

In hot pursuit: do high temperatures make it harder for wild dogs to find prey?

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Abstract

Climate change is a growing threat to biodiversity, and identifying the mechanisms by which species are affected is imperative for conservation. The African wild dog (*Lycaon pictus*) may be particularly vulnerable; wild dogs hunt less on hotter days, and persistent hot weather is associated with increased mortality and reduced reproductive success. This study investigated the hypothesis that these effects result from wild dogs' main prey species (impala, *Aepyceros melampus*, and dik-diks, *Madoqua guentheri*) spending more time in dense, shady cover on hot days. This might make them harder to locate, forcing wild dogs to compensate by hunting more at night when impala are predictably located in open areas ("glades").

While impala used denser cover on hotter days, dik-diks did not. However, rather than becoming harder to locate, impala were likely to have been more vulnerable to predation, as wild dogs preferred to hunt in denser cover. Wild dogs did not preferentially visit glades following hot days, suggesting that they were not compensating for high daytime temperatures by targeting aggregations of impala at night. The negative demographic effects of high ambient temperature on wild dogs are therefore unlikely to result from changes in the behaviour of their most important prey species.

Introduction

Climate change is a growing threat to biodiversity, with worst-case predictions forecasting the sixth mass extinction event in Earth's history¹. Many studies have attempted to predict the likely impacts of a changing climate on particular species, but these assessments are often constrained by limited knowledge of the mechanisms behind the effects of weather conditions on demography². In particular, while efforts have focused largely on temperate and polar regions, these mechanisms are less well understood for tropical species³. This study attempts to explore such effects in the African wild dog (*Lycaon pictus*).

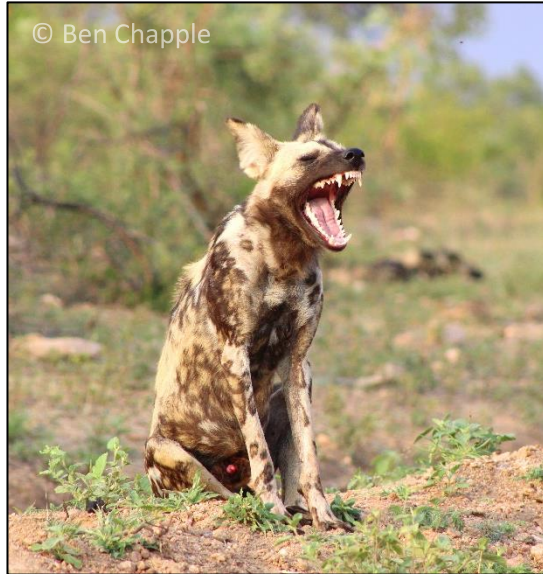


Figure 1: African wild dog

The African wild dog is an endangered species, with fewer than 700 packs remaining in the wild⁴. Native to sub-Saharan Africa, they are cursorial hunters, pursuing their prey at high speed and often over long distances^{5,6}. Although they possess few of the characteristics typically associated with climate change vulnerability^{2,7}, it has recently been suggested that wild dogs might be negatively impacted by increased ambient temperatures⁸. On hotter days, wild dogs spend less time hunting, potentially limiting food intake, and the persistence of hot weather is associated with reduced reproductive success and higher mortality⁸. Wild dogs appear to partially compensate for reduced diurnal activity by hunting more at night⁹.

The negative effects of high ambient temperatures on wild dogs may have a physiological basis; they may risk overheating while hunting⁸. However, meta-analyses of data from other species suggest that the impacts of climate change may be mediated more often by altered species interactions than by direct effects of temperature³. The effects of temperature on wild dogs might alternatively be explained by their prey spending more time in dense, shady cover on hot days, incidentally making them more difficult to locate (the “hidden prey hypothesis”). Similar heat sensitivity has been demonstrated in various ungulates, including the greater kudu (*Tragelaphus strepsiceros*) and Eurasian elk (*Alces alces*)^{10,11}. The challenge of finding prey on hot days could explain both the demographic impact of hot weather on wild dogs, and their greater nocturnality on subsequent nights⁹.

Although wild dogs hunt mainly by day, their prey may be more predictably located by night. At our study site in Kenya, wild dogs' main prey species are impala (*Aepyceros melampus*, mean 40kg), and dik-diks (*Madoqua guentheri*, mean 5kg)¹². While dik-diks live in territorial pairs¹³, impala often aggregate in ~0.5-hectare clearings called "glades"¹⁴. Glades are derived from abandoned cattle bomas, and persist for decades after their original clearance^{15,16}. 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^{14,16}. Consequently, the greatest aggregations of impala in glades occur at night when most predators are principally active, and when impala largely avoid foraging¹⁷. Wild dogs might therefore locate impala more easily by night than by day, potentially reducing the energetic cost of hunting, and allowing compensation for reduced daytime activity.

Regardless of which mechanism is responsible (overheating or hidden prey), increased nocturnal activity with higher temperature could explain the negative impacts of climate change on wild dogs. Under normal circumstances, wild dogs show strong spatial and temporal avoidance of other predators¹⁸; predation by nocturnally-active lions, hyaenas and leopards is the most important cause of natural mortality for wild dogs^{19,20}, and dogs are vulnerable to kleptoparasitism by hyaenas²¹. More frequent nocturnal hunting would be expected to raise wild dog mortality and reduce reproductive success by exposing both adults and pups to increased predation.

Distinguishing between these two hypotheses could inform wild dog conservation. If the overheating hypothesis is correct then stemming climate change, or focusing efforts on more temperate parts of the species' range, could be the only available conservation measures. However, if the impacts of temperature are mediated by interactions between habitat, competitors and prey, then wild dogs could be effectively conserved in areas with low densities of competing predators, even in the face of climate change; alternatively, there may be targeted forms of habitat management which could benefit the species.

In this study, I test the hidden prey hypothesis, using fine-scale data on the movements of wild dogs and their two main prey species to address three questions:

- 1. *Do wild dogs' prey spend more time in dense cover on hot days?***
- 2. *Do wild dogs hunt in denser cover on hot days?***
- 3. *When hunting at night, do wild dogs preferentially visit glades?***

Answering the first two questions should help to shed light on whether prey are indeed harder to find on hot days, and whether wild dogs shift their hunting behaviour, either in response to prey or to avoid the heat themselves. A resolution of the third question would show whether wild dogs seek out aggregations of impala in glades at night as a means of compensating for the negative impacts of reduced diurnal activity. In addition, I discuss the wider implications of my results for the relationships between wild dogs and their prey; I also address potential limitations of this study, and make recommendations for future research.

