**Impacts of temperature on predator-prey interactions in an African savanna**

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**Abstract**

Climate warming impacts species indirectly via interactions with other species, and such indirect interactions can arise through shifts in individual behaviour. It is therefore important to consider the potential for such indirect effects in anticipating whether and how climate change will affect biodiversity. Through changes in the escape speed of prey, attack speed of predators, or habitat use of both predators and prey, climate warming may alter predator-prey dynamics. We examined how high temperatures can impact individual behaviour and spatial overlap of predators and prey in a three-species system composed of a predator, the African wild dog, *Lycaon pictus*, and two species of prey: impala, *Aepyceros melampus* , which are larger than wild dogs, and dik-dik, *Madoqua guentheri* , which are smaller than wild dogs. When temperatures were high, wild dogs hunted for shorter periods and were less likely to engage in evening hunts. At high temperatures, impala selected habitats with more woody cover, thereby increasing spatial overlap with wild dogs. However, this increased spatial overlap did not translate to an increase in the consumption of impala by wild dogs: when temperatures were high, fewer wild dog scats contained impala, and wild dogs did not preferentially hunt impala, potentially because the duration of hunting periods was shorter. Our findings are consistent with predictions of optimal foraging theory, whereby predators with limited time should select for abundant, lower value prey over rare, high value prey.

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

**Introduction**

Climate change has far-reaching impacts on both species and ecosystems (Parmesan & Yohe 2003). Meta-analyses suggest that climate impacts on individual species often operate indirectly, through their effects on species interactions such as competition, herbivory, predation, and parasitism (Cahill *et al.* 2012; Ockendon *et al.* 2014). Therefore, understanding how weather affects species interactions may help to make general predictions about which species are most vulnerable to climate change, and therefore in need of conservation interventions.

The effect of climate on species interactions also has impacts beyond individual species. Global Ecosystem Models, such as the Madingley Model, are designed to predict worldwide ecosystem responses to climate change, with a view to informing policy decisions about activities such as carbon emissions and land use planning (Harfoot *et al.* 2014). Such models are likely to be sensitive to assumptions about how climate influences species interactions, because interactions between species play a central role in shaping ecosystems.

Shifts in individual behaviour can buffer against or exacerbate the influence of climate on species interactions. For example, rising ambient temperatures may allow ectotherms to move more rapidly, potentially making them more efficient predators and more challenging prey, with cascading consequences for community structure (Dell, Pawar & Savage 2014). It is usually assumed that temperature has no similar impacts on predation involving endotherms (e.g., Dell, Pawar & Savage 2014; Harfoot *et al.* 2014); however, 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 (Austin 1976; Pigeon *et al.* 2016), and choosing different foods (Doolan & Macdonald 1996; Garcia-Heras *et al.* 2017), all of which are likely to influence their impacts on the species that they consume, or that consume them. Moreover, it has been suggested that predator-prey interactions involving large-bodied endotherms might be especially sensitive to temperature, because the low surface-to-volume ratios of large animals may make it difficult to dissipate the heat generated by pursuing or avoiding predation (Speakman & Krol 2010; Creel *et al.* 2016). Hence, with respect to the outcome of predator-prey interactions, high ambient temperatures might potentially favour (1) endothermic prey that are smaller than their endothermic predators; and (2) endothermic predators that are smaller than their endothermic prey (Creel *et al.* 2016). Predation by and on large-bodied endotherms can have cascading effects on community structure (e.g., Fortin *et al.* 2005; Johnson, Isaac & Fisher 2007), and these effects might therefore be sensitive to changes in ambient temperature.

These examples demonstrate the multiple ways in which one element of climate change (rising ambient temperature) might shift the individual behaviours that underlie predator-prey interactions among endotherms. We quantified the relative importance of these potential mechanisms using a three-species predator-prey system in an African savanna, where two ungulate species, impala (*Aepyceros melampus*) and Guenther’s dik-dik (*Madoqua guentheri*), share a common predator, the African wild dog (*Lycaon pictus*). At our study site in Kenya, impala and dik-diks are the two most abundant ungulates, and their browsing shapes the structure of plant communities (Ford *et al.* 2014; Ford *et al.* 2015). Wild dogs are crepuscular, and hunt their prey by running them 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 four sets of hypotheses about the impacts of ambient temperature on predation by wild dogs, based on predicted behavioural changes by predator and prey (Table 1). First, we explored the potential consequences for predation of reduced activity time during daytime, when solar radiation makes ambient temperatures highest. Previously, we have shown that wild dogs are less active on hot days (Rabaiotti & Woodroffe 2019), which may reflect shorter hunting periods (Woodroffe 2011b). Optimal foraging theory suggests that, when foraging opportunities are limited, individuals should accept lower-value prey when encountered, rather than continuing to search for higher-value prey (Lucas 1983). Therefore, we expected that wild dogs with reduced foraging time, through reductions in bout length, intensity, or number of activity bouts, would increase predation on dik-diks (which are encountered more frequently but are too small to feed a whole pack) over impala, which are larger but encountered less frequently (Woodroffe *et al.* 2007). We term this the ‘Optimal foraging scenario’.

Second, we investigated whether increased nocturnal activity influenced the outcome of interactions between wild dogs and their prey. Following hot days, wild dogs are more active at night, which we have suggested might reflect increased nocturnal hunting (Rabaiotti & Woodroffe 2019). We predicted that this change might increase predation on impala, which aggregate at night in small clearings (“glades”), apparently as a form of anti-predator behaviour (Augustine 2004; Otieno et al. 2019). Similarly, we predicted that wild dogs should select areas in and around glades when hunting on nights following hot days (Table 1). We term this the ‘Nocturnal compensation scenario’.

Third, we quantified whether habitat selection might be affected by ambient temperatures, with consequences for predation. Many large mammals select shaded habitat in hot 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). Further, we predicted that such a change would increase predation by wild dogs on impala, since we have shown previously that impala face higher *per capita* predation rates in habitats characterized by woody cover (and thus shade; Ford *et al.* 2014). We term this the ‘Increased habitat overlap’ scenario.

