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

D. Rabaiotti[1,2], Adam T. Ford[3], Ben Chapple[2], Sophie Morrill[2],
Jacob R. Goheen[4] and Rosie Woodroffe[1]

[1]Institute of Zoology, Regents Park, London, UK, NW1 4RY

[2]Department of Genetics, Evolution and Environment, University College London, Gower Street, London, UK, WC1H 0AG

[3]Departent of Biology, University of British Columbia, 3187 University Way, ASC 413, Kelowna, BC Canada V1V 1V7

[4]Departent of Zoology and Physiology, University of Wyoming, 1000 E. University Ave., Laramie, USA, WY 82071

Abbreviated title: Temperature affects predator-prey interactions

Article type: Research article

Number of words: Abstract = 316, Main text = 7867

Corresponding author: D. Rabaiotti, Daniella.Rabaiotti@ioz.ac.uk, +447968018087

Abstract

1. Climate warming may alter predator-prey dynamics by changing predator attack speed and prey escape speed, and by impacting the daily activity rhythms and habitat use of both predators and prey. As there is no direct link between metabolic rates and temperature in endotherms, it is widely assumed that climate warming will not affect interactions between endothermic predators and prey.

2. This assumption ignores evidence that many endotherm species change their habitat use and behaviour at high temperatures. Moreover, predator-prey chases generate metabolic heat, which larger-bodied endotherms may be less able to dissipate, potentially altering chase outcomes at high ambient temperatures.

3. We investigated how ambient temperature impacted predator-prey interactions in a three-species system comprising one predator species, the African wild dog (*Lycaon pictus*), and two prey species, dikdik (*Madoqua guentheri*) and impala (*Aepyceros melampus*).

4. We predicted that African wild dogs would kill more impala at high ambient temperatures via three mechanisms. Firstly, we predicted that African wild dog activity would be reduced in the day, but increase at night, enabling them to target impala, which are predictably located in glades during this time period. Secondly, we predicted that all three species would seek shade at high temperatures, using closed habitat where impala face higher predation rates. Third, we predicted that difficulties of dissipating metabolic heat during chases at high ambient temperatures would affect impala (40kg) more than dikdiks (5kg).

5. Although prey habitat selection and wild dog activity patterns changed with temperature as predicted, we found that fewer, not more, wild dog scats contained impala remains when ambient temperatures were high. Wild dogs spent less time hunting on hot days and, consistent with models of optimal foraging under time constraints, appeared to select abundant, lower-value dikdiks over rarer but higher-value impala.

6. Our findings show that weather can influence predator-prey interactions among endotherms, and suggest that studies assuming otherwise should be interpreted with caution.

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

Introduction

54 *Introduction*

55   Climate change has far-reaching impacts on both species and ecosystems (Parmesan &

56 Yohe 2003). Meta-analyses suggest that many climate impacts on individual species operate

57 indirectly, through their effects on species interactions such as competition, herbivory,

58 predation, and parasitism (Cahill *et al.* 2012; Ockendon *et al.* 2014). As weather patterns will

59 shift under novel climate regimes, understanding how ambient temperature and other abiotic

60 processes influence species interactions will become critical to wildlife conservation in the

61 coming decades.

62   Climate is particularly critical for ectothermic species, which rely on environmental

63 temperatures to regulate their body temperature, meaning that high ambient temperatures

64 directly lead to changes in physiology, movement and behaviour. These individual

65 behavioural shifts can drive climate impacts on species interactions. For example, high

66 ambient temperatures allows ectotherms to move more rapidly, potentially making them

67 more efficient predators and more challenging prey, with cascading consequences for

68 community structure (Dell, Pawar & Savage 2014). It is usually assumed that ambient

69 temperature has no similar impacts on predation involving endotherms (e.g., Dell, Pawar &

70 Savage 2014; Harfoot *et al.* 2014); however, birds and mammals may respond to high

71 ambient temperatures by curtailing their foraging time (Ricklefs & Hainsworth 1968;

72 Quaglietta, Mira & Boitani 2018), switching from diurnal to nocturnal foraging (Levy *et al.*

73 2018), selecting different habitats (Austin 1976; Pigeon *et al.* 2016), and choosing different

74 foods (Doolan & Macdonald 1996; Garcia-Heras *et al.* 2017), all of which are likely to

75 influence their impacts on the species that they consume, or that consume them.

76   Predator-prey interactions involving large-bodied endotherms might be especially

77 sensitive to rising environmental temperatures, because the low surface-area-to-volume ratios

78 of large animals may make it difficult to dissipate heat generated by pursuing or avoiding

– 3 –

79   predation (Speakman & Krol 2010; Creel *et al.* 2016). Hence, with respect to the outcome of

80   predator-prey interactions, high ambient temperatures might favour endothermic prey that are

81   smaller than their endothermic predators, as the predators' large body size would mean that

82   they overheat faster than their smaller prey, leading to decreased predation rates on smaller

83   prey species. Similarly, high ambient temperatures may also benefit endothermic predators

84   that are smaller than their endothermic prey, as the large bodied prey would overheat faster

85   than the smaller bodied predator, leading to shorter chase times and higher hunting success

86   (Creel *et al.* 2016). Predation by and on large-bodied endotherms can have cascading effects

87   on community structure (e.g. Hebblewhite et al 2005), hence any effect of temperature on

88   endotherm predation might have broader impacts on ecological communities.

