From coursers to croppers: temperature mediated diet shifts in African wild dogs in a two-prey system

# Abstract

How species are impacted by climate change is dependant on species interactions. There has been suggestions that predators will benefit from rising temperatures because larger bodied prey is impacted more, decreasing chase times. African wild dogs, however, negatively impacted by high temperatures. This paper investigates how wild dog and two primary prey species respond to high temperatures.

# Introduction

Climate change is increasingly impacting species globally, leading to range contraction, demographic impacts and even extinctions (Wolfe et al., 2005; Parmesan, 2006; Pounds et al., 2006; Welbergen et al., 2008; Waller et al., 2017). Predicting the impacts of climate change on species will be key to implementing conservation interventions designed to mitigate the worst impacts of changes in temperature and rainfall on species. Species interactions are key in structuring ecological communities and many species interactions are modified by climatic factors (Rall et al. 2010; Harley 2011; Allan et al. 2015). The ways in which species respond to changing environments is often altered by, or even a result of, species interactions (Petchey et al. 1999; Wilmers et al. 2007; Guiden et al. 2019). Despite this, the vast majority of the literature on climate change impacts focuses on single species, and the majority of papers looking at multiple species have focused on exothermic species, particularly arthropod-plant systems and the marine environment (Petchey et al. 1999; Voigt et al. 2003; Harley 2011). Little work has been done on climate induced changes to species interactions in endotherms, and the applicability of the studies on fish and arthropods to mammalian and avian species is unclear. Despite this, large-scale models of climate change impacts on ecosystems base numerous assumptions on predation and ecosystem dynamics, such as increased attack rate at high temperatures, on findings from exothermic species (Newbold 2018).

In exothermic species higher temperatures generally leads to predation rates through higher attack speeds (Wollkind and Logan 1978; Petersen and DeAngelis 1992; Vucic-Pestic et al. 2011), although this is not universally the case (Englund et al. 2011). As a result it is often assumed that exothermic predators will benefit from warming as capture rates of prey will increase as temperatures rise (Weetman et al. 1998; Vucic-Pestic et al. 2011). For endotherms, however, Bergman’s rules states that larger species are found more in cooler climates (Bergmann 1847), as they have a lower surface area to body size ratio and therefore dissipate less body heat into their environment (Peters 1986). This means that larger species would be expected to struggle to thermoregulate at high temperatures (Gardner et al. 2011). In cases where an endothermic predator is larger than its prey species it would be expected to have a lower capture rate at higher temperatures, and where the predator was smaller than the prey species it would be expected to have a higher capture rate at higher temperatures. Because of this, species are often predicted to decrease in size as the climate warms (Edeline et al. 2013).

In contrast to this, the trophic sensitivity hypothesis states that predators are expected to be less tolerant of environmental stress than prey species (Cheng et al. 2016). Similarly, a review of species in grasslands across trophic groups found that organisms higher up the food chain were more sensitive to changes in climate, with producers the least affected and carnivores the most affected (Voigt et al. 2003). The decoupling of predator-prey interactions is a key way in which climatic changes can impact both predator and prey population dynamics, and which commonly negatively impacts predator species (Winder and Schindler 2004; Durant et al. 2007; Guiden et al. 2019). Particular focus in the literature has been given to the uncoupling of predator-prey dynamics through phenological shifts, whereby timing of breeding events or migration changes, leading to important life history events becoming asynchronous (Yang and Rudolf 2010). Predation rates can be lowered through smaller scale behavioural changes in either predator or prey however, through changes in behaviours such as timing of activity and habitat use (Cunningham et al. 2013; Martin et al. 2015). In order for predators to feed successfully on prey species there must be overlap in habitat use in both space and time, and lower overlap results in lower predation rates, and consequently lower energy take for the predator (Guiden et al. 2019). Both space use (Cunningham et al. 2015; Pigeon et al. 2016) and timing of activity (Oseen and Wassersug 2002; Hetem et al. 2012; Rabaiotti and Woodroffe 2019) have been shown to shift in response to climate in a variety of species, and this can result in lower levels of habitat overlap between predators and prey.