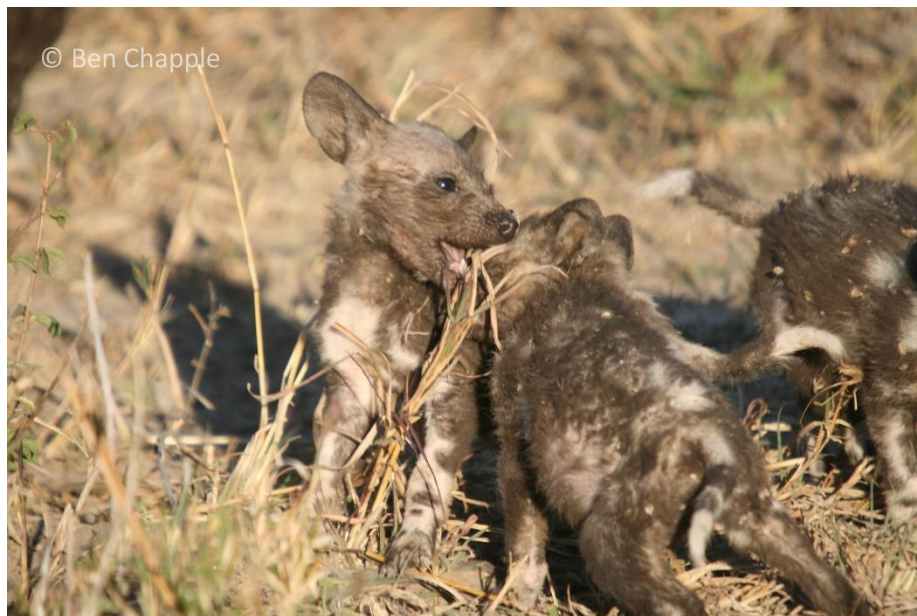


Figure 2: wild dog pups are vulnerable to predation by lions and hyaenas, especially when the adults hunt at night

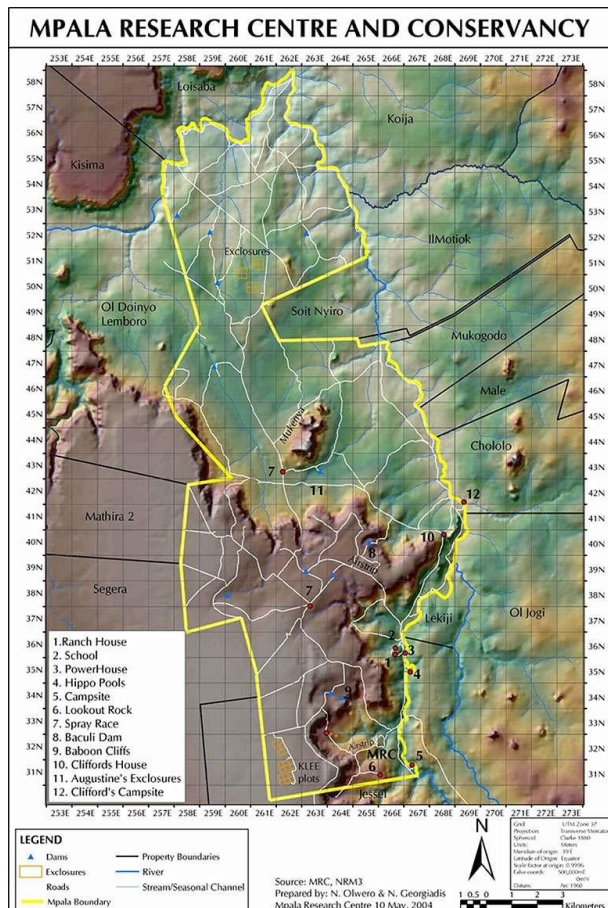


Figure 3: map of the Mpala Research Centre

(source: www.mpala.org)

Materials and 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 respectively^{23,24}. 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 ranching²⁴.

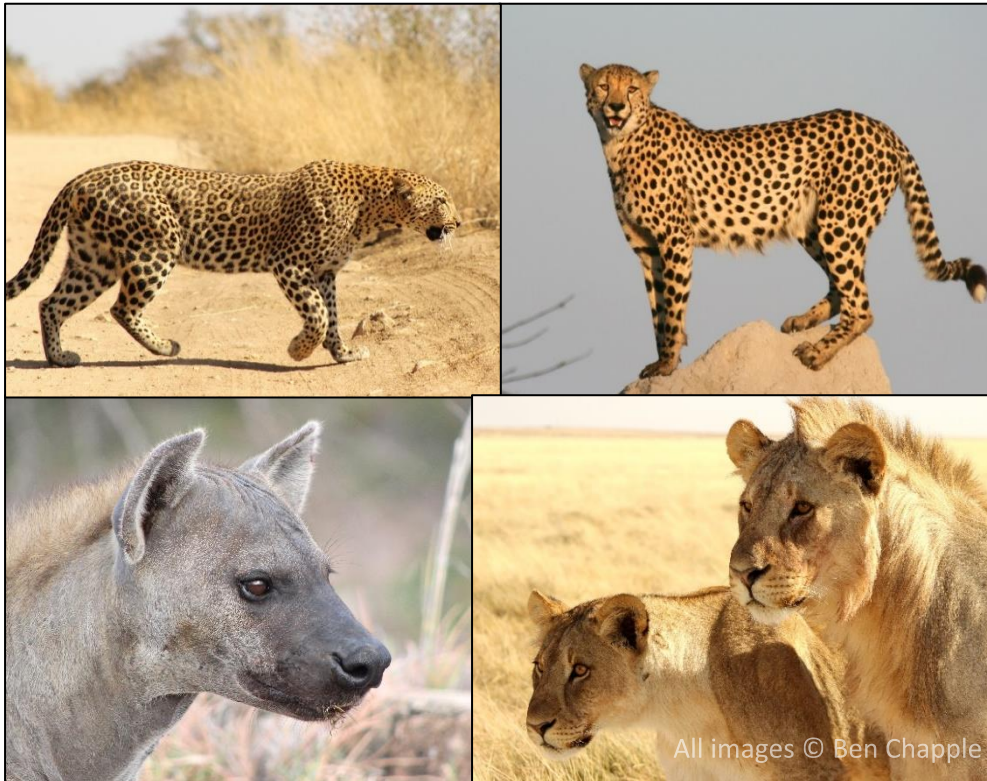


Figure 4: some of the large carnivores which occur alongside wild dogs at MRC. Clockwise from top left: leopard, cheetah, lion and spotted hyaena

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.



Figure 5: impala (left) and dik-dik (right, source: Wikimedia Commons)

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.



Figure 6: GPS-collared wild dog at MRC
(source: www.mpala.org)

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-diks^{9,13,28,29}.

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). Following Morrill (2017)³¹, 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. In reality, hunts had mean duration of 230 minutes and mean total activity of

6707, emphasising the bimodal nature of wild dog behaviour. These conditions excluded bouts which were too short to relate to hunting periods, or which related to less energetic behaviours, such as socialising.

The timestamp associated with each wild dog GPS-collar location was then used to identify locations associated with hunts; the remaining data were excluded.