89   Using a three-species predator-prey system in an African savanna, we measured the

90   impact of ambient temperature on predator-prey interactions. Specifically, we examined how

91   ambient temperature affected the habitat use and activity patterns of a small-bodied prey

92   species (the 5kg Guenther's dikdik *Madoqua guentheri*), a larger-bodied prey species (the

93   40kg impala *Aepyceros melampus*), and their shared predator (the 23kg African wild dog

94   *Lycaon pictus*). At our study site in Kenya, impala and dikdiks are the two most abundant

95   ungulates, and their browsing shapes plant communities (Ford *et al.* 2014; Ford *et al.* 2015).

96   Wild dogs are crepuscular, and hunt by running prey down (Creel & Creel 1995); dikdiks and

97   impala together comprise 82% of the prey biomass that wild dogs consume at our study site

98   (Woodroffe et al. 2007).

99   We evaluated five hypotheses about the impacts of ambient temperature on predation by

100   wild dogs on impala and dikdik (Table 1). First, we hypothesised that predator-prey

101   interactions would be impacted by reduced predator activity on hot days (Table 1).

102   Previously, we have shown that wild dog activity declines as ambient temperatures increase

103   (Woodroffe et al 2017, Rabaiotti & Woodroffe 2019), which may reflect shorter hunting

104 periods (Woodroffe 2011b). Optimal foraging theory suggests that, when foraging time is

105 limited, individuals should accept lower-value prey, rather than continuing to search for

106 higher-value prey (Lucas 1983). Therefore, we predicted that, if wild dogs had reduced

107 foraging time, they would increase predation on dikdik (which are encountered more

108 frequently but are too small to feed a whole pack) over impala, which are larger but

109 encountered less frequently (Woodroffe *et al.* 2007). We term this, Hypothesis 1, the

110 'reduced daytime foraging hypothesis'.

111   Second, we hypothesised that predator-prey interactions would be impacted by greater

112 predator nocturnality in hot weather (Table 1). We have shown previously that wild dogs are

113 more nocturnal when daytime temperatures are high (Rabaiotti & Woodroffe 2019). While

114 impala herds are scattered during daylight hours, at night they aggregate in clearings

115 ("glades") as a form of anti-predator behaviour (Augustine 2004; Otieno et al. 2019), and are

116 therefore predictably located. We predicted that wild dogs would target glades at night to

117 hunt impala, and termed this, Hypothesis 2, the 'nocturnal prey concentration hypothesis'.

118 We would expect that, if Hypothesis 2 was upheld, increased nocturnal wild dog activity at

119 high ambient temperatures would lead to increased targeting of predictably located impala

120 over less predictably located dikdik, increasing predation risk on impala (Table 1).

121   Third, we quantified whether habitat selection by both predators and prey might be

122 affected by ambient temperatures, with consequences for predation. Many large mammals

123 select shade in hotter weather (Mole *et al.* 2016; Pigeon *et al.* 2016), and we predicted that

124 wild dogs, impala, and dikdik would do the same (Table 1). Further, we predicted that such a

125 change would increase predation by wild dogs on impala, since impala face higher *per capita*

126 predation rates in habitats characterised by higher woody cover (and thus shade; Ford *et al.*

127 2014). We term this, Hypothesis 3, the 'shade-seeking hypothesis'.

128   Finally, we explored the potential consequences of both predators and prey overheating

129 during chases. Creel *et al.* (2016) suggested that, during chases, wild dogs would overheat

130 more slowly than their larger-bodied prey, leading to shorter and more successful chases at

131 higher ambient temperatures. Larger species have more difficulty dissipating metabolic heat

132 due to their lower surface-area-to-volume ratio (Peters 1986), potentially making such

133 species more vulnerable to coursing predators. By extension, we predicted that wild dogs

134 would overheat less rapidly than impala but more rapidly than dikdiks, leading to increased

135 predation on impala relative to dikdiks at higher ambient temperatures (Table 1). We termed

136 this, Hypothesis 4, the 'prey overheating hypothesis'.

137   These hypothesised behavioural responses to high ambient temperatures generated

138 contrasting sets of predictions about trophic interactions between wild dogs, impala, and

139 dikdik (summarised in Table 1). By testing these predictions, we explored the behavioural

140 mechanisms underlying whether, and how, ambient temperature influenced interactions

141 between predators and prey, in an attempt to evaluate how climate change might affect this

142 ecosystem through predator-prey interactions.

143

144 ***Methods***

145 *Study area*

146   The focal area for this study was the Mpala Conservancy, Kenya (0°17' N, 36°53' E), a

147 200 km^2 area of semi-arid savanna managed jointly for livestock production and wildlife

148 conservation. Mpala experiences little seasonal variation in ambient temperature; daily

149 maximum temperature ranges from 20-37°C, and mean annual rainfall is 590mm, varying

150 substantially both within and between years (Caylor, Gitonga & Martins 2017).