The African wild dog, *Lycaon pictus,* an endangered species of canid, has been found to change its activity levels and distances travelled in response to high temperatures (Rabaiotti and Woodroffe 2019). These lower levels of activity at high temperatures may be energetically positive (Creel et al. 2016) or negative (Woodroffe et al. 2017) to the species. African wild dogs feed on a variety of prey species, ranging in size from wildebeest to hares (Woodroffe et al. 2005, 2007; Davies-Mostert et al. 2013). In Laikipia, Kenya, where wild dogs have been shown to increase nocturnal activity in response to higher temperatures, wild dogs’ main prey species are impala (*Aepyceros melampus*, mean 40kg), and dik-diks (*Madoqua guentheri*, mean 5kg) (Woodroffe et al. 2007). High temperatures could influence the predator-prey relationship between wild dogs and both prey species by altering spatial overlap, temporal overlap, or hunting success.

Wild dogs are crepuscular, with the vast majority of hunts occurring at dawn and dusk, outside of the heat of the day when light levels are still high enough to hunt (Woodroffe et al. 2017). The timing of wild dog hunts has been shown to shift in response to high temperatures, with less activity and shorter distances travelled in the day, and higher activity and longer distances travelled at night (Rabaiotti and Woodroffe 2019). This change in activity could result in increased temporal and spatial overlap with prey species; through activity times aligning more closely with when prey species are easier to hunt; or decreased temporal overlap with prey species through an increase in activity when prey are harder to hunt, or due to shorter hunt periods leading to decreased prey capture.

While dik-diks live in territorial pairs (Komers 1997), impala often aggregate in ~0.5-hectare clearings called “glades”(Ford et al. 2014). Glades are derived from abandoned cattle bomas, and persist for decades after their original clearance (Young et al. 1995). Although impala and other herbivores are attracted to glades by their nutrient-rich grasses, they are primarily used because the open habitat facilitates better detection of predators (Augustine; Ford et al. 2015). We would expect larger bodied animals to have a greater need to seek shade, and therefore in hot weather impala should move away from glades to denser habitat. Similarly larger bodied African herbivores were found to experience the greatest decrease in time spent feeding on hot days, which would be energetically costly for the species (du Toit and Yetman 2005). Wild dogs have been found to have better capture rates in higher vegetation (Fanshawe and FitzGibbon 1993), and lower energy intake may make impala more vulnerable to predation. This means that both the change in habitat use by impala and lower energy intake as a result of high temperatures would likely be advantageous for wild dogs, increasing predation rates on impala, as a result of both increased habitat overlap and hunting success rate. Similarly, impala would be expected to overheat more quickly at high temperatures due to their large body size (Peters 1986), leading to shorter chase distances, reducing wild dog daytime activity levels whilst energetically benefitting the predator (Creel et al. 2016).

Although wild dogs hunt mainly by day, their prey may be more predictably located by night. The greatest aggregations of impala in glades occur at night, when most predators are principally active, and when impala largely avoid foraging (Jarman and Jarman 1973). Wild dogs might therefore locate impala more easily by night than by day, meaning that increased nocturnal activity at high temperatures increases the spatial and temporal overlap between wild dogs and impala, compensating for decreased temporal overlap at high temperatures in the day. This would lead to greater predation risk on impala in hot weather.

Here we investigate movement and habitat use in the African wild dog and two of its key prey species, impala and dikdik, change in response to rising temperatures, and examine how wild dog diet is influenced as a result. We expect to see hunts in wild dog becomes shorter at higher temperatures. Animals with larger body size would have a greater need to thermoregulate, and therefore impala, but not dikdik, would be expected to move into more shaded areas, increasing habitat overlap between predator and prey. We would expect wild dog diet shift towards impala at high temperatures as a result. On the other hand, high temperatures may reduce the habitat overlap between wild dogs and impala through shorter foraging times in impala and wild dogs when the weather is hotter. We would therefore expect to see lower proportion of diet made up of impala at high temperatures.