Finally, we explored the potential consequences of overheating during chases. Creel *et al.* (2016) suggested that, during high-speed chases, wild dogs would overheat more slowly than their larger-bodied prey, leading to shorter, successful chases at high ambient temperatures as a result of larger species having more difficulty dissipating heat due to their lower surface area to body size ratio (Peters 1986) . By extension, we predicted that wild dogs (23kg) would overheat less rapidly than impala (40kg) but more rapidly than dik-diks (5kg), leading to increased predation on impala relative to dik-diks (Table 1). We termed this the ‘Decreased chase time’ scenario.

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

**Methods**

*Study area*

The focal area for this study was the Mpala Conservancy, a 200 km2 semi-arid savanna in Kenya managed jointly for livestock production and wildlife conservation (0°17’ N, 36°53’ E). Due to its equatorial location, Mpala experiences little predictable seasonal variation in temperature; daily maximum temperature ranges from 20-37°C years (Caylor, Gitonga & Martins 2017), and mean annual rainfall is 590mm, which varies 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). Large predators comprise lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*), striped hyaena (*Hyaena hyaena*) and African wild dog (Frank, Woodroffe & Ogada 2005).

*Data collection*

We used Global Positioning System (GPS) collars to measure daytime and night-time activity, and habitat use. GPS-collars (Savannah Tracking Ltd, Nairobi, Kenya) were fitted to 20 adult female impala (each from a different herd) between May and June 2011, as described in Ford *et al.* (2014). Each impala GPS-collar recorded a location every 20 minutes, for an average of 245 days. Additionally, 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. Finally, 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) every five minutes, for 218 days on average.

We used faecal analysis to quantify the relative rate of predation by wild dogs on impala and dik-diks. Wild dog scats were collected during 2001-4 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).

We drew on daily meteorological data collected at Mpala Research Centre, within the study site (Caylor, Gitonga & Martins 2017). We also recorded pack size of wild dogs through visual observation at least once a month. Finally, we used GPS-collar data to identify periods when wild dog packs were denning (raising small pups in a den, recognisable from the movement path which shows a characteristic “starburst” pattern of repeat visits to the same location, Woodroffe, Groom & McNutt 2017).

*Identifying hunting periods of wild dogs*

To quantify wild dog activity, and to compare prey and predator behaviour at times when predation risk was highest, we used accelerometry data to identify wild dog hunting periods. First, we summed the two accelerometer measurements for each 5-minute period, to give an overall measure of activity (from 0 to 510). We then defined hunt periods based on three criteria: (i) activity >0 for >20 minutes; (ii) total activity during the activity bout >500; (iii) followed by three or more consecutive records of 0 activity. These criteria excluded activity bouts which were too short to relate to hunting periods, or which related to less energetic behaviours, such as socialising. Because this method did not allow us to distinguish chases from other parts of the hunt (e.g. seeking prey, feeding from a kill) we could not measure the duration or speed of chases. For each hunting period, 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 Figure S1. We classified hunting periods as “morning”, “evening”, “night” or “midday”, based on their start and stop times and as detailed in Table S1. These will subsequently collectively be referred to as ‘time periods’. Start and stop times between which bouts of activity were allocated to a particular period of the day were determined. Hunting periods were classified by plotting histograms of the data and observing where peaks of activity in morning and evening started and stopped (Figure S1). After using accelerometry data to delineate hunting periods, we categorized each wild dog location as falling either inside or outside a hunting period.

Similarly, we identified dik-dik and impala GPS collar locations as occurring within the wild dog hunting periods. We defined “morning” as the time elapsed between sunrise (taken from the *R* package *suncalc*, Agafonkin & Thieurmel 2017) and the third quartile of end times for hunting periods (approximately 3.5h after sunrise; Figure S2). For example, if sunrise was at 0600h (sunrise at the site varied between 0552h and 0623h), any impala or dik-dik GPS-collar locations recorded between 0600h and 0930h were categorized to occur within the “morning” period. We likewise classified impala and dik-dik “evening” GPS-locations as those recorded between the first quartile of start times for hunting periods (approximately 2hr10min before sunset; Figure S2) and sunset (which fell between 1841h and 1912h). We then categorized impala and dik-dik GPS-locations as “midday” if they were recorded between the “morning” and “evening” periods, and “night” if they were recorded between sunset and sunrise.

*Habitat use*

We analysed habitat use with an existing habitat map of Mpala, which had been created from a 2011 Quickbird satellite image (Digital Globe, Longmont, CO, USA) by Ford *et al.* (2014). We characterised 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.

We used the same habitat map to classify each GPS-collar location in relation to glades. For impala and dik-diks, we recorded whether each location fell inside or outside a glade. As <1% of wild dog hunting locations fell inside glades, we recorded the distance to the nearest glade for each wild dog location, using the plugin “*NNJoin*” in *QGIS* (QGIS Development Team 2018).

*Statistical analyses*

We used multi-model inference to evaluate associations between each outcome variable (distance to glades, use of glades, woody cover, distance travelled, probability of wild dog hunt, wild dog hunt duration, wild dog hunt intensity, hunt start and stop times and presence of impala in wild dog scat) and a range of explanatory variables. For each outcome variable, we built a series of statistical models from explanatory variables (see below) and biologically-meaningful interactions between explanatory variables (Table 2, 3, 4, 5, S2, S3, S4, S5). We then used Akaike’s Information Criterion (AIC) to compare models using the *R* package *MuMIn* (Bartoń 2017). We considered all models with AIC scores within 7 units of the best (lowest AIC) model (*i.e.,* ΔAIC<7) to have a moderate level of support (Burnham et al. 2002), referring to this array of models as the “top set”. We used model averaging to estimate the effect on the outcome variable of each explanatory variable in the top set.

In order to investigate the optimal foraging scenario, whereby wild dogs were expected to reduce their hunting activity on hot days, we analysed continuous outcome variables describing hunt duration, start time, stop time, and intensity within the morning, evening, and night-time periods, as well as a binary outcome variable describing whether or not a hunt was recorded during each period. Only 10% of hunting periods occurred during midday (accounting for 2% of daily activity), so these were not subjected to statistical analyses. For each outcome variable, we constructed Generalised Linear Mixed Models (GLMMs) using the package *nlme* (Pinheiro *et al.* 2015) in *R* (R Core Team 2015), with Gaussian error distribution for the continuous variables and binomial error distribution for the binary variables. Each model included the identity of individual animals as a random effect. Temperature was included as an explanatory variable; for morning and evening hunts the temperature variable was maximum temperature (in °C) on the day of the hunt, while the variable for night-time hunts was maximum temperature during the preceding daytime period.