151   Mpala hosts 22 species of wild ungulate, of which dikdiks and impala are the two most

152 abundant (Ford *et al.* 2015), at 139 individuals per km^2 and 20.3 individuals per km^2

153   respectively (Augustine et al 2004). Mpala also supports five species of large carnivore in

154   addition to wild dogs: lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*),

155   spotted hyaena (*Crocuta crocuta*), and striped hyaena (*Hyaena hyaena*), all of which have

156   dietary overlap with wild dogs (Frank, Woodroffe & Ogada 2005).

157

158   *Data collection*

159   We used Global Positioning System (GPS) collars to measure daytime and night-time

160   activity, movement, and habitat use. GPS-collars (Savannah Tracking Ltd, Nairobi, Kenya)

161   were fitted to 20 adult female impala (each from a different herd) between May and June

162   2011, as described in Ford *et al.* (2014). Each impala GPS-collar recorded a location every 20

163   minutes, for an average of 245 days. Likewise, GPS-collars (Savannah Tracking Ltd, Nairobi,

164   Kenya) were fitted to 15 adult female dikdik between July 2010 and September 2011, as

165   described in Ford & Goheen (2015). Each dikdik GPS-collar recorded a location every 10

166   minutes, for 18 days on average. Additionally, GPS collars (Vectronic Aerospace GmbH,

167   Berlin, Germany) were fitted to 18 wild dogs in 13 packs between 2011 and 2016, using

168   capture methods described in Woodroffe (2011a); all of these packs had home ranges

169   overlapping Mpala, although none remained on Mpala year-round. Data were collected from

170   one collar per pack at any one time. Each wild dog GPS-collar recorded locations at 01:00,

171   06:30, 07:00, 07:30, 08:00, 13:00, 18:00, 18:30, 19:30, and also recorded average

172   acceleration in two planes (on a scale of 0 to 255 units) every five minutes, for 218 days on

173   average.

174   We used faecal analysis to quantify the relative frequency of predation by wild dogs on

175   impala and dikdik. Wild dog scats were collected during 2001-2004 across a 5,700km^2 study

176   area which included Mpala Conservancy, and analysed as described in Woodroffe *et al.*

177   (2007). We avoided pseudoreplication by including only one randomly-selected scat

– 7 –

178 collected from each pack on each occasion (Woodroffe *et al.* 2007). Because the GPS-collar

179 data were collected ≥7 years after the scat samples, they came from the descendants of the

180 individuals which deposited the scats. There were no major shifts in temperature and rainfall

181 between the two time periods, however (Table S1).

182   Daily rainfall and daily maximum ambient temperature were collected from a weather

183 station at Mpala Research Centre (Caylor, Gitonga & Martins 2017). Data on the timing of

184 sunrise and sunset were taken from the *R* package *suncalc* (Agafonkin & Thieurmel 2017).

185 Moonlight was calculated by multiplying percentage illumination by the number of hours the

186 moon was in the sky between sunset and sunrise. Finally, we used GPS-collar data to identify

187 periods when wild dog packs were denning (raising pups in a den, recognisable from the

188 movement path which shows a "starburst" pattern of repeat visits to the same location,

189 Woodroffe *et al* 2017) as activity levels have been shown to increase during this period

190 (Woodroffe *et al* 2017). Mornings and evenings where individuals were babysitting

191 (guarding the pups and therefore not hunting) were defined as days where the individual did

192 not move from the den site during the morning or evening – these were removed from the

193 analyses.

194

195 *Identifying hunting periods of wild dogs*

196   To estimate the time that wild dogs spent hunting, and to compare prey and predator

197 behaviour at times when predation risk was highest, we used accelerometry data collected by

198 GPS-collars to identify wild dog hunting bouts. First, we summed the two accelerometer

199 measurements for each 5-minute period, to give an overall measure of activity. We then

200 defined hunting bouts based on three criteria: (i) activity >0 units for >20 minutes; (ii) total

201 activity during the activity bout >500 units; (iii) followed by three or more consecutive

202 records of 0 unit activity. These criteria excluded activity bouts which were too short to

203 represent hunting, or which related to less energetic behaviours, such as socialising. Criteria

204 were derived using visual inspection of activity plots and examining the characteristics of

205 activity bouts in time periods during which wild dogs are typically observed hunting. For

206 each hunting bout identified in this way, we recorded start time, end time, duration (in

207 minutes), and intensity (total activity divided by duration). The distributions of start and stop

208 times are shown in Fig. S1. We classified hunting bouts as "morning", "evening", "night" or

209 "midday", based on their start and stop times, as detailed in Table S2 and Fig. S1. Bouts that

210 spanned multiple time periods were excluded from the analysis. After using accelerometry

211 data to identify specific hunting bouts, we categorised each wild dog location as falling inside

212 or outside a hunting bout.

213

214 *Categorising activity periods of prey species*

215 We categorised dikdik and impala GPS collar locations into four time periods, reflecting

216 diel variation in wild dog hunting activity and hence predation risk. We defined "morning" as

217 the time period between sunrise (taken from the *R* package *suncalc*, Agafonkin & Thieurmel

218 2017) and the third quartile of end times for wild dog hunting bouts (approximately 3.5h after

219 sunrise; Fig. S1). We classified impala and dikdik "evening" GPS-locations as those recorded

220 between the first quartile of start times for hunting bouts (approximately 2hr10min before

221 sunset; Fig. S1) and sunset (which fell between 1841h and 1912h). We categorised impala

222 and dikdik GPS-locations as "midday" if they were recorded between the "morning" and

223 "evening" periods, and "night" if they were recorded between sunset and sunrise.