# Hypotheses

H1: Hot weather benefits African wild dogs

H1a) On hot days African wild dogs have fewer, shorter and less intense hunts  but compensate for this by increasing the frequency, length and intensity of nocturnal hunts

H1b) African wild dogs find it easier to hunt impala at night

H1bi) Impala congregate in glades at night

H1bii) Wild dogs hunts target glades when hunting at night

H1c) Prey are easier to hunt when it is hot

H1ci)  Habitat use by impala and wild dogs is more similar when it is hot

H1cii) Habitat use by dikdik and wild dogs is more similar when it is hot

H1d) Wild dogs are more likely to eat impala when it is hot

H0: Hot weather does not benefit African wild dogs

H0a) On hot days African wild dogs do not compensate for changes to crepuscular hunts by increasing the frequency, length and intensity of nocturnal hunts

H0b) African wild dogs do not find it easier to hunt impala at night

H0bi) Impala do not congregate in glades at night

H0bii) Wild dogs hunts do not target glades when hunting at night

H0c) Prey are not easier to hunt when it is hot

H0ci) Habitat use by impala and wild dogs is not more similar when it is hot

H0cii) Habitat use by dikdik and wild dogs is not more similar when it is hot

H0d) Wild dogs are less likely to eat impala when it is hot

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| --- | --- | --- | --- | --- | --- | --- | --- |
| Behaviour | Explanation | Predicted change at high temperature | | | Consequence for predation risk | | |
| wild dog (23kg) | impala (40kg) | dikdik (5kg) | impala | dikdik | relative risk |
| Habitat selection | All move to more shaded habitat. Predict greatest change for larger-bodied species, which need largest shade patches. | intermediate increase in preference for dense habitat    **NOT UPHELD** | greatest increase in preference for dense habitat    **UPHELD** | smallest increase in preference for dense habitat  **UPHELD** | Increased predation risk due to increased spatial overlap | Smaller increase in predation risk as less habitat overlap | impala>dikdik        **NOT UPHELD** |
| Chase distance | All species overheat when running, but largest-bodied species overheat first | intermediate reduction in chase distance      **CAN’T TEST** | greatest reduction in chase distance      **CAN’T TEST** | smallest reduction in chase distance    **CAN’T TEST** | Increased predation risk as larger than wild dogs and overheats first | Reduced predation risk as smaller than wild dog and overheats less | impala>dikdik          **NOT UPHELD** |
| Time spent foraging during daylight | All spend less time foraging in daylight, predator shows greatest response because hunting generates more body heat than grazing/browsing | Greatest reduction in daytime foraging      **UPHELD** | Little/no reduction in daytime foraging      **INCREASE STEP LENGTH** | Little/no reduction in daytime foraging      **NO DIFFERENCE** | Reduced predation risk: less temporal overlap. Less abundant so less likely to be found before wild dogs stop hunting | Increased predation risk: on shorter hunts wild dogs select less rewarding but more abundant prey | dikdik>impala          **UPHELD** |
| Time spent foraging at night | All species take advantage of cooler temperatures at night. Predict greatest response for species which lose most daytime foraging time. | Greatest increase in nocturnal activity        **UPHELD** | Little/no increase in nocturnal activity      **NO DIFFERENCE** | Little/no increase in nocturnal activity      **NO DIFFERENCE** | Increased predation risk as predictably located in glades, which wild dogs can target. Increased spatial and temporal overlap.  **NOT UPHELD** | No increase in predation risk as no increase in spatial or temporal overlap | impala>dikdik              **NOT UPHELD** |

# Methods

## Study area

The focal area for this study was the Mpala Research Centre (MRC), a 200 km2 private wildlife conservancy in Laikipia County, Kenya (0°17’ N, 36°53’ E). Principal habitats are semi-arid savanna, acacia bushland, wooded grassland, rocky escarpments, and riverine thickets22. Due to its location close to the equator, MRC experiences little seasonal variation in temperature; daily maximum temperature ranges from 20-37°C. Mean annual rainfall is 500-600mm, and precipitation varies both seasonally and between years23.

MRC hosts 22 species of wild ungulate, of which dik-diks (Madoqua guentheri) and impala (Aepyceros melampus) are the first and second most abundant respectively23,24. Large predators are common, and include lion (Panthera leo), leopard (P. pardus), cheetah (Acinonyx jubatus), spotted hyaena (Crocuta crocuta) and African wild dog (Lycaon pictus). The predominant human activity in the area is cattle ranching.

## Data collection

### Impala

Between May and June 2011, 20 adult female impala (each from a different herd) were caught with drive nets (Kenya Wildlife Service) or net guns operated from a helicopter (Frontier Helicopters, Whakatane, New Zealand). Each individual was fitted with a Global Positioning System (GPS) collar (Savannah GPS-UHF, Savannah Tracking Ltd, Nairobi, Kenya), which recorded a location every 20 minutes. Full details of collaring procedures are provided in Ford et al. (2014)14.