Although our hypotheses concerned the potential effects of temperature, we included three other explanatory variables known to influence activity patterns of wild dogs (Woodroffe, Groom & McNutt 2017; Rabaiotti & Woodroffe 2019). The first of these variables described whether or not the pack was denning. This is because African wild dogs are more active during the denning period due to the energetic demands of raising a litter (Rabaiotti and Woodroffe 2019). The second variable was rainfall (in mm) on the day of the hunt. This was included as rainfall has been shown to mitigate the impact of high temperatures on activity levels(Rabaiotti and Woodroffe 2019). The third variable was moonlight, expressed in full-moon-hour equivalents, calculated from *suncalc* (Agafonkin & Thieurmel 2017) in *R* by multiplying the proportion of the moon that was illuminated, by the number of hours the moon was in the sky between sunset and sunrise. This was included as wild dogs are more active on moonlit nights (Cozzi et al. 2012). Models of night-time activity included moonlight on the same night, while models of morning activity included the previous night’s moonlight, and models of evening activity included moonlight the subsequent night. For models of night-time activity, the time of moonrise and moonset were also included as explanatory variables.

To investigate the increased habitat overlap scenario, where temperature was hypothesised to increase the use of shaded habitat by wild dogs, impala, and dik-diks, 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. Only wild dog locations from hunting periods were included. We analysed these using GLMMs with individual identity as a random effect, building a separate array of models for each time of day, and all times of day together. Candidate explanatory variables were the same as for the analyses of wild dog activity (i.e. temperature, rainfall, moonlight, and, for wild dogs, denning), but we also included a variable describing rainfall phase. Reflecting the unpredictable rainfall at our study site, and following Ford *et al.* (2014), we considered days to fall within “wet phases” if >50mm of rain had fallen in the previous four weeks, with all other days classed as “dry phases”. In constructing the array of models for multi-model inference, this rainfall phase variable was never included in the same model as daily rainfall, because the two were correlated.

To investigate the nocturnal compensation scenario, under which impala and dik-diks were expected to use glades more at night following hot days, and wild dogs were expected to preferentially target glades at night, we calculated the proportion of each individual’s locations falling within glades during the morning, midday, evening, and night periods for each 24-h period. To test the hypothesis that wild dogs hunted in glades more often at night following hot days, we similarly calculated the mean distance to the nearest glade for each night-time hunt period. We analysed these outcome variables using GLMMs, using time of day, temperature, rainfall, and rainfall phase as candidate explanatory variables. For wild dogs, we also included explanatory variables describing denning and pack size.

We further analysed glade use at night, using the outcome variables described above, but only for the night-time period. We fitted GLMMs including, as candidate explanatory variables, temperature on the previous day, moonlight, rainfall, rainfall phase and, for wild dogs, denning and pack size.

Finally, we analysed whether or not wild dog scats were more likely to contain impala remains on hot days. This investigated the decreased chase time scenario, whereby impala would be impacted more than wild dogs at high temperatures, increasing wild dog predation rates on impala, and also the other three scenarios, through testing whether predation rates on impala increased or decreased at high temperatures. We analysed this outcome variable using a GLM with binomial error distribution. Candidate explanatory variables were temperature during the previous seven days (to account for delays between a scat being deposited and collected), and land use type (as a previous study showed that impala were consumed far less frequently on community land, relative to private land, Woodroffe *et al.* 2007). Impala densities remain stable throughout the year and do not fluctuate seasonally, and therefore availability would not be associated with temperature (Ford et al. 2015). Pack or individual identity were often unknown for wild dog scats, so these models did not include random effects.

**Results**

*Daily movement patterns*

African wild dogs showed a strongly crepuscular activity pattern, with morning and evening activity accounting for 47% of bouts and 70% of total activity (Figure 1A). Forty-two percent of wild dog hunting periods occurred at night. Due to the low intensity levels of night-time hunts, however, only 17% of total wild dog activity occurred during the night. The rest of the activity occurred either during the midday period (10% of bouts accounting for 2% of total activity) or spanned multiple time periods. Impala showed the lowest levels of displacement during the morning and evening time periods, with slightly higher displacement distances in the midday time period, and the greatest displacement distances during the night period (Figure 1B). Dik-dik showed low amounts of displacement throughout the 24h period, with the greatest displacement distances at night and in the morning periods (Figure 1B).

*Effects of ambient temperature on wild dog hunting patterns*

As predicted under Scenario 1: Optimal foraging, at high ambient temperatures wild dogs’ daytime hunting periods were of shorter duration in both the morning and evening time periods (Table 2). These shorter hunting periods reflected earlier start and stop times in the morning (Table S2) and later start times in the evening (Table S3). As well as being shorter, both morning and evening hunts entailed less intense activity on hotter days (Table S2, Table S2). Evening hunts were less likely to occur at all on days with higher ambient temperatures (Table S3). Rainfall might have mitigated the effects of high ambient temperatures, with rainfall:temperature interactions included in some of the top models for hunt duration and intensity (Table S2, Table S3). Denning packs were consistently more active during daytime (Table S2, Table S3).

Likewise, as predicted under Scenario 2 wild dogs were more likely to hunt at night following daytime periods with high ambient temperatures (Table 2), with some evidence that temperature also affected the duration and intensity of night-time hunts (Table S3). Nocturnal activity was strongly linked to moonlight (Table 2, Table S4), with corresponding reductions in daytime activity on dates with strong moonlight (Table 2, Table S2, Table S3).

*Habitat selection*

Impala used areas with less woody cover than both dik-dik and wild dogs across all times of day. Dik-dik used areas with intermediate woody cover levels in comparison to impala and wild dogs across the 24h period, and wild dogs used the areas with the highest levels of woody cover on average at all time periods (Figure 1C). Impala were found in the lowest levels of woody cover during the morning and night-time periods, in comparison to wild dogs which used the highest levels of woody cover during the night (Figure 1C). The use of woody cover by dik-diks was relatively consistent throughout the day (Figure 1C).

As predicted under Scenario 3, impala selected land with denser woody cover on hotter days, with positive effects of ambient temperature included in the top model sets for morning, midday, and evening (Table 3). In contrast, there was only weak and inconsistent evidence for dik-diks selecting woody cover based on ambient temperature, and no evidence of such selection by hunting wild dog packs (Table 3).