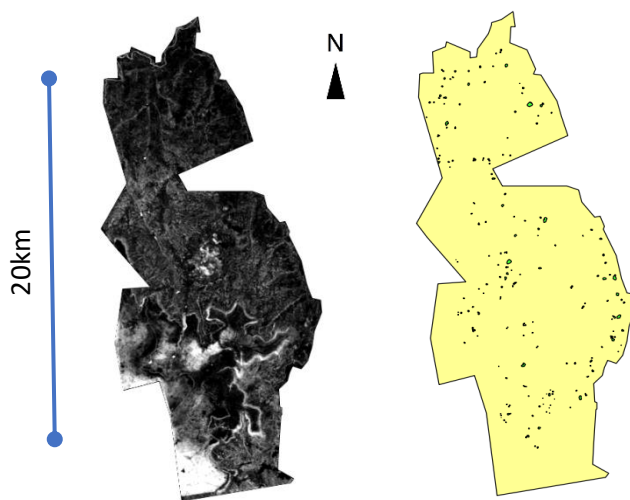


Figure 7: Maps showing woody cover (left, with woodier areas in white), and the locations of glades (right) at MRC.

(source: Ford et al. 2014)

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

Table 1: predictor and response variables used in linear mixed-effects models

| Predictor Variables | Response Variables |
|--|---|
| Part of day/period, rainfall, phase (wet/dry), daily maximum temperature | Woody cover |
| Moonlight (night only), previous night's moonlight (day only) | Distance to nearest glade |
| Pack size, pack status (wild dogs only) | Proportion of locations within glades (impala/dik-dik only) |

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 activity^{13,17}. 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 behaviour^{12,33,34}.

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

Habitat selection

Impala were found in areas with a lower proportion of woody cover than expected ($W = 3.07 \times 10^{10}$, $p < 0.001$). This effect was consistent for crepuscular ($W = 1.09 \times 10^{10}$, $p < 0.001$) and nocturnal hunting periods ($W = 4.73 \times 10^9$, $p < 0.001$).

Impala were found closer to glades than expected ($W = 3.62 \times 10^{10}$, $p < 0.001$). This was true for crepuscular ($W = 1.08 \times 10^{10}$, $p < 0.001$) and nocturnal periods ($W = 7.45 \times 10^9$, $p < 0.001$).

There was no difference between dik-dik use of woody cover and random locations within their home ranges ($W = 4.80 \times 10^8$, $p = 0.1045$). This was true for crepuscular ($W = 1.38 \times 10^8$, $p = 0.1029$) and nocturnal periods ($W = 1.03 \times 10^8$, $p = 0.5257$).

Dik-diks were found further from glades than expected ($W = 1.40 \times 10^8$, $p < 0.001$). This was true for crepuscular ($W = 4.03 \times 10^7$, $p < 0.001$) and nocturnal hunting periods ($W = 3.01 \times 10^7$, $p < 0.001$).

Overall, wild dogs hunted in areas with a lower proportion of woody cover than expected ($W = 2228900$, $p < 0.001$). 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 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 tended to hunt in areas of denser cover than those preferred by either of their prey species.

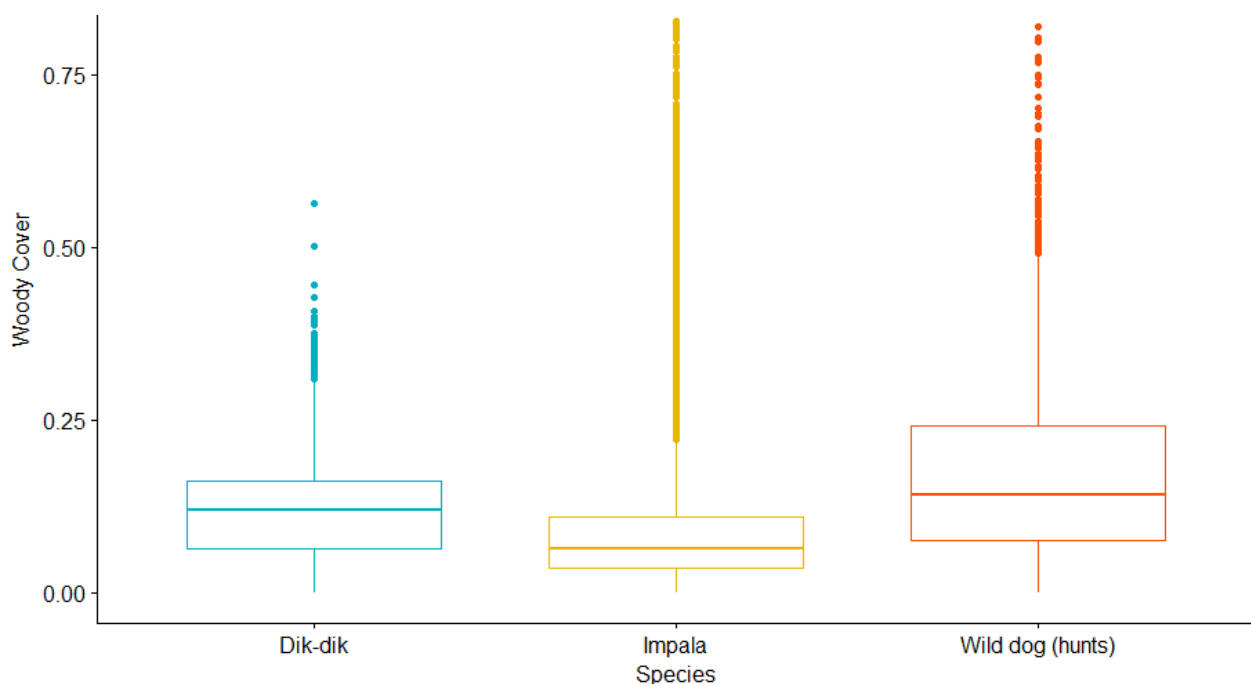


Figure 8: boxplots showing differences in overall woody cover use for dik-diks, impala and hunting wild dogs

Linear mixed-effects models

Table 2A – Impala: woody cover (overall)

| <u>Model</u> | <u>Part of day – Middle</u> estimate (±SE) | <u>Part of day – Evening</u> estimate (±SE) | <u>Part of day – Night</u> estimate (±SE) | <u>Maximum temperature (° C)</u> estimate (±SE) | <u>phase – Wet</u> estimate (±SE) | <u>ΔAIC</u> |
|--------------|--|---|---|---|---|-------------|
| 1 | 0.017 (±0.0008) | -0.0028 (±0.0008) | -0.039 (±0.0008) | 0.00098 (±0.0002) | -0.0015 (±0.0009) | 0 |
| 2 | 0.017 (±0.0008) | -0.0028 (±0.0008) | -0.039 (±0.0008) | - - | - - | 4.85 |

Both alternative overall models indicate that, relative to morning, impala used woody cover more in the middle of the day, less in the evening, and least at night. Model 1 additionally indicates that impala used more woody cover on days with higher maximum temperature, and less woody cover during wet phases.