224

225 *Habitat use*

226 We analysed habitat use from a vegetation map of Mpala created from a 2011 Quickbird

227 satellite image (Digital Globe, Longmont, CO, USA) by Ford *et al.* (2014). We estimated the

– 9 –

228 woody cover (a measure of shadiness) associated with each impala, dikdik, and wild dog

229 GPS-collar location as the proportion of woody cover within a circular area of radius 40m,

230 centred on the collar location, calculated in *QGIS* (QGIS Development Team 2018).

231   We used the same habitat map to classify each GPS-collar location in relation to glades.

232 For impala and dikdik, we recorded whether each location fell inside or outside a glade. As

233 <1% of wild dog hunting locations fell inside glades, we recorded the distance to the nearest

234 glade for each wild dog location, using the plugin "*NNJoin*" in *QGIS* (QGIS Development

235 Team 2018).

236

237 *Statistical analyses*

238   We used multi-model inference to evaluate associations between wild dog hunting

239 outcome variables (start time, stop time, duration, probability of occurrence, and intensity of

240 morning, evening and night time hunts) and a range of explanatory variables (Table S3, Table

241 S4). The reduced daytime foraging time hypothesis (Table 1, Hypothesis 1) predicted that

242 wild dogs would spend less time hunting on hot days. To test this hypothesis, we split the

243 activity data into morning, midday and evening. We analysed continuous outcome variables

244 describing hunt duration, start time, stop time, and hunt intensity, as well as a binary outcome

245 variable describing whether or not a hunt was recorded for each time period. Only 10% of

246 hunting bouts occurred during the midday period (accounting for 2% of daily activity), so we

247 considered these abnormal events and did not subject them to further statistical analyses.

248 Morning and evening hunt periods were analysed separately as a number of the covariates

249 (Table S3) were predicted to impact morning and evening hunts in different ways. For each

250 outcome variable, we constructed Generalised Linear Mixed Models (GLMMs) using the

251 package *nlme* (Pinheiro *et al.* 2015) in *R*, with Gaussian error distribution for the continuous

252 outcome variables and binomial error distribution for the binary outcome variable. Each

253   model included the identity of individual animals and the date as random effects. Although

254   our hypotheses concerned the potential effects of ambient temperature, we included several

255   other explanatory variables known to influence activity patterns of wild dogs, namely

256   denning status, rainfall, moonlight and, in models of night-time activity, time of moonrise

257   and moonset. Detailed justifications for including each explanatory variable are shown in

258   Table S3.

259   For each outcome variable, we built a series of statistical models using explanatory

260   variables and biologically-meaningful interactions between explanatory variables, with

261   individual identity as a random variable. We then used Akaike's Information Criterion (AIC)

262   to compare models using the *R version 3.3.2* (version 3.3.2, R Core Team 2017) package

263   *MuMIn* (Bartoń 2017). We considered all models with delta AIC scores within 2 units of the

264   lowest AIC model (*i.e.,* ΔAIC< 2) to have a high level of support (Burnham et al. 2002),

265   referring to this array of models as the "top set". We used model averaging (Burnham et al.

266   2002) to estimate the effect on the outcome variable of each explanatory variable in the top

267   set.

268   In the nocturnal prey selection hypothesis (Table 1, Hypothesis 2), we predicted that

269   impala would use glades more at night (Table 1, 2a: nocturnal prey concentration). To test

270   this hypothesis, we calculated the proportion of each impala's locations falling within glades

271   during the morning, midday, evening, and night periods for each 24-h period. We used mixed

272   effects models with in glade (1) or not (0) as the independent variable and time period (day

273   (morning, evening and midday combined) or night) as the explanatory variable and individual

274   identity and date as random variables to test whether prey species were significantly more

275   likely to be found in glades at night than during the day.

276

277   In the nocturnal prey selection hypothesis, we also predicted that wild dogs would be more

278   likely to hunt at night following hot days (Table 1, 2b: increased night-time hunting). To test

279   this hypothesis, we analysed continuous outcome variables describing the duration, start time,

280   stop time, and intensity of hunts occurring between sunset and sunrise, as well as a binary

281   outcome variable describing whether or not a hunt was recorded each night. These outcome

282   variables were compared with the same explanatory variables used in Hypothesis 1 except

283   that, as nocturnal periods span dates, the maximum ambient temperature for the proceeding

284   daytime period was used. As in the models of daytime hunting behaviour (Hypothesis 1), we

285   constructed Generalised Linear Mixed Models (GLMMs), with Gaussian error distribution

286   for the continuous outcome variables and binomial error distribution for the binary outcome

287   variable, for each outcome variable using the package *nlme* (Pinheiro *et al.* 2015) in *R* (R

288   Core Team 2015), and each model included the identity of individual animals as a random

289   effect. Model selection was performed using model averaging in the same way as when

290   investigating daytime hunts (Hypothesis 1).

291   In the nocturnal prey selection hypothesis, we also predicted that wild dogs would

292   preferentially target glades at night (Table 1, 2c: night-time habitat selection). To test this

293   hypothesis, we calculated the mean distance to the nearest glade for each night-time hunt

294   period. As when investigating prey use of glades, we analysed this outcome variable using. a

295   mixed effects model with time period (day (morning, evening and midday combined) or

296   night) as the explanatory variable and individual identity and date as random variables, in

297   order to test whether wild dogs were significantly closer to glades at night than during the

298   day.