Dik-dik were found closest to glades, followed by impala, with wild dogs being found further from glades than the two prey species, irrespective of time period (Figure 1D). Impala were more likely to be located in glades at night than at other times, although there was no such pattern for dik-diks (Table 4). In contrast with predictions under Scenario 2, wild dogs were not located closer to glades at night than at other times of day, and were no more likely to be found close to glades at night when temperatures were high (Table 4). Impala were less likely to be located in glades on moonlit nights, and following days with high temperatures, whereas dik-diks appeared more likely to use glades on moonlit nights (Table 4). Pack size was the most consistent predictor of wild dog proximity to glades (Table 4).

*Prey selection*

Among 795 wild dog scats, 71 (9%) contained impala remains and 609 (77%) contained dik-dik remains. As predicted under the optimal foraging scenario (Scenario 1), but not the nocturnal compensation, increased habitat overlap or decreased chase distance scenarios (Scenarios 2, 3 and 4), there was strong evidence that wild dog scats were less likely to contain impala remains when temperatures had been higher during the previous seven days (Table 5).

**Discussion**

Our analyses revealed clear associations between ambient temperature and the behaviour of both predator and prey species, which appeared to influence predation risk. Our findings were most consistent with expectations from optimal foraging theory, under which we predicted that wild dogs would spend less of the daytime hours hunting on hot days. On hot days, morning hunts ended earlier (Table S2), and evening hunts started later (Table S3) so that, overall, less time was spent hunting during daytime hours. Further, we predicted that such curtailed hunting would affect prey selection. In a previous comparison we concluded that, on private ranches like Mpala, hunting dik-diks and impala would have similar profitability, because the greater energy intake achievable by hunting impala (the larger prey species) was offset by the shorter travel distances associated with hunting dik-diks (the more abundant prey species, Woodroffe *et al.* 2007). However, optimal foraging theory predicts that a predator with limited time should select a more abundant but lower-value prey (such as dik-diks) rather than waiting to locate a rarer but higher value prey (such as impala, Lucas 1983). High ambient temperatures would therefore be expected to favour wild dogs eating dik-diks more than impala, and our observations were consistent with this prediction (Table 4).

Under the nocturnal compensation scenario (Scenario 2), we predicted that, when ambient temperatures were high, wild dogs would hunt at night, targeting impala which are predictably located in glades. Although wild dogs hunted more often at night in hot weather (Table 2), and impala were predictably located in glades at night (Table 4), there was no evidence that wild dogs targeted impala at night. Wild dogs were no closer to glades at night than at other times of day, and were no closer to glades on nights when daytime temperatures had been high (Table 4). Interestingly, impala were less frequently located in glades on moonlit nights, when wild dogs were more active (Table 4). Moonlight is associated with reduced hunting success in lions (Funston, Mills & Biggs 2001), so it is possible that impala relax their antipredator behaviour and abandon glades on moonlit nights. In contrast with the predictions of Scenario 2, impala remains were less likely to be found in wild dog scats following periods of high ambient temperature (Table 4). Hence, Scenario 2 did not generate the predicted consequences for predation risk.

Under the increased habitat overlap scenario (Scenario 3), we predicted that all three species would increase their daytime use of woody cover at high ambient temperatures. However, we found that only impala did so (Table 3). Of the three species, impala used the most open habitat (Figure 1C), which may have resulted in a greater need to seek shade at high temperatures. Physiological studies suggest that dik-diks are dependent upon shade to thermoregulate (Kamau & Maloiy 1985) but, being small-bodied, they may be able to use small patches of shade without moving into denser habitat. Wild dogs rest in woody cover during the midday period (Figure 1C) but there was no evidence that they hunted in denser cover on hot days (Table 3), perhaps because hunting periods occurred before and after the hottest times of day (Figure 1A). Impala’s tendency to move into denser cover at high temperatures would be expected to increase their risk of being killed, since wild dogs (and leopards, another major predator of impala) typically occupied denser cover (Figure 1C), and impala arere more likely to be killed (by any predator species) in denser cover (Ford *et al.* 2014). Despite this prediction, we found that impala remains were less likely to be found in wild dog scats following periods of high ambient temperature (Table 4). Hence, although impala behaviour changed in line with the predictions of Scenario 3, this change did not generate the predicted impact on predation risk.

Under the decreased chase time scenario (Scenario 4), we predicted that high ambient temperatures would reduce chase distances for impala and increase them for dik-diks, as larger-bodied animals would be slowed down by the heat to a greater extent than smaller-bodied animals (Creel *et al.* 2016). We were not able to test these hypotheses directly because our monitoring methods did not allow us to measure chase distance or speed. However, under this scenario we also predicted that predation upon impala would increase, relative to predation on dik-diks, when ambient temperatures were high, in contrast with our observations (Table 4). Hence, a key prediction of Scenario 4 was not upheld by our analyses.

Demographic evidence provides further support for Scenario 1 over Scenarios 2-4. Under Scenario 1, we would expect energy intake by wild dogs to be reduced at high ambient temperatures, due to constrained foraging time and a consequent acceptance of lower-energy prey. This prediction is consistent with our observations that this study population experiences higher mortality and lower reproductive success at high ambient temperatures (Woodroffe, Groom & McNutt 2017; Rabaiotti *et al.* in review). In contrast, under the other three scenarios, wild dogs’ food intake (and potentially survival and reproductive success), would be expected to improve at high temperatures, because impala (a higher-value prey) would be more accessible due to their being predictably-located (Scenario 2, nocturnal compensation), in dense cover where they are vulnerable to predators (Scenario 3, increased habitat overlap), or more easily captured due to their tendency to overheat during high speed chases (Scenario 4, decreased chase time). Hence, while demographic patterns cannot confirm the optimal foraging scenario (Scenario 1) as the most likely mechanism whereby temperature influences predator-prey interactions in this system, they do contribute to refuting Scenarios 2-4.

Climate change could intensify wild dog predation on dik-diks at our study site, and perhaps other high-density, small-bodied prey elsewhere. Predation on dik-diks did not trigger cascading effects on vegetation, even though wild dogs suppressed dik-dik numbers, and dik-dik browsing influenced tree abundance (Ford *et al.* 2015). However, if rising temperatures intensify predation on dik-diks, wider impacts on community structure might be expected.