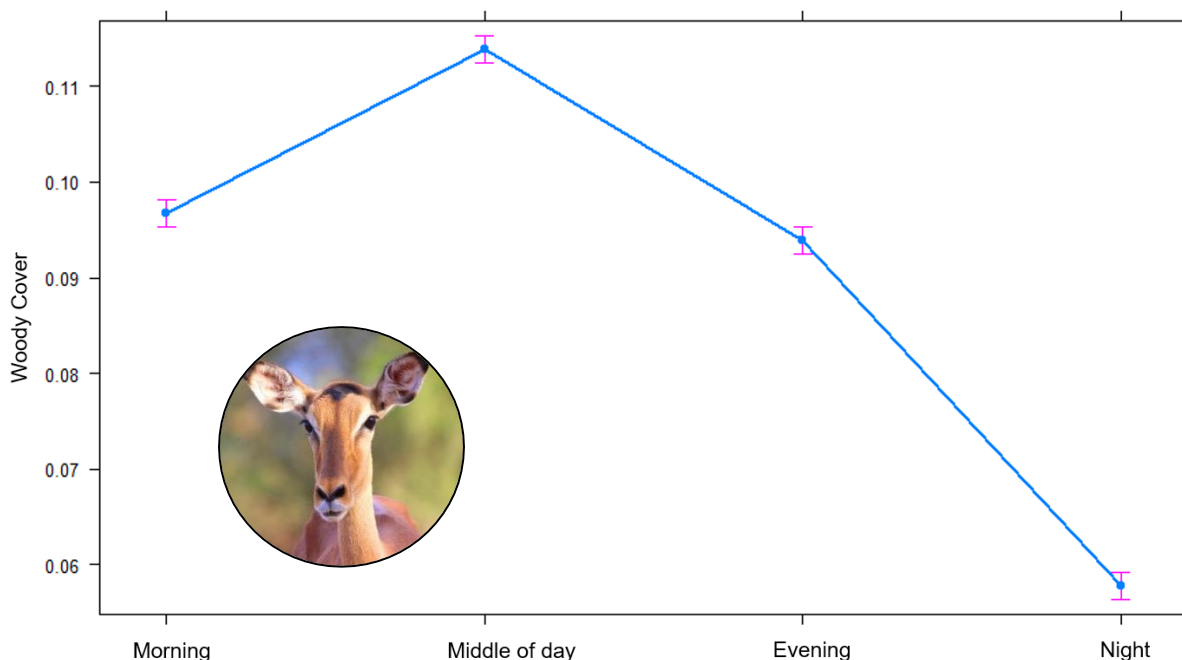


Figure 9: graph showing how use of woody cover by impala varies over the course of the day

Table 2B – Impala: woody cover (by part of day)

| <u>Part of day</u> <u>(Model)</u> | <u>Maximum temperature</u> <u>(° C)</u> estimate (±SE) | <u>Phase – Wet</u> estimate (±SE) | <u>Previous night's moonlight</u> estimate (±SE) | <u>Rainfall (mm)</u> estimate (±SE) | <u>Moonlight</u> estimate (±SE) | <u>ΔAIC</u> |
|--------------------------------------|---|---|--|---|---------------------------------------|-------------|
| Morning (1) | 0.0019 (±0.0003) | - - | - - | - - | - - | 0 |
| Middle (1) | 0.0014 (±0.0003) | - - | - - | - - | - - | 0 |
| Evening (1) | - - | -0.0021 (±0.001) | - - | - - | - - | 0 |
| Evening (2) | 0.00052 (±0.0003) | - - | - - | - - | - - | 2.6 |
| Night (1) | - - | - - | - - | 0.00027 (±0.00007) | - - | 0 |
| Night (2) | - - | -0.0026 (±0.001) | - - | - - | - - | 5.34 |
| Night (3) | - - | - - | - - | - - | 0.0028 (±0.002) | 6.49 |

In the morning and the middle of the day, the models indicate that impala used woodier areas on days with higher maximum temperature.

For evening, model 1 indicates that impala used less woody cover during wet phases. Alternatively, model 2 indicates that impala used more woody cover on days with higher maximum temperature.

Three alternative models are reported for the night. Model 1 indicates that impala used woodier areas with higher rainfall. Model 2 indicates that impala used less woody areas during wet phases. Model 3 indicates that impala used more woody cover on nights with more moonlight.

Table 2C – Impala: glade distance (overall)

| <u>Model</u> | <u>Part of day – Middle</u> estimate (±SE) | <u>Part of day – Evening</u> estimate (±SE) | <u>Part of day – Night</u> estimate (±SE) | <u>ΔAIC</u> |
|---------------------|--|---|---|--------------------|
| 1 | -0.00023 (±0.00002) | 0.000078 (±0.00002) | -0.000060 (±0.00002) | 0 |

Relative to morning, the overall model indicates that impala were further from glades in the evening, and closer to glades both in the middle of the day and at night.

Table 2D – Impala: glade distance (by part of day)

| <u>Part of day (Model)</u> | <u>Maximum temperature (° C)</u> estimate (±SE) | <u>Phase – Wet</u> estimate (±SE) | <u>ΔAIC</u> |
|---------------------------------------|--|--|--------------------|
| Morning (1) | -0.000036 (±0.00001) | - - | 0 |
| Morning (2) | - - | 0.00013 (±0.00005) | 0.25 |
| Middle (1) | -0.000029 (±0.00001) | - - | 0 |
| Middle (2) | - - | 0.000090 (±0.00005) | 0.63 |
| Evening (1) | - - | -0.000051 (±0.00006) | 0 |
| Evening (2) | -0.000011 (±0.00001) | - - | 2.96 |
| Night (1) | -0.000038 (±0.00001) | - - | 0 |
| Night (2) | - - | 0.000092 (±0.00006) | 2.62 |

For all four parts of day, one alternative model includes maximum temperature, and another includes phase. The daytime temperature models indicate that impala were closer to glades on hotter days; at night, impala were closer to glades following days with higher maximum temperature. The phase models indicate that impala were further from glades during wet phases for all periods except evening, when they were closer.

Table 2E – Impala: proportion in glades (overall)

| <u>Model</u> | <u>Part of day – Middle</u> estimate (\pm SE) | <u>Part of day – Evening</u> estimate (\pm SE) | <u>Part of day – Night</u> estimate (\pm SE) | <u>ΔAIC</u> |
|--------------|---|--|--|-------------------------------|
| 1 | 0.0091 (\pm 0.004) | 0.070 (\pm 0.004) | 0.20 (\pm 0.004) | 0 |

The overall model indicates that, relative to morning, a greater proportion of impala locations were in glades in the middle of the day and the evening. The greatest proportion of locations were in glades at night.