299   In the shade-seeking hypothesis (Table 1, Hypothesis 3) we predicted that wild dogs,

300   impala, and dikdiks would increase their use of shaded habitat at high ambient temperatures.

301   To test this hypothesis, we constructed a series of models with use of woody cover as the

302   outcome variable. To avoid pseudoreplication, we averaged the woody cover values for each

303   individual across each morning, midday, evening or night-time period. For wild dogs, we

304   only included measurements of woody cover at locations taken during hunting bouts. We

305   analysed these outcome variables using GLMMs with individual identity as a random effect,

306   building a separate array of models for each time of day, and for all times of day together.

307   Candidate explanatory variables were the same as for the analyses of wild dog activity (i.e.,

308   temperature, rainfall, moonlight, and, for wild dogs, denning), but also included a variable

309   describing rainfall phase (Table S4), which was predicted to impact herbivore behaviour and

310   location (Goheen et al 2013). Following Ford *et al.* (2014), we considered days to fall within

311   "wet phases" if >50mm of rain had fallen in the previous four weeks, and classed all other

312   days as falling in "dry phases". In constructing the array of models for multi-model inference,

313   this rainfall phase variable was never included in the same model as daily rainfall, because

314   the two were correlated. Model selection was performed using model averaging in the same

315   way as when investigating wild dog hunting (Hypothesis 1 and 2b).

316   The prey overheating hypothesis (Table 1, Hypothesis 4) could not be tested directly from

317   our datasets, because our GPS-collar locations were recorded too infrequently to estimate

318   chase speeds, so our evaluation of this scenario relied on testing the prediction that wild dogs

319   killed impala more frequently on hot days (Table 1). This outcome was also predicted under

320   Hypotheses 2 and 3, however, and could not be used to specifically support Hypothesis 4. We

321   tested this prediction by using a GLM with binomial error distribution to analyse whether or

322   not wild dog scats contained impala remains. In this model, candidate explanatory variables

323   were ambient temperature during the previous seven days (to account for delays between a

324   scat being deposited and collected), and land use (as a previous study showed that impala

325   were consumed far less frequently on community land, relative to private land, Woodroffe *et*

326   *al.* 2007). Pack or individual identity were often unknown for wild dog scats, so these models

327 did not include random effects. Model selection was performed using model averaging in the

328 same way as when investigating wild dog hunting (Hypothesis 1 and 2b) and woody cover

329 selection (Hypothesis 3).

330

331 ***Results***

332 *Daily movement patterns*

333 African wild dogs showed a strongly crepuscular activity pattern, with hunts and daily

334 activity concentrated in the morning and evening time periods (Fig. 1). Sixteen percent of

335 wild dog hunting periods, and 17% of total daily activity, occurred at night (Fig. 2).

336 Impala had the highest levels of displacement between GPS locations at night (1.24km

337 ±2.11(s.d.)) and lower displacement distances in the morning (0.90km ±1.4), daytime

338 (0.97km ±1.7) and evening (0.89km ±1.3) time periods.

339 Dikdik had similar levels of displacement between GPS locations throughout the day, with

340 the higher levels of displacement in the morning (0.27km ±0.3) and at night (0.26km ±0.27)

341 and slightly lower displacement distances in the daytime (0.20km ±0.27) and evening

342 (0.19km ±0.23) time periods.

343

344 *Associations between ambient temperature and wild dog hunting*

345 Consistent with the reduced daytime foraging time hypothesis (Hypothesis 1), wild

346 dogs' daytime hunting periods were shorter in both the morning and evening time periods at

347 high ambient temperatures (Table 2, Fig. 3d). These shorter hunting periods reflected earlier

348 start and stop times in the morning (Table S5) and later start times in the evening (Table S6).

349 In addition to being shorter, both morning and evening hunts entailed less intense activity on

350 hotter days (Table S5, Table S6). Evening hunts were less likely to occur at all on days with

351 higher ambient temperatures (Table S6), though there was no such effect on morning hunts

– 14 –

(Table S5). Rainfall may have mitigated the effects of high ambient temperatures, with rainfall:temperature interactions included in some of the top models for hunt duration (Table S5, Table S6). Packs were consistently more active during daytime when they were denning (Table S5, Table S6).

Similarly, and as predicted under the increased nocturnal prey selection hypothesis (Hypothesis 2), wild dogs were more likely to hunt at night following daytime periods with high ambient temperatures (Table 2). There was also some evidence that the duration and intensity of night-time hunts increased following hot days (Table 2). Nocturnal hunting activity was increased at higher levels of moonlight (Table 2, Table S6), with corresponding reductions in daytime activity on dates with high moonlight indices (Table 2, Table S5, Table S6).

Habitat selection

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

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

The three species also varied in their use of glades. Consistent with the nocturnal prey selection hypothesis (Hypothesis 2a), impala were significantly more likely to be located in

– 15 –

glades at night than in the day (Table 4, Fig. 3c), although there was no such pattern for

dikdiks (Table 4, Fig. 3c). In contrast with predictions under Hypothesis 2c, however, wild

dogs were significantly further from glades when hunting at night than when hunting in the

day (Table 4, Fig. 3b).