Our study site is unusual both in the density of dik-dik it houses (Augustine 2010; Ford et al. 2015) and the degree to which wild dogs rely on dik-dik as primary 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 assumed for our study site. Low reproductive success and high mortality at high ambient temperatures have been reported for wild dogs from two sites where impala are wild dogs’ principal prey (Woodroffe, Groom & McNutt 2017; Rabaiotti *et al.* In Review), although site-specific conditions complicate any comparison of the magnitude of temperature effects at different sites.

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

More generally, we have shown that ambient temperature can influence patterns of predation, even when both predator and prey are tropical endotherms. This finding contrasts with the assumptions of several models (e.g., Dell, Pawar & Savage 2014), and suggests that such models may not accurately represent the responses of ecological communities in which endotherms play important roles. However, our findings also highlight the difficulty of accurately predicting exactly how temperature would be expected to influence predation involving endotherms: the temperature-related changes in behaviour that we observed generated conflicting hypotheses about how predation on impala and dik-diks might vary in response to weather conditions, and only empirical testing within this specific study system indicated the true direction of the impact. Further investigations of how temperature-induced changes in the behaviour of predator and prey influence trophic interaction are needed to build a more general picture of the relationship between ambient temperature and endotherm predation within ecological communities.

**Acknowledgements**

To add.

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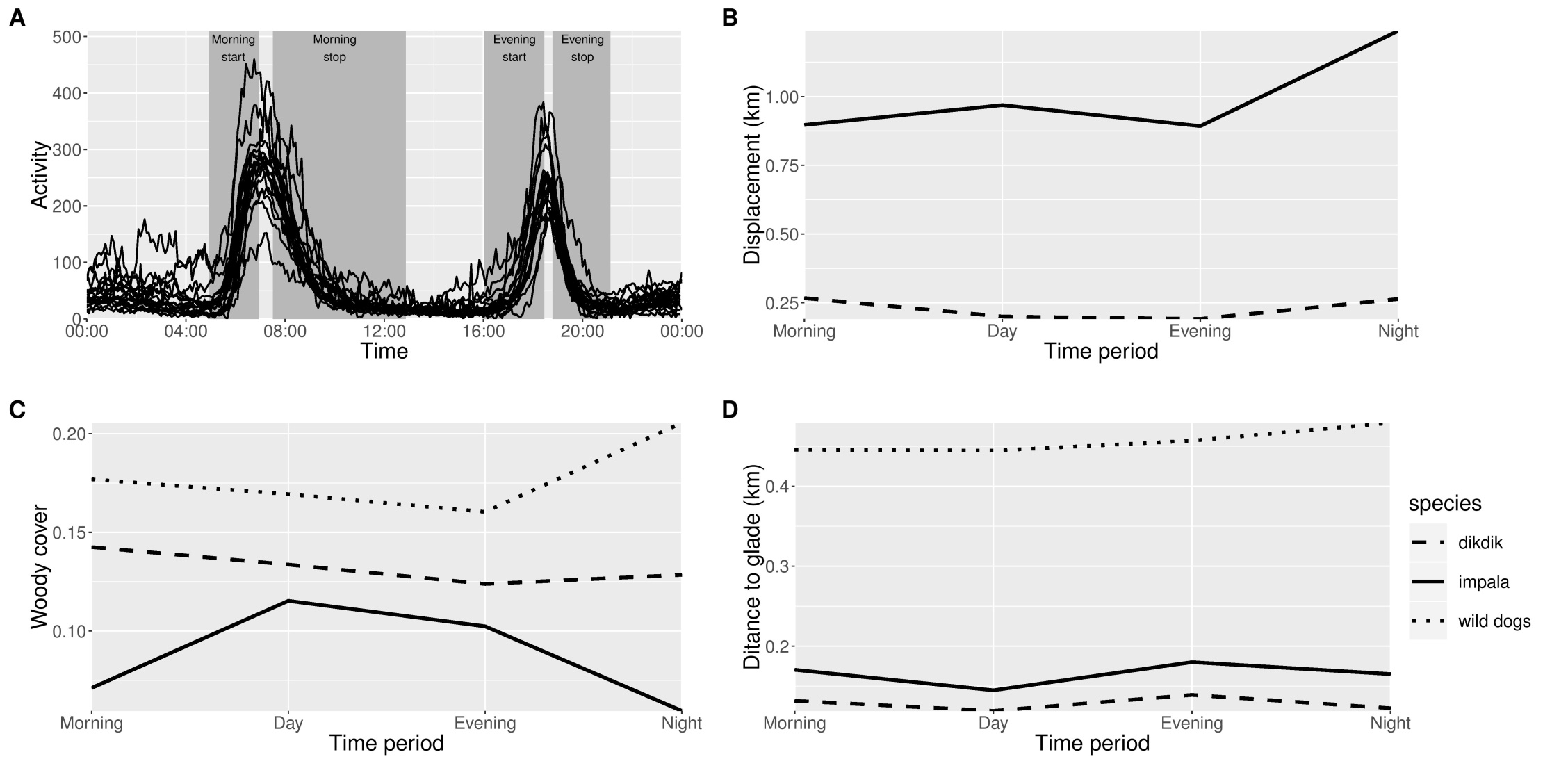
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**Figure 1** Daily movement patterns of sympatric African wild dogs, impala, and dik-diks. (A) activity measured by collar-mounted accelerometers fitted to 18 wild dogs – grey bands indicate the times in which the hunting periods had to start and stop to be classified as morning and evening hunts (B) mean distance moved between successive GPS-collar locations for 20 impala (solid line) and 15 dik-diks (dashed line) during Morning, Day, Evening and Night periods, (C) mean woody cover measures, and (D) mean distances to the nearest glade, at GPS-locations for the same 18 wild dogs (dotted line), 20 impala and 15 dik-diks during Morning, Day, Evening and Night periods.