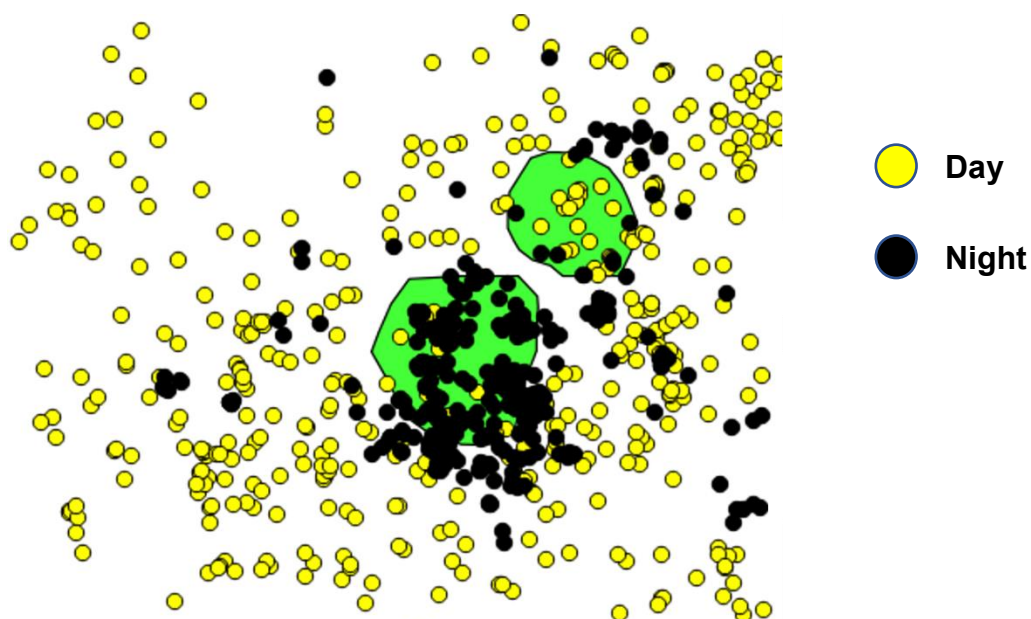


Figure 10: QGIS plot showing the aggregation of impala in glades at night

Table 2F – Impala: proportion in glades (by part of day)

| <u>Part of day</u> <u>(Model)</u> | <u>Maximum temperature</u> <u>(° C)</u> estimate (±SE) | <u>Phase – Wet</u> estimate (±SE) | <u>Previous night's moonlight</u> estimate (±SE) | <u>Rainfall (mm)</u> estimate (±SE) | <u>Moonlight</u> estimate (±SE) | <u>ΔAIC</u> |
|--|---|--|---|--|--|--------------------|
| Morning (1) | - - | -0.0013 (±0.003) | - - | - - | - - | 0 |
| Middle (1) | - - | 0.0057 (±0.003) | - - | - - | - - | 0 |
| Evening (1) | - - | 0.0043 (±0.006) | - - | - - | - - | 0 |
| Evening (2) | - - | - - | - - | -0.00072 (±0.0003) | - - | 1.79 |
| Night (1) | - - | - - | - - | -0.0025 (±0.0005) | -0.072 (±0.01) | 0 |
| Night (2) | 0.0055 (±0.002) | - - | - - | -0.0023 (±0.0005) | -0.068 (±0.01) | 5.76 |

For morning, the model indicates that a lower proportion of impala locations were in glades during wet phases.

For the middle of the day, the model indicates that a greater proportion of impala locations were in glades during wet phases.

For evening, model 1 indicates that a greater proportion of impala locations were in glades during wet phases. Alternatively, model 2 indicates that a lower proportion of locations were in glades on days with higher rainfall.

Both alternative night models indicate that higher rainfall and more moonlight were associated with a lower proportion of locations falling within glades. Model 2 additionally indicates that a greater proportion of locations were in glades following days with higher maximum temperature.

Table 3A – Dik-diks: woody cover (overall)

| <u>Model</u> | <u>Phase - Wet</u> estimate (±SE) | <u>Maximum temperature (° C)</u> estimate (±SE) | <u>ΔAIC</u> |
|---------------------|---|---|--------------------|
| 1 | 0.0024 (±0.003) | - - | 0 |
| 2 | - - | -0.00039 (±0.0005) | 3.8 |

Model 1 indicates that dik-diks used more woody cover during wet phases. Alternatively, Model 2 indicates that dik-diks may have used less woody cover on days with higher maximum temperature.

Table 3B – Dik-diks: woody cover (by part of day)

| <u>Part of day</u> <u>(Model)</u> | <u>Maximum</u> <u>temperature</u> <u>(° C)</u> estimate (±SE) | <u>Phase –</u> <u>Wet</u> estimate (±SE) | <u>Previous</u> <u>night's</u> <u>moonlight</u> estimate (±SE) | <u>Moonlight</u> estimate (±SE) | <u>ΔAIC</u> |
|--|--|---|---|--|--------------------|
| Crepuscular (1) | - - | 0.0055 (±0.006) | - - | - - | 0 |
| Crepuscular (2) | -0.00072 (±0.0008) | - - | - - | - - | 4.08 |
| Middle (1) | - - | -0.0077 (±0.005) | - - | - - | 0 |
| Middle (2) | - - | - - | 0.00091 (±0.0004) | - - | 2.58 |
| Night (1) | - - | - - | - - | -0.022 (±0.004) | 0 |

For crepuscular periods, model 1 indicates that dik-diks used more woody cover during wet phases. Alternatively, model 2 indicates that dik-diks may have used less woody cover on days with higher maximum temperature.

For the middle of the day, model 1 indicates that dik-diks used less woody cover during wet phases. Alternatively, model 2 indicates that dik-diks used more woody cover when the previous night had been more moonlit.

At night, the model indicates that dik-diks used less woody cover when there was more moonlight.

Table 3C – Dik-diks: distance to glades (overall)

| <u>Model</u> | <u>Rainfall (mm)</u> estimate (±SE) | <u>ΔAIC</u> |
|--------------|--|-------------|
| 1 | -0.000027 (±0.000006) | 0 |

The overall model indicates that dik-diks were closer to glades on days with higher rainfall.