### Dik-diks

Between July 2010 and September 2011, 15 adult female dik-diks were caught on moonless nights, using portable spotlights and long-handled nets. Each individual was fitted with a 200g GPS collar (Savannah Tracking Ltd, Nairobi, Kenya), which was programmed to record a location every 10 minutes. The capture methods are described in Komers (1996)25, and full details of collaring procedures can be found in Ford and Goheen (2015)24.

### Wild dogs

Between 2011 and 2016, GPS collars were fitted to 15 wild dogs (GPS-Plus, Vectronic Aerospace GmbH, Berlin, Germany). Although there was a brief period when two dogs in the same pack were collared, the data for the overlap period had been deleted for one of the animals to ensure independence. As well as recording locations at specific times over 24 hours (01:00, 06:30, 07:00, 07:30, 08:00, 13:00, 18:00, 18:30, 19:30), the collars also contained accelerometers, which provided a recording (every five minutes) of acceleration on a scale of 0 to 255, both in the horizontal and vertical plane. Capture was achieved by darting from a vehicle at a distance of 10-20m. Full details of the collaring procedures are provided in Woodroffe 201126. Denning periods were identified by the characteristic pattern of dogs returning repeatedly to the same location. Pack size was recorded by observation whenever a pack was relocated.

### Environmental variables

The environmental conditions associated with each GPS-collar location were characterised. The timings of dawn, dusk, moonrise and moonset, and lunar illumination (the proportion of the moon illuminated on a given night) at MRC were estimated using data from the US Naval Observatory (http://www.usno.navy.mil/) and the R package “suncalc”27. Day and night were separated by dawn and dusk. For night-time locations, “moonlight” was the lunar illumination at that point in time. For locations recorded during the day, the previous night’s lunar illumination was multiplied by the time for which the moon had been visible, to give a measure of total moonlight on the previous night. Both of these variables relating to moonlight are known to affect the activity of wild dogs, impala and dik-diks9,13,28,29.

Weather conditions were represented as daily maximum temperature (°C), and total daily rainfall (mm), recorded on site at MRC30. As we were interested in the effects of daytime temperature on behaviour during the subsequent night, maximum temperature referred to the highest recorded temperature in a 24-hour period from dawn to dawn, following Rabaiotti and Woodroffe (in review)9. Following Ford et al. (2014)14, wet “phases” were periods for which > 50mm of rain had fallen in the previous four weeks; periods with ≤ 50mm of rain in the previous four weeks were classed as dry “phases”. This definition reflects the unpredictable seasonal rainfall pattern at MRC.

## Linking locations to habitat features

The habitat features associated with each GPS-collar location were characterised using Geographic Information System (GIS) software and maps of habitat features at MRC provided by Ford et al. (2014)14. Using QGIS (QGIS Desktop 2.18.16), locations which fell outside MRC were removed from the data; this was a negligible proportion for impala and dik-diks, but led to the exclusion of data for six wild dogs which did not visit MRC while collared. For all remaining locations, a value for woody cover was extracted from a raster layer, which had been created from a 2011 Quickbird satellite image (Digital Globe, Longmont, CO, USA). Woody cover was characterised as the proportion of overstory cover within a circular area of radius 40m14.

The QGIS plugin “NNJoin” was then used to calculate the shortest straight-line distance (in decimal degrees) between each location and the nearest glade (glades had been manually digitised from the same satellite image). It was assumed that shorter distances indicated greater likelihood of glade usage; points falling within glades produced a distance value of 0. For impala and dik-diks, whether each location fell inside (1) or outside (0) of a glade was recorded as an additional metric of glade usage; this variable was not calculated for wild dogs, due to very low numbers (19/2176) of hunt locations falling within glades. While all wild dogs and impala had home ranges (calculated as 100% minimum convex polygons) which contained at least one glade, the same was true for only 9/15 dik-diks. Data for the remaining six dik-diks were therefore excluded from the glade calculations, as measures of glade use would not be ecologically relevant for dik-diks which cannot visit glades.

## Linking wild dog locations to behaviour

For wild dogs, GPS-collar locations recorded during hunts were identified by using the accelerometers to recognise periods of intense activity. Accelerometer measurements in the horizontal and vertical planes were summed to give an overall measure of activity (from 0 to 510). An activity bout was defined as a period with activity >0 followed by three consecutive records of 0 activity, and a hunt was defined as a bout lasting >20 minutes with a total activity >500. These conditions excluded bouts which were too short to relate to hunting periods, or which related to less energetic behaviours, such as socialising.