Prey selection

Among 795 wild dog scats, 71 (9%) contained impala remains and 609 (77%)

contained dikdik remains. As predicted under the restricted foraging time hypothesis

(Hypothesis 1) but not the other three hypotheses, wild dog scats were less likely to contain

impala remains when ambient temperatures had been higher in the previous seven days

(Table 5, Fig. 3e).

Discussion

Our analyses revealed clear associations between ambient temperature and the

behaviour of both predator and prey species, which appeared to influence trophic

interactions. Our findings were most consistent with the restricted foraging time hypothesis

(Hypothesis 1), under which we predicted that, on hot days, wild dogs would spend less of

the daylight period hunting, and therefore prefer abundant small prey over larger but less

abundant prey. Consistent with these predictions, we found that wild dogs spent less time

hunting during daytime hours (Fig. 3d, Table S5, Table S6). Previously we posited that, on

average, dikdik and impala would yield comparable returns, because the greater energy

intake achievable by hunting impala was offset by the shorter travel distances associated with

hunting dikdik (Woodroffe *et al.* 2007). However, optimal foraging theory predicts that a

predator with limited time should select more abundant but lower-value prey (such as

dikdiks) rather than waiting to locate rarer, higher value prey (such as impala, Lucas 1983).

402 High ambient temperatures would therefore be expected to favour wild dogs eating dikdiks

403 more than impala, and our observations were consistent with this prediction (Table 5).

404   Under the nocturnal prey selection hypothesis (Hypothesis 2), we predicted that, when

405 ambient temperatures were high, wild dogs would hunt at night, targeting impala which are

406 predictably located in glades. Although wild dogs hunted more often at night in hot weather

407 (Table 2), and impala were located in glades at night (Table 4, Fig. 3c), there was no

408 evidence that wild dogs targeted impala at night. Wild dogs were no closer to glades at night

409 than at other times of day, were no closer to glades on nights when ambient daytime

410 temperatures had been high (Table 4), and were less likely to consume impala in hot weather

411 (Table 5, Fig. 3e). Hence, patterns of predator behaviour and prey selection were not

412 consistent with Hypothesis 2.

413   Under the shade-seeking hypothesis (Hypothesis 3), we predicted that all three

414 species would increase their daytime use of woody cover at high ambient temperatures.

415 However, we found that only impala did so (Table 3). Of the three species, impala used the

416 most open habitat (Fig. 3a, b and c), which may have resulted in a greater need to seek shade

417 at high ambient temperatures. Physiological studies suggest that dikdiks are dependent upon

418 shade to thermoregulate (Kamau & Maloiy 1985) but, being small-bodied and less gregarious

419 than impala, they may be able to use small patches of shade without moving into denser

420 habitat. There was no evidence that wild dogs hunted in denser cover on hot days (Table 3),

421 perhaps because hunting periods occurred before and after the hottest times of day (Fig. 3a).

422 The tendency of impala to move into denser cover at high ambient temperatures would be

423 expected to increase their risk of being killed, since wild dogs typically occupied denser

424 cover (Fig. 3a), and impala are more likely to be killed in denser cover (Ford *et al.* 2014).

425 Nevertheless, we found that impala remains were less likely to be found in wild dog scats

426 following periods of high ambient temperature (Table 5). Hence, although impala behaviour

427 changed in line with the predictions of the shade-seeking hypothesis (Hypothesis 3), this

428 change did not generate the predicted impact on predation.

429   Under the prey overheating hypothesis (Hypothesis 4) we predicted that high ambient

430 temperatures would reduce chase distances for impala and increase them for dikdiks, as

431 larger-bodied animals would be slowed down by the heat to a greater extent than smaller-

432 bodied animals (Creel *et al.* 2016). We were not able to test this hypothesis directly because

433 our monitoring methods did not allow us to measure chase distance or speed. However, under

434 this scenario we also predicted that predation upon impala would increase, relative to

435 predation on dikdiks, when ambient temperatures were high. Our observations showed the

436 opposite pattern (Table 5, Fig. 3e); hence, a key prediction of the prey overheating hypothesis

437 was not upheld by our observations. Dikdiks make up a higher proportion of prey consumed

438 by wild dogs than at other sites and are not typically considered to be within the species'

439 range of preferred prey sizes (Clements et al. 2014). The prey overheating hypothesis may be

440 more relevant in areas that have greater fluctuations in temperature (e.g. as seen in other parts

441 of wild dogs species range) or where larger prey are more abundant (e.g., wildebeest).