**Table 1** Scenarios and predictions relating to changes in individual behaviour of African wild dogs, impala and dik-diks under different weather scenarios. Shading indicates predictions which were upheld by our statistical models.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Scenario** | **Explanation** | **Predicted behaviour change at high ambient temperature** | | | **Predicted change in predation rate** |
| *wild dog (23kg)* | *impala (40kg)* | *dik-dik (5kg)* |
| Scenario 1: Optimal foraging | Reduced foraging by wild dogs in daytime when temperatures are highest | reduced foraging during daytime  upheld: yes | unchanged foraging during daytime  not tested | unchanged foraging during daytime  not tested | dik-dik>impala  dik-diks live at higher densities so are predicted to be selected by a predator with limited time3  upheld: yes |
| Scenario 2: Nocturnal compensation | Wild dogs increase activity at night, because daytime foraging is constrained and impala occur predictably in glades | increased foraging at night  upheld: yes | unchanged foraging at night  not tested | unchanged foraging at night  not tested | impala>dik-dik:  at night, impala are predictably located in glades4  upheld: no |
| increased use of glades  upheld: no |
| Scenario 3: Increased habitat overlap | All species predicted to select shade at high temperatures. | increased preference for dense habitat  upheld: no | increased selection for dense habitat    upheld: yes | increased preference for dense habitat  upheld: no | impala>dik-dik:  predation on impala is higher in denser habitat1  upheld: no |
| Scenario 4: Decreased chase time | All species overheat when running, but largest-bodied species overheat first | intermediate reduction in running speed  not tested | greatest reduction in running speed  not tested | smallest reduction in running speed  not tested | impala>dik-dik:  impala are larger and hence predicted to be more affected by overheating2  upheld: no |

1(Ford *et al.* 2014);2(Creel *et al.* 2016);3(Lucas 1983);4(Augustine 2004).

**Table 2** Variables associated with the **duration of hunting periods** of African wild dogs during daytime, and the **occurrence** of night-time hunts. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 5) for the duration of hunting periods in the morning and evening (in minutes), and the occurrence (or not) of hunts at night. 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). Bold highlighting indicates estimates for which the 95% confidence interval excluded zero.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Outcome variable** | **Explanatory variable** | **Estimate** | | | **Lower**  **95% CI** | | **Upper**  **95% CI** | | | **Variable**  **Importance (n)** |
| Morning hunt duration (minutes) | Intercept | | | 220.06 | 198.78 | | 241.33 | | | — (4) |
| Denning (Yes) | | | -57.48 | -137.38 | | 22.41 | | | 1.00 (4) |
| **Temperature (°C)** | | | **-1.33** | **-2.007** | | **-0.66** | | | **0.88 (3)** |
| Moonlight night before | | | 0.054 | -0.24 | | 0.35 | | | 0.68 (2) |
| Rainfall (mm) | | | -2.97 | -6.31 | | 0.36 | | | 0.60 (1) |
| Rainfall:Temperature | | | 0.13 | 0.004 | | 0.25 | | | 0.60 (1) |
| **Denning:Temperature** | | | **5.015** | **2.83** | | **7.19** | | | **0.58 (1)** |
| Evening hunt duration (minutes) | Intercept | | | 226.49 | 213.95 | | 239.04 | | | — (2) |
| **Temperature (°C)** | | | **-3.01** | **-3.45** | | **-2.57** | | | **1.00 (2)** |
| **Moonlight** | | | **-1.84** | **-2.063** | | **-1.62** | | | **1.00 (2)** |
| Moonrise | | | -0.006 | -0.12 | | 0.11 | | | 1.00 (2) |
| Denning (Yes) | | | 7.43 | -18.14 | | 33.003 | | | 1.00 (2) |
| Rainfall (mm) | | | -0.14 | -2.30 | | 2.16 | | | 0.20 (1) |
| Rainfall:Temperature | | | 0.013 | -0.071 | | 0.098 | | | 0.20 (1) |
| Denning:Temperature | | | 2.04 | 0.50 | | 3.58 | | | 0.15 (1) |
| Night-time hunt occurrence | Intercept | | -0.41 | | | -0.52 | | -0.30 | — (2) | | |
| **Temperature** | | **0.019** | | | **0.016** | | **0.023** | **1.00 (2)** | | |
| **Moonlight** | | **0.031** | | | **0.028** | | **0.033** | **1.00 (2)** | | |
| Denning | | -0.069 | | | -0.094 | | -0.044 | 0.52 (1) | | |

**Table 3** Variables associated with **selection of woody cover** by African wild dogs, impala, and dik-dik. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 5). 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). Bold highlighting indicates estimates for which the 95% confidence interval excluded zero.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Outcome variable** | **Explanatory variable** | **Estimate** | **Lower**  **95% CI** | **Upper**  **95% CI** | **Variable**  **importance (n)** |
| impala - morning | Intercept | 0.048 | 0.03 | 0.06 | * (1) |
| **Temperature** | **0.002** | **0.001** | **0.002** | **0.98 (1)** |
| impala - midday | Intercept | 0.076 | 0.06 | 0.09 | * (1) |
| **Temperature** | **0.001** | **0.001** | **0.002** | **1.00 (1)** |
| impala - evening | Intercept | 0.091 | 0.09 | 0.1 | * (2) |
| Season (Wet) | -0.002 | -0.004 | -0.0006 | 0.73 (1) |
| Temperature | 0.0005 | 0.0001 | 0.0008 | 0.2 (1) |
| impala - night | Intercept | 0.057 | 0.05 | 0.06 | * (1) |
| Rainfall | 0.00024 | -0.0001 | 0.0006 | 0.86 (1) |
| dik-dik - crepuscular | Intercept | 0.12 | 0.1 | 0.2 | (2) |
| Season (Wet) | 0.0055 | -0.0004 | 0.01 | 0.78 (1) |
| Temperature | -0.0008 | -0.001 | 0.000003 | 0.11 (1) |
| dik-dik - midday | Intercept | 0.12 | 0.1 | 0.2 | (4) |
| Season (Wet) | -0.0002 | -0.006 | 0.006 | 0.59 (1) |
| Moonlight | 0.0009 | 0.0003 | 0.001 | 0.21 (1) |
| Rain (mm) | 0.0005 | 0.0002 | 0.0009 | 0.10 (1) |
| Temperature | 0.0004 | -0.0004 | 0.001 | 0.09 (1) |
| dik-dik - night | Intercept | 0.13 | 0.1 | 0.2 | (2) |
| **Moonlight** | **-0.022** | **-0.03** | **-0.01** | **0.71 (1)** |
| **Season (Wet)** | **0.023** | **0.02** | **0.03** | **0.32 (1)** |
| wild dog - crepuscular | Intercept | 0.16 | 0.1 | 0.2 | - (1) |
| **denning vs not** | **-0.036** | **-0.05** | **-0.02** | **1.00 (1)** |
| wild dog - night | Intercept | 0.15 | 0.1 | 0.2 | - (1) |
| **denning vs not** | **-0.12** | **-0.14** | **-0.09** | **1.00 (1)** |