For analyses of habitat use the timestamp associated with each wild dog GPS-collar location was then used to identify locations associated with hunts; the remaining data were excluded. For analyses of hunting behaviour all activity bouts classified as hunts were included in the analysis.

## Spatial and temporal autocorrelation

As the dik-dik and impala GPS collars recorded locations at a relatively high frequency, these data were vulnerable to both spatial and temporal autocorrelation. To control for these effects, the data were divided into four separate time periods (“parts of day”): Morning, Middle of Day, Evening, and Night. “Night” was defined as the period between dusk and the subsequent dawn. Daylight hours were divided with reference to the times when wild dogs were typically hunting, as these were the periods of greatest relevance to this study. “Morning” was between dawn and the third quartile of morning hunt stop times (approximately 3hr30min later); so, if dawn was at 06:00 (it varied from 05:52-06:23), any GPS-collar locations recorded between then and 09:30 were within the morning hunting period. “Evening” was between the first quartile of evening hunt start times (approximately 2hr10min before dusk) and dusk (18:41-19:12). “Middle of Day” referred to times that fell outside those periods, and contained just 20/1724 daytime hunt locations.

For each part of day, the average value for woody cover, the minimum glade distance, and the proportion of points within glades were taken. For nights, an average of the moon’s illumination was also calculated. Rainfall, maximum temperature, phase (wet/dry), and previous night’s moonlight were recorded at daily intervals and did not require averaging.

## Statistical analyses

### Habitat selection

In order to assess habitat use, each species’ GPS locations were compared with an equal number of random points. For impala and dik-diks, a number of random points equal to the number of GPS locations was generated within each individual’s home range (calculated as a 100% minimum convex polygon). As individual wild dogs were wide-ranging, the random points (equal to the number of recorded hunt locations) were generated within a single MCP encompassing the full range of wild dog movement on MRC. The MCP did not therefore include the south-west corner of MRC, which wild dogs rarely visit.

For each random point, values for woody cover and distance to nearest glade were extracted. The values for the random points were then compared to those for the real GPS locations, using Mann-Whitney U tests.

Analyses were carried out for all hunting periods combined, as well as subsets of the data for nocturnal and crepuscular hunting periods, allowing assessment of whether each species used glades and woody cover in proportion to their availability. Finally, a Kruskal-Wallis test was used to determine whether different species exhibited divergent habitat preferences.

### Linear mixed-effects models

Linear mixed-effects models (R package “lme4”32) were used to test the associations between the response variables and the predictor variables (see Table 1 above). Individual identity (all models), and date (overall models only) were included as random effects; this accounted for individual or date specific effects, which were not relevant to this study.

Separate models were used for each response variable. Overall models were run for all parts of day combined, to facilitate comparisons between morning, middle of day, evening and night. If the results revealed significant differences between time periods, then separate analyses were conducted for each part of day; if not, then morning and evening were combined in a single “crepuscular periods” model. Crepuscular periods contain both the majority of wild dog hunts and the highest levels of prey feeding activity13,17. The middle of the day was modelled separately for prey only (wild dogs were exclusively resting) to investigate the behaviour of impala and dik-diks at times when wild dogs rarely hunted. Night was modelled separately to assess the effects of moonlight.

All daytime models included the variable describing the previous night’s moonlight. The night models included the measure of average lunar illumination. Wild dog models included two additional variables: pack size (6-24) and status (denning/not denning), both of which influence wild dog hunting behaviour12,33,34.

For each response variable, a list of at least 15 potential models was created, each containing different combinations of the individual predictor variables, and interactions between them. Combinations of predictor variables and interactions were only included in the potential models if they were considered to be ecologically relevant, based on this study’s hypotheses and the literature. The variables “phase” and “rainfall” were never included in the same models as, although they relate to distinct properties of the environment, they are nevertheless positively correlated (days with high rainfall usually occur in association with wet phases). The R package “MuMIn”35 was used to produce a model selection table from our list of potential models. Models were compared using their Akaike Information Criterion (AIC); models with lower AIC values are of higher statistical quality. The “best” model was compared to all the others by the difference in their AIC values (Δ AIC). A Δ AIC < 2 suggests substantial evidence for a model, and a Δ AIC < 7 suggests a moderate level of support. Alternative models with a Δ AIC < 7 were reported.

