7427 | 0.4771 | 1.0083 |
| Mean maximum temperature over the previous 7 days | -0.0207 | -0.0298 | -0.0117 |

**Figure 1** Daily movement patterns of African wild dogs. Activity measured by collar-mounted accelerometers fitted to 18 wild dogs (A); blue bands denote the start and stop times used to classify morning and evening hunts. Hunts tend to fall before and after the daily maximum air temperature (B).

A screenshot of a cell phone

Description automatically generated**Figure 2** Percentage of hunts and total activity which fall in Morning (start between 04:55:39 and 06:56:04 and end between 07:30:41 and 12:51:33), Midday (start between 06:56:05 and 16:01:54 and end between 12:51:34 and 18:47:02), Evening (start between 16:01:55 and 18:26:52 and end between 18:47:03 and 21:06:56) and Night (start between 18:26:53 and 04:55:38 and end between 21:06:57 and 07:30:40) 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, dik-diks and African wild dogs across time periods. Locations recorded between sunrise and the third quartile of end time for wild dog hunting bouts were classed as morning; locations recorded between the first quartile of the start time of evening hunting bouts and sunset were classified as evening; locations between morning and evening were classified as midday and locations between sunset and sunrise were classified as night.



Chart

Description automatically generated with medium confidence

**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. Points represent the means for each 1°C interval, vertical bars indicate the standard errors. 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.