**Table 4** Variables associated with **use of glades** by wild dogs, impala, and dik-dik. The table presents Estimated effects of explanatory variables included in the top model sets (ΔAICc < 5. 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). Bold highlighting indicates estimates for which the 95% confidence interval excluded zero.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Outcome variable** | **Explanatory variable** | **Estimate** | | **Lower**  **95% CI** | **Upper**  **95% CI** | **Variable**  **importance (n)** |
| impala in glade – 24h | Intercept | | 0.039 | 0.022 | 0.055 | * (1) |
| **morning *vs* midday** | | **0.06** | **0.06** | **0.07** | **1.00 (1)** |
| **evening *vs* midday** | | **-0.009** | **-0.01** | **-0.005** | **1.00 (1)** |
| **night *vs* midday** | | **0.19** | **0.18** | **0.20** | **1.00 (1)** |
| impala in glade - night | Intercept | | 0.26 | -0.007 | 0.03 | * (1) |
| **Moonlight** | | **-0.072** | **-0.08** | **-0.06** | **1.00 (1)** |
| **Rainfall** | | **-0.0025** | **-0.003** | **-0.002** | **0.94 (1)** |
| **Temperature** | | **0.006** | **0.004** | **0.008** | **0.06 (1)** |
| dik-diks in glade – 24h | Intercept | | 0.030 | 0.02 | 0.04 | * — (1) |
| wet *vs* dry phase | | -0.015 | -0.02 | -0.006 | 0.96 (1) |
| dik-diks in glade - night | Intercept | | 0.012 | -0.007 | 0.03 | * (1) |
| **Moonlight** | | **0.042** | **0.03** | **0.05** | **0.97(1)** |
| wild dog distance to glade – 24h | Intercept | | 0.58 | 0.5 | 0.6 | — (1) |
| **Pack size** | | **-0.012** | **-0.01** | **-0.02** | **0.90 (1)** |
| wild dog distance to glade – night | Intercept | | 0.55 | 0.4 | 0.7 | (5) |
| **Pack Size** | | **-0.020** | **-0.03** | **-0.01** | **0.67(2)** |
| Moonlight | | 0.064 | 0.03 | 0.1 | 0.27 (2) |
| denning *vs* not | | -0.051 | -0.004 | -0.1 | 0.11 (1) |
| wet *vs* dry phase | | -0.039 | -0.08 | -0.001 | 0.08 (1) |

**Table 5** Variables associated with **African wild dog consumption of impala**. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc<5) for African wild dog consumption of impala. The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n). Bold highlighting indicates estimates for which the 95% confidence interval excluded zero.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Explanatory variable** | **Estimate** | **Lower 95% CI** | **Upper 95% CI** | **Variable importance (n)** |
| Intercept | 0.74 | 0.5 | 1.01 | — (2) |
| **Temperature in previous 7 days** | **-0.021** | **-0.03** | **-0.01** | **1.00 (1)** |
| Community vs private land | -0.63 | -0.1 | -0.02 | 0.10 (1) |

**Impacts of temperature on predator-prey interactions in an African savanna**

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

and Rosie Woodroffe1

***Supporting Information***

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



**A**

**B**

**Time**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Table S1** Start and stop times of hunting periods allocated to each time period within the analysis. | | | | |
| **Type of Bout** | **Earliest start time** | **Latest start time** | **Earliest stop time** | **Latest stop time** |
| Morning | 04:55:39 | 06:56:04 | 07:30:41 | 12:51:33 |
| Midday | 06:56:05 | 16:01:54 | 12:51:34 | 18:47:02 |
| Evening | 16:01:55 | 18:26:52 | 18:47:03 | 21:06:56 |
| Night | 18:26:53 | 04:55:38 | 21:06:57 | 07:30:40 |

**Table S2** Variables associated with the characteristics of African wild dog hunting periods in the **morning**. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 5) for each outcome variable. The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n). Bold highlighting indicates estimates for which the 95% confidence interval excluded zero.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Outcome variable** | **Explanatory variable** | | **Estimate** | **Lower**  **95% CI** | **Upper**  **95% CI** | **Variable**  **importance (n)** | |
| Occurrence | Intercept | | 0.80 | 0.77 | 0.83 | | — (1) |
| **Moonlight before** | | **-0.0097** | **-0.011** | **-0.0079** | | **1.00 (1)** |
| Duration  (minutes) | Intercept | | 220.06 | 198.78 | 241.33 | | — (4) |
| Denning (Yes) | | -57.48 | -137.38 | 22.41 | | 1.00 (4) |
| **Temperature (°C)** | | **-1.33** | **-2.007** | **-0.66** | | **0.88 (3)** |
| Moonlight before | | 0.054 | -0.24 | 0.35 | | 0.68 (2) |
| Rainfall (mm) | | -2.97 | -6.31 | 0.36 | | 0.60 (1) |
| Rainfall:Temperature | | 0.13 | 0.004 | 0.25 | | 0.60 (1) |
| **Denning:Temperature** | | **5.015** | **2.83** | **7.19** | | **0.58 (1)** |
| Intensity | Intercept | | 51.43 | 46.78 | 56.076 | | **— (3)** |
| **Denning (Yes)** | | **1.56** | **0.14** | **0.16** | | **0.89 (2)** |
| **Temperature (°C)** | | **-0.26** | **-0.38** | **-0.14** | | **0.57 (2)** |
| Start time | Intercept | 06:31:41 | | 06:24:07 | 06:39:14 | | * (1) |
| **Denning (Yes)** | **-00:07:46** | | **-00:06:14** | **-00:09:18** | | **1(1)** |
| **Temperature (°C)** | **-00:01:15** | | **-00:01:01** | **-00:01:29** | | **0.99(1)** |
| Stop time | Intercept | | 09:54:52 | 09:20:48 | 10:28:56 | | * (3) |
| **Temperature (°C)** | **-00:02:28** | | **-00:01:53** | **-00:03:03** | | **0.72(2)** |
| **Denning (Yes)** | **00:13:25** | | **00:09:37** | **00:17:14** | | **0.57(2)** |