442   Other evidence also favours the reduced foraging time hypothesis (Hypothesis 1) over

443 the other hypotheses. Under Hypothesis 1, we would expect energy intake by wild dogs to be

444 reduced at high ambient temperatures, due to constrained foraging time and a consequent

445 acceptance of lower-energy prey. This prediction is consistent with our observations that this

446 study population experiences higher mortality and lower reproductive success at high

447 ambient temperatures (Woodroffe, Groom & McNutt 2017; Rabaiotti *et al.* in review). In

448 contrast, under the other three scenarios, wild dogs' food intake (and thus potentially their

449 survival and reproductive success), would be expected to improve at high temperatures,

450 because impala (higher-value prey) would be more accessible due to being predictably

451 located (Hypothesis 2), in dense cover where they are vulnerable to predators (Hypothesis 3),

– 18 –

452 or more easily captured due to their tendency to overheat during high speed chases

453 (Hypothesis 4). Hence, while demographic patterns cannot confirm the reduced foraging time

454 hypothesis (Hypothesis 1) as the most likely mechanism whereby ambient temperature

455 influences predator-prey interactions in this system, they do contribute to refuting

456 Hypotheses 2-4.

457 Our findings suggest that climate change might have two wider impacts through its

458 effect on predation by wild dogs. First, we have shown previously that wild dogs suppressed

459 dikdik numbers, and dikdik browsing influenced tree abundance (Ford *et al.* 2015). Although

460 we found that wild dog predation on dikdiks did not trigger cascading effects on vegetation

461 (Ford *et al.* 2015), rising environmental temperatures would be expected to intensify wild dog

462 predation on dikdiks, which might generate wider impacts on community structure.

463 Second, our findings suggest that wild dog populations' resilience in the face of

464 climate change might be affected by the abundance of small, abundant prey. Our study site is

465 unusual both in the density of dikdiks it supports (Augustine 2010; Ford et al. 2015) and the

466 degree to which wild dogs rely on dikdiks as prey (Woodroffe *et al.* 2007). Across much of

467 the geographic range of wild dogs, dikdiks are altogether absent (Kingdon & Hoffman 2013),

468 and impala comprise the bulk of wild dog diets (Creel, Mills & McNutt 2004; Mbizah,

469 Marino & Groom 2012). Without abundant small prey to hunt on hot days, we would expect

470 wild dogs to more frequently make no kill at all, with potentially greater impacts on energy

471 intake than may occur at our study site. Low reproductive success and high mortality at high

472 ambient temperatures have been reported for wild dogs from two sites where impala are wild

473 dogs' principal prey (Woodroffe, Groom & McNutt 2017; Rabaiotti *et al.* In Review),

474 although site-specific conditions complicate any comparison of the magnitude of temperature

475 effects at the different sites.

476   Our results help to explain the negative impacts of high ambient temperatures on the

477   survival and reproductive success of the African wild dog, an endangered species (Woodroffe

478   & Sillero-Zubiri 2013). Our findings suggest that prey diversity may help to buffer wild dog

479   populations against the effects of climate change, because abundant prey are readily located

480   even when hunting time is constrained. Measures which maintain prey densities and diversity

481   (such as limiting offtake by people) may help to conserve wild dogs in a warming climate.

482   However, interventions which artificially raise prey densities (such as installation of

483   waterholes) may risk increasing the densities of wild dogs' predators (Creel & Creel 1996;

484   Mills & Gorman 1997), and might have harmful consequences for wild dog conservation.

485   More generally, we have shown that ambient temperature can influence patterns of

486   predation, even when both predator and prey are tropical endotherms. This finding contrasts

487   with the assumptions of several general ecosystem and community ecology models (e.g.,

488   Dell, Pawar & Savage 2014 , Harfoot et al 2014), and suggests that such models may not

489   accurately represent the responses of ecological communities in which endotherms play

490   important roles. However, our findings also highlight the difficulty of accurately predicting

491   exactly how environmental temperature would be expected to influence predation involving

492   endotherms: all four of the hypotheses that we investigated were plausible, but they generated

493   conflicting predictions about how predation on impala and dikdiks might vary in response to

494   weather conditions, and only empirical testing indicated the true direction of the impact.

495   Further investigations of how temperature-induced changes in the behaviour of predator and

496   prey species together influence trophic interactions would help to build a more general

497   picture of the relationship between ambient temperature and endotherm predation within

498   ecological communities.

499

500

508
509 *Author Contributions*

510   D. Rabaiotti, Rosie Woodroffe and Adam Ford, designed the research questions. D.

511 Rabaiotti organised the datasets, designed and carried out the final analyses and wrote the

512 paper. Rosie Woodroffe oversaw data collection on wild dogs and contributed to the writing

513 of the paper. Adam Ford and Jacob Goheen collected the dikdik and impala data and

514 contributed to the writing of the paper. Ben Chapple helped design and carry out the analyses

515 on the impala and dikdik data and African wild dog habitat use. Sophie Morrill assisted in

516 designing and carrying out the analyses on wild dog hunt times.

517

518 *Data Availability Statement*

519   Should the article be accepted, the data will be deposited on Dryad and the DOI included

520 at the end of the article

521

522   *References*

523

524   Agafonkin, V. & Thieurmel, B. (2017) *suncalc: compute sun position, sunlight phases, moon*

525   *position and lunar phase.* https://CRAN.R-project.org/package=suncalc.

526   Augustine, D.J. (2004) Influence of cattle management on habitat selection by impala on

527   central Kenyan rangeland. *Journal of Wildlife Management,* 68(4)**,** 916-923.

528   Augustine, D.J. and Mcnaughton, S.J., (2004). Regulation of shrub dynamics by native

529   browsing ungulates on East African rangeland. Journal of Applied Ecology, 41(1), pp.45-58.

530   Augustine, D.J., 2010. Response of native ungulates to drought in semi-arid Kenyan

531   rangeland. *African Journal of Ecology*, 48(4), pp.1009–1020. Available at:

532   http://doi.wiley.com/10.1111/j.1365-2028.2010.01207.x.