Table 3D – Dik-diks: distance to glades (by part of day)

| <u>Part of day</u> <u>(Model)</u> | <u>Rainfall (mm)</u> estimate (±SE) | <u>Moonlight</u> estimate (±SE) | <u>ΔAIC</u> |
|--------------------------------------|---|---------------------------------------|-------------|
| Crepuscular (1) | -0.000023 (±0.000006) | - - | 0 |
| Middle (1) | -0.000035 (±0.000009) | - - | 0 |
| Night (1) | -0.000029 (±0.000007) | - - | 0 |
| Night (2) | - - | -0.00031 (±0.0001) | 3.71 |

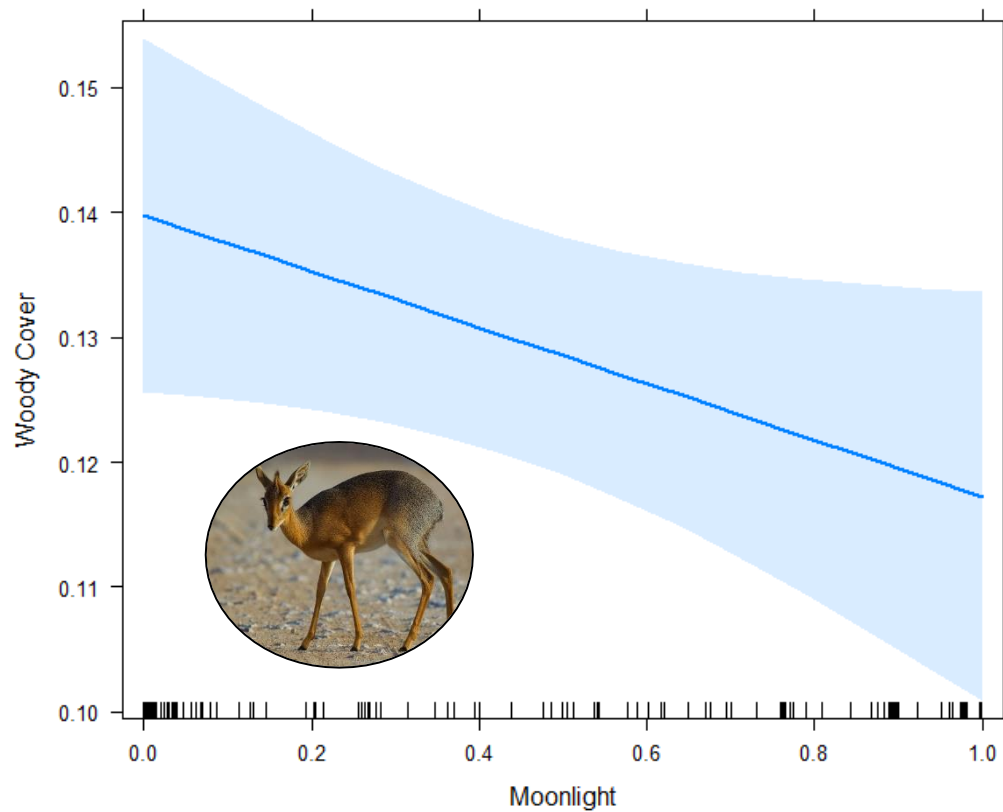


Figure 11: graph showing the effect of moonlight on dik-diks' use of woody cover at night

For crepuscular periods, the middle of the day, and the night, a model indicates that dik-diks were closer to glades in association with higher rainfall. An alternative model indicates that dik-diks were closer to glades on more moonlit nights.

Table 3E – Dik-diks: proportion in glades (overall)

| <u>Model</u> | <u>Phase – Wet</u> estimate (\pmSE) | <u>ΔAIC</u> |
|---------------------|---|--------------------------------------|
| 1 | -0.016 (\pm 0.009) | 0 |

The overall model indicates that a lower proportion of dik-dik locations were in glades during wet phases.

Table 3F – Dik-diks: proportion in glades (by part of day)

| <u>Part of day</u> <u>(Model)</u> | <u>Maximum</u> <u>temperature (° C)</u> estimate (±SE) | <u>Phase – Wet</u> estimate (±SE) | <u>Moonlight</u> estimate (±SE) | <u>ΔAIC</u> |
|--|---|--|--|--------------------|
| Crepuscular (1) | - - | -0.011 (±0.01) | - - | 0 |
| Crepuscular (2) | 0.00059 (±0.002) | - - | - - | 4.64 |
| Middle (1) | - - | -0.011 (±0.007) | - - | 0 |
| Middle (2) | -0.00096 (±0.0009) | - - | - - | 5.4 |
| Night (1) | - - | - - | 0.042 (±0.01) | 0 |
| Night (2) | - - | -0.029 (±0.01) | - - | 0 |

For both crepuscular periods and the middle of the day, model 1 indicates that a lower proportion of dik-dik locations were in glades during wet phases. Both second models alternatively indicate that a greater proportion of dik-dik locations were in glades on days with higher maximum temperature.

For night, model 1 indicates that a higher proportion of locations were in glades with more moonlight. Alternatively, model 2 indicates that a lower proportion were in glades during wet phases.