# Results

## Time spent foraging

Hunts had mean duration of 230 minutes and mean total activity of 6707, emphasising the bimodal nature of wild dog behaviour. African wild dog hunts were most likely to happen in the morning, followed by the evening and then at night (Table 1-3). Temperature was strongly associated with the duration, intensity, start time and stop time of morning and evening hunts, and the occurrence of night-time hunts (Table 1-3). At high temperatures wild dogs had shorter, less intense morning (Table1) and evening hunts, and evening hunts were less likely to occur (Table 2). Night time hunts were more likely to occur following hot days and there a weaker association with length and duration, with hunts following hot days longer and of greater intensity (Table3). There was a strong association between temperature and the start time of morning and evening hunts (Table 1 and 2), and a weak association with the start and stop time of night-time hunts (Table 3). At higher temperatures morning hunts started and ended earlier (Table 1), evening hunts started later (Table 2) and night time hunts started earlier and ended later (Table 3). There was a positive interaction between temperature and rainfall on the duration of morning  (Table 1) and evening hunts and the intensity of evening hunts (Table 2).

Levels of moonlight and the time of moonrise were the variables with the strongest influence on all aspects of nocturnal hunts (Table 3). Night time hunts were more likely to occur and were longer and more intense when moonlight levels were higher, starting and ending earlier, with the start time of night time hunts strongly associated with the timing of moonrise (Table 3). The intensity, duration, start and stop times of evening hunts were associated with moonlight - evening hunts were shorter, started and ended later, and less intense when proceeding nights with greater levels of moonlight (Table 2). The occurrence of morning hunts was strongly associated with moonlight the previous night, with morning hunts less likely to occur when the previous night had higher moonlight levels (Table1).

Denning was strongly associated with the intensity and duration of morning and evening hunts, which were longer and more intense during the denning period (Table 1 and 2). Denning was also associated with the start and stop times of morning and evening hunts, with both morning and evening hunts starting and ending later when wild dogs are denning (Table 1 and 2). There was a weak positive association between denning and the likelihood of occurrence of evening hunts (Table 2), and a negative association between denning and the occurrence of night-time hunts (Table 3). There was a positive interaction between the effect of denning and temperature on the duration of morning hunts (Table 1), and a negative interaction between the effect of denning and temperature on the duration of night-time hunts (Table 3). Denning had a small positive interaction with the effect of temperature on the duration of evening hunts but a negative interaction with the effect of temperature on intensity (Table 3). This indicates that evening hunts were shorter when it was hot but less so during the denning period, but were even less intense on hot days during the denning period than outside it.

Impala had longer shorter distances between GPS points (step length) in the day when maximum temperatures were higher. Impala had longer step lengths in the morning compared to the middle of the day, and shorter step lengths in the evening. Impala had longer step lengths in the day during periods of wetter seasonality. There was a negative interaction between the impacts of maximum temperature and season on step length. At night Impala had shorter step lengths when there was more moonlight and in the wet season, with a negative interaction between season and moonlight.

Dikdik had longer step lengths in the day at higher rainfall levels. At night dikdik had shorter step lengths at higher moonlight levels and during periods of wetter seasonality.

## Habitat Use

There were significant differences between woody cover use for each of the three species (Kruskal-Wallis chi-squared = 13151, df=2, p<0.001). Dik-diks preferred woodier areas than impala, and wild dogs hunted in areas of significantly denser cover on average than those preferred by either of their prey species.

### Impala

Impala were found in areas with a lower proportion of woody cover than would be expected at random (W = 3.07 x 1010, p < 0.001). This effect was consistent for crepuscular (W = 1.09 x 1010, p<0.001) and nocturnal hunting periods (W = 4.73 x 109, p<0.001). Impala were also found closer to glades than expected at random (W = 3.62 x 1010, p<0.001). This was true for crepuscular (W = 1.08 x 1010, p<0.001) and nocturnal periods (W = 7.45 x 109, p<0.001). There was a significant difference between probability of being in glades and woody cover use between the morning and evening periods (Table 4).