**Table S3** Variables associated with the characteristics of African wild dog hunting periods in the **evening**. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 5) for each outcome variable. The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n). Bold highlighting indicates estimates for which the 95% confidence interval excluded zero.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Outcome variable** | **Explanatory variable** | | **Estimate** | **Lower 95% CI** | **Upper 95% CI** | **Variable**  **importance (n)** | |
| Occurrence | Intercept | | 1.21 | 1.08 | 1.35 | | — (2) |
| **Moonlight** | | **-0.010** | **-0.012** | **-0.008** | | **1.00 (2)** |
| **Temperature (°C)** | | **-0.017** | **-0.021** | **-0.013** | | **0.97 (2)** |
|  | Denning (Yes) | | 0.042 | 0.016 | 0.069 | | 0.08 (1) |
| Duration  (minutes) | Intercept | | 226.49 | 213.95 | 239.04 | | — (2) |
| **Temperature (°C)** | | **-3.01** | **-3.45** | **-2.57** | | **1.00 (2)** |
| **Moonlight** | | **-1.84** | **-2.06** | **-1.62** | | **1.00 (2)** |
| Moonrise | | -0.006 | -0.12 | 0.11 | | 1.00 (2) |
| Denning (Yes) | | 7.43 | -18.14 | 33.00 | | 1.00 (2) |
| Rainfall (mm) | | -0.14 | -2.30 | 2.16 | | 0.20 (1) |
| Rainfall:Temperature | | 0.013 | -0.071 | 0.098 | | 0.20 (1) |
| Denning:Temperature | | 2.04 | 0.50 | 3.58 | | 0.15 (1) |
| Intensity | Intercept | | 62.98 | 46.78 | 56.08 | | — (4) |
| **Temperature (°C)** | | **-0.83** | **-0.96** | **-0.70** | | **1.00 (4)** |
| Denning (Yes) | | 7.50 | 2.55 | 12.45 | | 1.00 (4) |
| **Moonlight** | | **-0.21** | **-0.27** | **-0.15** | | **0.45 (3)** |
| Moonrise | | -0.006 | -0.038 | 0.027 | | 0.45 (3) |
| Rainfall (mm) | | -1.14 | -2.04 | -0.78 | | 0.14 (1) |
| Rainfall:Temperature | | 0.058 | 0.034 | 0.082 | | 0.14 (1) |
| Denning:Temperature | | -0.58 | -1.01 | -0.13 | | 0.07 (1) |
| Start time | Intercept | 15:43:55 | | 15:34:49 | 15:53:01 | | * (2) |
| **Temperature (°C)** | **00:03:30** | | **00:03:11** | **00:03:49** | | **1.00 (2)** |
| **Denning (Yes)** | **-00:10:49** | | **-00:08:52** | **-00:09:18** | | **1.00 (2)** |
| **Moonlight** | **00:01:01** | | **00:00:52** | **00:01:10** | | **0.90 (1)** |
| Moonrise | -00:00:01 | | -00:00:05 | 00:00:05 | | 0.90 (1) |
| Stop time | Intercept | 19:42:14 | | 19:38:50 | 19:45:39 | | * (2) |
| **Denning (Yes)** | **00:13:25** | | **00:09:37** | **00:17:14** | | **0.55(1)** |
| **Moonlight** | **00:00:52** | | **00:00:43** | **00:01:02** | | **0.44(1)** |
| Moonrise | 00:00:01 | | -00:00:04 | 00:00:06 | | 0.44(1) |

**Table S4** Variables associated with the characteristics of African wild dog hunting periods **at night**. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 5) for each outcome variable. The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n). Bold highlighting indicates estimates for which the 95% confidence interval excluded zero.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Outcome variable** | **Explanatory variable** | | **Estimate** | **Lower 95% CI** | **Upper 95% CI** | **Variable importance (n)** | |
| Occurrence | Intercept | | -0.41 | -0.52 | -0.30 | | — (2) |
| **Temperature** | | **0.019** | **0.016** | **0.023** | | **1.00 (2)** |
| **Moonlight** | | **0.031** | **0.028** | **0.033** | | **1.00 (2)** |
| Denning | | -0.069 | -0.094 | -0.044 | | 0.52 (1) |
| Duration  (minutes) | Intercept | | 80.69 | 47.72 | 113.66 | | — (4) |
| **Moonlight** | | **5.59** | **5.00** | **6.18** | | **1.00 (4)** |
| **Moonrise** | | **0.83** | **0.42** | **1.25** | | **1.00 (4)** |
| Denning (Yes) | | 102.12 | -52.87 | 257.11 | | 0.94 (4) |
| Temperature (°C) | | 0.71 | -0.55 | 1.97 | | 0.79 (3) |
| Rainfall (mm) | | -0.54 | -7.66 | 6.57 | | 0.53 (2) |
| Rainfall:Temperature | | 0.004 | -0.27 | 0.27 | | 0.51 (1) |
| Denning:Temperature | | -7.42 | -13.76 | -1.10 | | 0.47 (2) |
| Intensity | Intercept | | 28.51 | 20.67 | 36.36 | | — (4) |
| **Moonlight** | | **0.86** | **0.75** | **0.98** | | **1.00 (4)** |
| Moonrise | | -0.011 | -0.10 | -0.072 | | 1.00 (4) |
| Denning (Yes) | | 1.82 | -3.17 | 6.84 | | 0.75 (2) |
| **Temperature (°C)** | | **0.42** | **0.18** | **0.66** | | **0.52 (2)** |
| Start time | Intercept | 15:52:55 | | 09:34:32 | 22:11:08 | | * (2) |
| **Moonrise** | **00:24:22** | | **00:20:30** | **00:24:22** | | **1.00 (2)** |
| Moonlight | -00:05:15 | | -00:10:38 | 00:00:08 | | 1.00 (2) |
| **Temperature (°C)** | **-00:29:38** | | **-00:18:57** | **-00:40:20** | | **0.22 (1)** |
| Stop time | Intercept | 09:14:33 | | 06:28:31 | 12:00:35 | | * (3) |
| **Moonlight** | **-00:24:17** | | **-00:20:20** | **-00:28:14** | | **1.00 (3)** |
| Moonrise | 00:03:22 | | 00:00:31 | 00:06:12 | | 1.00 (3) |
| **Denning (Yes)** | **02:22:25** | | **01:11:11** | **03:33:39** | | **0.25 (1)** |
|  | **Temperature** | **00:19:04** | | **00:11:10** | **00:26:57** | | **0.08 (1)** |