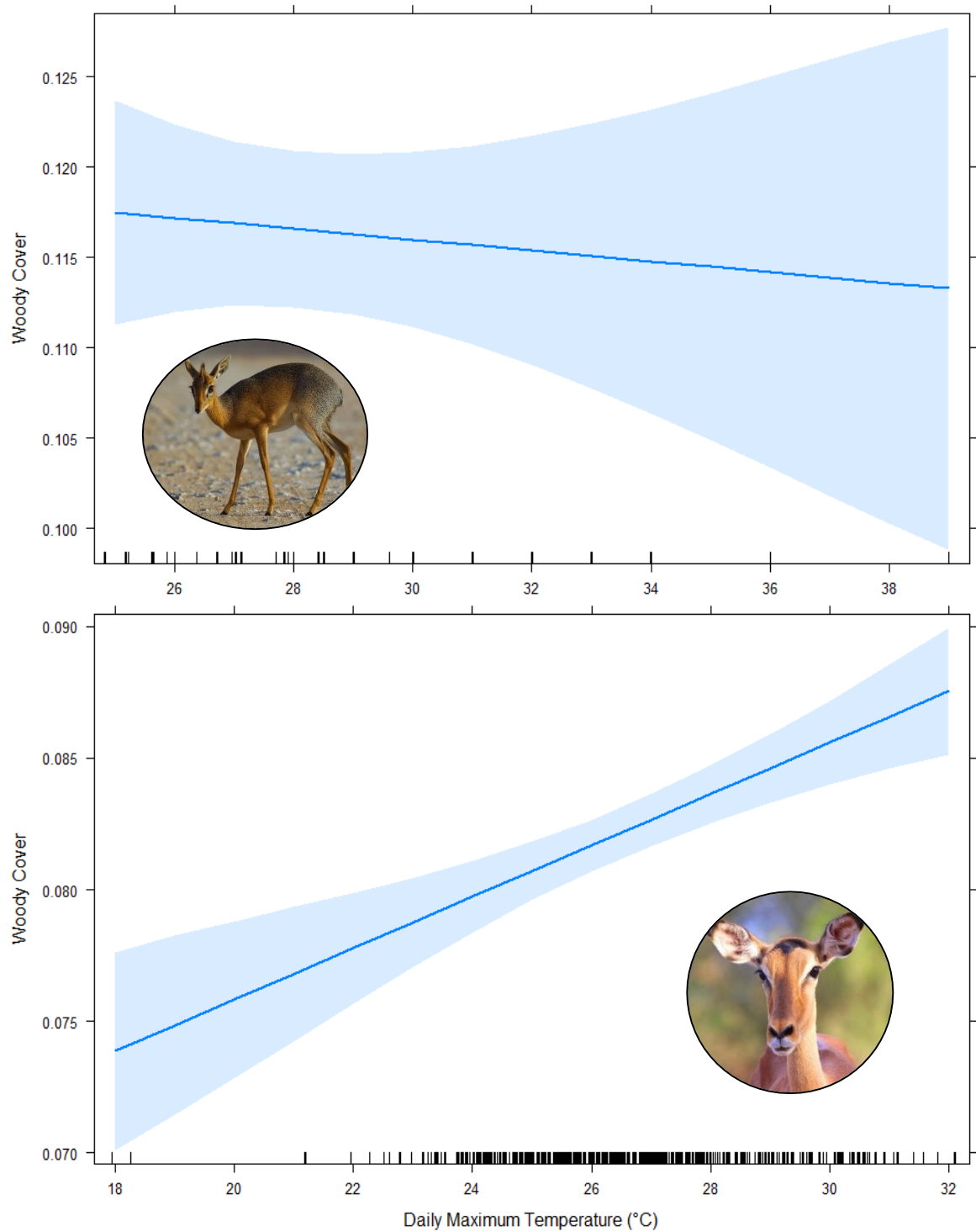


Figure 12: graphs showing how daily maximum temperature affected woody cover use for dik-diks (top) and impala (bottom)

Table 4A – Hunts: woody cover (all models)

| <u>Part of day</u> <u>(Model)</u> | <u>Status – Denning</u> estimate (±SE) | <u>Moonlight</u> estimate (±SE) | <u>ΔAIC</u> |
|--|---|--|--------------------|
| Overall (1) | -0.047 (±0.01) | - - | 0 |
| Crepuscular (1) | -0.036 (±0.01) | - - | 0 |
| Night (1) | -0.12 (±0.02) | - - | 0 |
| Night (2) | -0.12 (±0.02) | -0.026 (±0.02) | 5.75 |

Both the overall model and the model for crepuscular periods indicate that wild dogs hunted in less woody areas when they were denning.

For night, model 1 indicates that wild dogs hunted in less woody areas during the denning period. Alternatively, model 2 indicates that wild dogs hunted in less woody areas on more moonlit nights.

Table 4B – Hunts: distance to glades (all models)

| <u>Part of day</u> <u>(Model)</u> | <u>Pack size</u> estimate (±SE) | <u>Status – Denning</u> estimate (±SE) | <u>Moonlight</u> estimate (±SE) | <u>ΔAIC</u> |
|--|--|---|--|--------------------|
| Overall (1) | -0.00012 (±0.00003) | - - | - - | 0 |
| Crepuscular (1) | -0.00012 (±0.00003) | - - | - - | 0 |
| Crepuscular (2) | - - | 0.00048 (±0.0002) | - - | 4.27 |
| Night (1) | -0.00018 (±0.00005) | - - | - - | 0 |
| Night (2) | - - | - - | 0.00058 (±0.0003) | 2.44 |

The first of each set of models (overall/crepuscular/night) indicates that wild dogs in larger packs hunted closer to glades.

For crepuscular periods, an alternative model indicates that wild dogs hunted further from glades during the denning period.

For night, an alternative model indicates that wild dogs hunted further from glades on more moonlit nights.

Discussion

This study investigated whether the negative effects of high temperature on wild dogs result from changes in prey behaviour. Three main questions were posed:

1. Do wild dogs' prey spend more time in dense cover on hot days?

Impala, wild dogs' most important prey species across Africa as a whole³⁶, did spend more time in dense cover on days with higher maximum temperature. Dik-diks, however, did not. Dik-diks are physiologically adapted for high temperatures³⁷; adaptations include a long proboscis, lined with blood vessels, through which they can dissipate heat by panting¹³. Gunther's dik-dik, which occurs at MRC, is the most heat-tolerant species; this could explain the lack of any significant response to high temperatures. By contrast, impala are relatively more heat-sensitive; activity levels decline in hot weather³⁸, and they are strongly dependent on shade during periods of high temperatures¹³. This is consistent with our finding that impala sought out areas of denser woody cover on days with higher maximum temperature.

As expected, impala moved into more open areas at night, congregating in glades. This behaviour has evolved to improve visual detection of their predators¹⁴. However, it is mostly effective against stalking predators, like leopards, which require dense cover to approach their prey³⁹; it is unlikely therefore to be an adaptation against predation by cursorial predators, and could actually increase impala's vulnerability to wild dogs at night, by making them easier to locate.

2. Do wild dogs hunt in denser cover on hot days?

We found no evidence that wild dogs hunted in denser cover on hotter days. On days with higher maximum temperature, wild dog hunts are limited to narrower time windows in the early morning and late afternoon⁹. It is possible therefore that wild dogs simply avoided hunting when temperatures were sufficiently high to drive impala into denser, shadier cover. Alternatively, wild dogs may avoid moving into woodier areas because the dense vegetation disrupts their cursorial hunting style.

Impala moved into denser cover on hotter days. We originally hypothesised that this would make them harder to locate for wild dogs, and that hunting success would consequently fall. However, wild dogs actually preferred to hunt in woodier areas than those frequented by their prey. This could be because prey are easier to

capture; in another study, 85% of hunts that ended in thicker cover were successful, compared with 37% in more open areas⁵. Additionally, leopards have been shown to prefer hunting in denser areas, where prey are less abundant but easier to approach unnoticed³⁹. This suggests that habitat selection by predators is often based on more than simply the probability of encountering prey. Furthermore, hunting in denser cover could lower the risk of a kill being lost to other predators. Wild dogs are vulnerable to kleptoparasitism, especially by spotted hyaenas, but the probability of kill detection is lower in areas of thick vegetation^{40,41}.

As a result, the movement of impala into areas of denser cover at high ambient temperatures seems unlikely to make them harder to locate. In fact, it may even benefit wild dogs; Ford et al. (2014) showed that impala experienced higher rates of predation by wild dogs and leopards in woodier cover¹⁴. The finding that impala selected more woody cover on hot days might reflect a trade-off between predation risk and behavioural thermoregulation.

While impala mostly rely on visual detection of predators, dik-diks' primary defence is crypsis, which may be more effective in areas of denser cover⁴². This may explain why dik-diks preferred woodier areas than impala. However, as dik-diks' use of woody cover was similar on hotter days, they were presumably no more or less vulnerable to wild dog predation.