Time of day had the greatest association with the distance of impala to glades, the likelihood of them being in glades and their use of woody cover. Impala were closest to glades in the day followed by at night (Table 4). They were furthest from glades in the evening, which was also the time period that they were least likely to be found in glades (Table 4). Impala were most likely to be found in glades, and in the lowest levels of woody cover, at night. The highest levels of woody cover were used by impala in the mornings (Table 4). Temperature, rainfall and seasonality both explained some of the patterns observed in distance to glades, with moonlight also associated with distance to glades at night. Temperature was strongly associated with woody cover use by impala in the morning and middle of the day, and somewhat associated with woody cover use in the evening. Impala were closer to glades and in greater levels of woody cover at higher maximum temperatures at all times of day(Table 4). Impala were less likely to be in glades in the morning and evening on hot days and more likely to be in glades on nights following hot days (Table 4).

The probability of impala being found in glades was associated with periods of wet seasonality in all daytime periods, particularly in the middle of the day (Table 4). Following wet seasonal periods impala were further from glades at all times of day other than during the evenings, and impala were more likely to be found in glades in daytime and evening periods following periods of wet seasonality. Wet seasonal periods were associated with woody cover use in the evenings and rainfall was associated with woody cover use at night. In evening periods impala were found in less dense woody cover following periods of wet seasonality (Table 4). Rainfall had a variable relationship with the likelihood of impala being in glades depending on the time of day. The likelihood of Impala glade use was strongly associated with and moonlight at night, with impala less likely to be in glades on nights with more moonlight (Table 4). There was some association between moonlight and distance to glades at night and in the evenings, with impala being found closer to glades at higher levels of moonlight. There was a weak association between the likelihood of impala being found in glades in the mornings and moonlight, with impala more likely to be found in glades in mornings following nights with high levels of moonlight (Table 4).

### Dikdik

There was no difference between dik-dik use of woody cover and random locations within their home ranges (W = 4.80 x 108, p = 0.1045). This was true for crepuscular (W = 1.38 x 108, p = 0.1029) and nocturnal periods (W = 1.03 x 108, p = 0.5257). Dik-diks were found further from glades than expected at random (W = 1.40 x 108, p<0.001). This was true for crespuscular (W = 4.03 x 107, p<0.001) and nocturnal hunting periods (W = 3.01 x 107, p<0.001). There was no significant between distance to glades, probability of being in glades and woody cover use between morning and evening (Table 5).

Rainfall variables – either seasonal periods of greater rainfall or rainfall on a daily scale – were most strongly associated with dikdik habitat use, with rainfall being strongly associated with distance to glades and season strongly associated with occurrence in glades and levels of woody cover in the day (Table 5). Dikdik were closest to glades when rainfall had been higher in that 24h period at all times of day (Table 5), and less likely to be in glades during seasonal periods with higher rainfall. During wetter seasonal periods dikdik were found in higher woody cover at all time periods other than the middle of the day, when they were found in more open areas (Table 5). There was a weak association between temperature and woody cover use during the middle of the day and in crepuscular periods, and a weak association between temperature and the likelihood of dikdik being found in glades during crepuscular periods (Table 5). At higher temperatures dikdik were more likely to be in glades, and in lower levels of woody cover, during crepuscular periods, and were found in higher levels of woody cover during the day. At night, there was an association between moonlight and habitat use, which was strongest for the likelihood of dikdik using glades (Table 5). Dikdik were found in areas with less woody cover, closer to glades and were more likely to be found in them at night when moonlight levels were higher (Table 5).

### Wild dogs

Wild dogs hunted in areas with a lower proportion of woody cover than expected at random (W = 2228900, p<0.001). While this effect was strong at night (W = 82250, p<0.001), there was no significant difference in woody cover between crepuscular hunt locations and random points (W = 1454100, p = 0.2744). There was no significant between distance to glades, probability of being in glades and woody cover use between morning and evening (Table 6).

Pack size was associated with distance to glades, particularly during crepuscular hunts (Table 6). African wild dogs hunted closer to glades at bigger pack sizes during both crepuscular periods and at night. Whether the wild dogs were denning was strongly associated with woody cover use(Table 6). When African wild dogs were denning they hunted closer to glades during crepuscular periods but further from glades during the night, and in less woody cover at all times of day. Wild dogs hunted further from glades at higher levels of moonlight. Temperature did not influence the location of wild dog hunts (Table 6).