Figure 13: a typically cryptic dik-dik

3. When hunting at night, do wild dogs preferentially visit glades?

The models provided no evidence that wild dogs preferentially visited glades when hunting at night. Furthermore, wild dogs did not preferentially visit glades at night following hot days, which suggests that they were not compensating for high daytime temperatures by targeting impala in glades at night. However, wild dogs did hunt closer to glades on nights with less moonlight. Previous studies have shown that wild dogs can compensate for reduced diurnal activity on hot days by hunting more at night, but this option is mostly limited by moonlight^{9,29}. These results suggest that wild dogs may be attracted to glades when there is insufficient moonlight to hunt elsewhere; the reliable presence of impala in glades might therefore facilitate hunting on moonless nights. If climate change does force wild dogs to hunt more at night, then, given that the cycle of the moon is set, glades could potentially enable more complete compensation for reduced diurnal activity. However, as wild dogs did not compensate for high temperatures by hunting more in glades at night, this behaviour may have to be learned. The aggregation at night of impala in open areas is a widespread behaviour¹⁷, and so a similar principle may hold across the two species' shared range.

Nevertheless, wild dogs remain more vulnerable to predation and kleptoparasitism at night, when other predators are more active²⁹. Dogs show temporal and spatial avoidance of lions¹⁸, which can be a significant cause of mortality for both adults and pups²⁰. While lions in Laikipia prefer different prey to wild dogs (chiefly Burchell's zebra and eland⁴³), these species are also attracted to glades⁴⁴. Lions also enjoy their highest levels of hunting success on night's without moonlight, when they are more difficult for their prey to detect⁴⁵. Therefore, visiting glades on moonless nights might lead to higher mortality for wild dogs.

Methodological issues

Our measure of woody cover related to the proportion of overstory in a circular area of radius 40m (5027m²). Given that this represents more than 20% of dik-dik average territory size⁴⁶, it may have had limited relevance for the spatial scales at which dik-diks operate. This could be responsible for our failure to find a relationship between temperature and woody cover use, for example.

All of the collared impala in this study were female, but hunting wild dogs have been shown to exhibit a stronger preference for males⁴⁷. Males tend to be found on the periphery of herds and are less vigilant, particularly during the rut when they are also tired and distracted⁴⁸. This makes them more profitable targets. Adult males also have a greater tendency to remain in dense vegetation¹³. Consequently, our results may not be fully representative of this predator-prey relationship. Future research should track the movements of both male and female impala.

Interpretation of other results

Impala used areas of less woody cover during wet phases, and more woody cover on nights with more moonlight. Impala have a flexible diet, which varies seasonally¹³; in general, grass makes up the majority of their diet during the wet season, while browse becomes more important in the dry⁴⁹. Females in particular prefer woodier browse during dry months⁵⁰. These dietary variations could explain the greater use of more open areas during wet phases, when the availability of grass is higher. At night, moonlight might improve detection of predators, allowing impala to continue feeding²⁸.

Unlike impala, dik-diks are generally browsers during wet seasons⁵¹. This might explain why dik-diks used denser cover during wet phases, when woody plants will have been producing fresh shoots. Additionally, dik-diks depend on areas without much grass cover¹³; grass growth in open areas might also be driving dik-diks into denser cover during wet phases.

Dik-diks' reduced use of woody cover on nights with greater moonlight may relate to the relative risk of predation by wild dogs. Ford and Goheen (2015) showed that dik-diks increased their use of more open habitats when presented with a cue of wild dog presence, especially at night²⁴. Dik-diks show increased vigilance in response to levels of heightened risk⁵², suggesting that crypsis and vigilance are not mutually exclusive²⁴. Dik-diks may therefore be using more open areas on moonlit nights as a response to greater wild dog nocturnality.

Wild dogs hunted in less dense areas when they were denning than when they were not. Reproduction is energetically costly for wild dogs, and each individual must

contribute to the energy requirements of 21.7% more dog biomass on average during the denning period⁸. It is possible that the wild dogs hunted in areas with higher prey density in order to fulfil this increased energetic demand, and that this explains the reduced use of woody cover. However, this would presumably increase encounter rates with lions¹⁸, as previous studies have suggested that wild dogs avoid areas of high prey density to reduce encounter rates with lions⁵; temporal and spatial avoidance of lions has also been shown to be highest during the denning period⁵³. An alternative explanation relates to the smaller monthly home ranges of denning dogs (e.g. 37.1 km² vs. 144.2 km² ⁸); low woody cover measurements could simply be an artefact of den location.

Wild dogs also hunted further from glades when they were denning. In Laikipia, dogs consume a greater proportion of dik-diks during the denning period¹². This may be because highly territorial dik-diks do not vacate their home ranges in response to the local presence of a den, whereas more mobile impala move away. Hunting further from glades may therefore reflect this shift towards dik-diks which, unlike impala, were on average further from glades than expected. Finally, larger packs of wild dogs hunted closer to glades. This may reflect a preference by larger packs of impala over dik-diks; prey mass has previously been shown to increase with pack size³³.

Conclusions

The answers to the three main questions suggest that the negative effects of high temperature on wild dogs do not result from changes in the behaviour of their most important prey species. Although impala used denser cover on hot days, this would be expected to improve rather than reduce wild dog hunting success, and wild dogs did not preferentially hunt in glades on nights following hot days. These findings are consistent with the alternative explanation that dogs reduce their activity at higher temperatures to avoid overheating⁸. Although wild dogs may be adapted for hunting at high temperatures⁵⁴, the maximal capacity to dissipate body heat imposes an upper limit on energy expenditure in endotherms⁵⁵. This hypothesis should be investigated in future research, perhaps following the methodology used in a study of overheating in cheetahs⁵⁶. Cheetahs did not overheat while hunting, but core body temperature rose significantly in association with vigilance and the defence of kills

against other predators. This raises the possibility that resisting kleptoparasitism may be harder at higher ambient temperatures; a similar mechanism leading to overheating in wild dogs offers another potential explanation for the negative demographic effects of high temperature on the species.

If the adverse effects of climate change on wild dogs have a direct physiological basis, then there may be few options for effective *in situ* conservation. Instead, action should focus on populations in areas with lower densities of competing predators, and in more temperate regions; for example, the managed metapopulation in South Africa⁵⁷ could become more important. However, if the nocturnal hunting of impala in glades does facilitate more complete compensation for low day-time activity, then it might be possible to create new glades in key locations, allowing more effective night-time hunting even when there is little moonlight. This coping mechanism may be less effective in community areas, where larger prey such as impala may be depleted¹².

While it was possible to infer changes in the behaviour of wild dogs, it is not clear how these relate to critical parameters such as net energetic intake, and risk of predation by lions. For example, wild dogs might visit glades on moonless nights because it is profitable to do so (i.e. they regularly succeed in making kills). On the other hand, wild dogs might rarely capture prey in glades (and frequently encounter other predators) but visit them anyway out of desperation. Alternatively, while wild dogs might well enjoy a higher success rate (per chase) on hot days, when impala move into denser cover, does this compensate for the reduced time available for hunting? Only through the integration of all these complex variables will the questions posed by this study be fully resolved.

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