## Wild dog diet

Wild dogs ate fewer impala at higher temperatures and when they were resident on pastoral land (Table 7)

# Discussion

On hot days African wild dogs have shorter, less intense crepuscular hunts with morning hunts occurring earlier and evening hunts later. Wild dogs were more likely to hunt at night following hot days, however nocturnal and evening hunts were more less likely to occur at lower moonlight levels. Impala selectively spend time in glades across the 24 hour period, and are most likely to be found in glades in the middle of the day and at night. Wild dogs do not appear to target glades when hunting at night, however, as there was no difference in the distance of wild dogs to glades between  crepuscular and nocturnal hunts. Both Impala and dikdik both occupied areas of lower woody cover on average than where wild dog hunts occurred. Impala were found in denser woody cover at high temperatures, more similar to that used by wild dogs, however they were also found closer to glades, particularly in the morning and at night, suggesting they are utilising woody cover closer to glades than that utilised most frequently by African wild dogs. Dikdik showed little response to high temperatures, and associations during the periods where wild dogs were hunting brought them into habitats that were less similar to those used on average for wild dog hunts. The results indicate that it is unlikely to be easier for wild dogs to predate on impala when it is hotter, and dietary analysis indicates that impala are less likely to be consumed at higher temperatures.

In line with Hypothesis 1a, temperature was an important determinant of wild dog hunt activity in the morning, evening and at night. During morning and evening periods hunts were shorter and less intense, and morning hunts were earlier, with evening hunts starting later. This is likely because on hot days the period when it is cool enough for wild dogs to hunt is shorter. Whilst wild dogs were more likely to hunt on nights following hot days, this appeared to be restricted by both denning and moonlight, with wild dogs 50% less likely to hunt during the denning period, and nearly 400% more likely to hunt on nights where there were twelve full moon hours as opposed to none. Night time hunts following hot days were longer and more intense. This suggests, in line with previous studies, that wild dogs were at least partially able to compensate for high temperatures by hunting at night.

Hypothesis 1b relates to whether this nocturnal activity meant that it was easier for African wild dogs to successfully hunt impala when engaging in night time hunts. Impala were more likely to be in and near glades at night compared to crepuscular periods and were in lower levels of woody cover, suggesting that impala congregate in glades, particularly during night-time hours. Wild dogs, however, did not appear to selectively target glades at night, as there was no difference in their distance to glades or use of woody cover between crepuscular and night time hunts.  This would suggest that wild dogs are not hunting impala selectively at night, and therefore that nocturnal hunts do not increase food intake over and above morning and evening hunts. Larger packs were found closer to glades at all times of day however which may indicate that larger packs selectively target impala more than smaller packs when hunting.

It has been suggested that hot weather may benefit African wild dogs by making prey, in particular prey with larger body sizes, easier to hunt as they overheat more quickly. Hypothesis 1c) suggests another mechanism by which it may be easier for wild dogs to hunt successfully in hot weather, through prey habitat use becoming more similar to wild dog habitat use. Impala moved into habitat with higher levels of woody cover on hot days, however the effect was small, and would not bring average woody cover use by impala in line with that of wild dogs even on hot days. Wild dog woody cover use did not change at high temperatures, again suggesting they do not selectively target impala when it is hotter. Impala used habitat closer to glades more in hot weather, areas that are spatially more dissimilar to those used by wild dogs when hunting. Dikdik habitat use was not greatly influenced by high temperatures, but where it was it was in a way that made habitat use less similar to that used by wild dogs. It would appear that while impala habitat use becomes more similar to the habitat wild dogs hunt in some ways, it becomes more dissimilar in others, and there is little change in the overlap of habitat use between wild dogs and dikdik. It seems therefore unlikely that wild dogs encounter prey at a significantly higher rate in hot weather.

Dietary analysis showed that Hypothesis 1d, that wild dogs consume impala at greater rates following periods of hot weather, was incorrect. Impala were found in a lower proportion of wild dog scats when it had been hotter over the previous 7 days, indicating that wild dogs are eating lower numbers of impala in comparison to dikdik. This reinforces our findings that wild dogs do not appear to be targeting impala during crepuscular periods or at night following periods of hot weather. It suggests alternatively that wild dogs may find it harder to successfully hunt impala during periods of hot weather, which indicates that the increase in nocturnal hunts does not compensate for the decrease in impala consumption due to the decrease in the occurrence, duration and intensity of daytime hunts. Shifts in hunt timings, and potentially prey habitat use, appear to be impacting the diet of African wild dogs.