533   Austin, G.T. (1976) Behavioral adaptations of verdin to desert. *Auk,* 93(2)**,** 245-262.

534   Bartoń, K. (2017) *MuMIn: Multi-Model Inference*. https://CRAN.R-

535   project.org/package=MuMIn.

536   Burnham, K.P., Anderson, D.R. & Burnham, K.P., 2002. *Model selection and multimodel*

537   *inference : a practical information-theoretic approach*, Springer.

538   Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y.,

539   Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O. & Wiens, J.J. (2012) How does climate

540   change cause extinction? *Proceedings of the Royal Society B-Biological Sciences,* 280(1750),

541   20121890.

542   Caylor, K.K., Gitonga, J. & Martins, D.J. (2017) Mpala Research Centre Meteorological and

543   Hydrological Dataset Mpala Research Centre, Kenya.

544   Clements, H.S., Tambling, C.J., Hayward, M.W., Kerley, G.I.H., 2014. An objective approach

545   to determining the weight ranges of prey preferred by and accessible to the five large

546   African carnivores. *PLoS ONE* 9(7), e101054.

547   Cozzi, G., Broekhuis, F., McNutt, JW., Turnbull, L, MAcDonald, D and Stable, B., 2012. Fear

548 of the dark or dinner by moonlight ? Reduced temporal partitioning among Africa's large

549 carnivores *Ecology*, 93(12), pp.2590–2599.

550   Creel, S. & Creel, N.M. (1995) Communal hunting and pack size in African wild dogs,

551 *Lycaon pictus. Animal Behaviour,* 50(5)**,** 1325-1339.

552   Creel, S., Creel, N.M., Creel, A.M. & Creel, B.M. (2016) Hunting on a hot day: effects of

553 temperature on interactions between African wild dogs and their prey. *Ecology*. *97*(11),

554 2910-2916.

555   Creel, S., Mills, M.G.L. & McNutt, J.W. (2004) Demography and population dynamics of

556 African wild dogs in three critical populations. *The biology & conservation of wild canids* (eds

557 D.W. Macdonald & C. Sillero-Zubiri), pp. 337-350. Oxford University Press, Oxford.

558   Creel, S.R. & Creel, N.M. (1996) Limitation of African wild dogs by competition with

559 larger carnivores. *Conservation Biology,* **10(2),** 1-15.

560   Davies-Mostert, H.T., Mills, M.G., Kent, V. and Macdonald, D.W., 2010. Reducing potential

561 sources of sampling bias when quantifying the diet of the African wild dog through scat

562 analysis. *African Journal of Wildlife Research*, 40(2), pp.105-113.

563   Dell, A.I., Pawar, S. & Savage, V. (2014) Temperature dependence of trophic interactions

564 are driven by asymmetry of species responses and foraging strategy. *Journal of Animal*

565 *Ecology,* **83(1),** 70-84.

566   Doolan, S.P. & Macdonald, D.W. (1996) Diet and foraging behaviour of group-living

567 meerkats, Suricata suricatta, in the southern Kalahari. *Journal of Zoology,* **239(4),** 697-716.

568   Ford, A.T. & Goheen, J.R. (2015) An experimental study on risk effects in a dwarf

569 antelope, Madoqua guentheri. *Journal of Mammalogy,* **96(5),** 918-926.

570   Ford, A.T., Goheen, J.R., Augustine, D.J., Kinnaird, M.F., O'Brien, T.G., Palmer, T.M., Pringle,

571 R.M. & Woodroffe, R. (2015) Recovery of African wild dogs suppresses prey but does not

572 trigger a trophic cascade. *Ecology,* **96(10),** 2705-2714.

573   Ford, A.T., Goheen, J.R., Otieno, T.O., Bidner, L., Isbell, L.A., Palmer, T.M., Ward, D.,

574   Woodroffe, R. & Pringle, R.M. (2014) Large carnivores make savanna tree communities less

575   thorny. *Science,* **346(6207),** 346-349.

576   Frank, L.G., Woodroffe, R. & Ogada, M.O. (2005) People and predators in Laikipia District,

577   Kenya. *People and wildlife - Conflict or coexistence?* (eds R. Woodroffe, S. Thirgood & A.R.

578   Rabinowitz), pp. 286-304. Cambridge University Press, Cambridge.

579   Funston, P.J., Mills, M.G.L. & Biggs, H.C. (2001) Factors affecting the hunting success of

580   male and female lions in the Kruger National Park. *Journal of Zoology,* **253(4),** 419-431.

581   Garcia-Heras, M.S., Mougeot, F., Simmons, R.E. & Arroyo, B. (2017) Regional and temporal

582   variation in diet and provisioning rates suggest weather limits prey availability for an

583   endangered raptor. *Ibis,* **159(3),** 567-579.

584   Goheen, J.R., Palmer, T.M., Charles, G.K., Helgen, K.M., Kinyua, S.N., Maclean, J.E., Turner,

585   B.L., Young, H.S. and Pringle, R.M., 2013. Piecewise disassembly of a large-herbivore

586   community across a rainfall gradient: the UHURU experiment. *PloS one*, 8(2).

587   Harfoot, M.B.J., Newbold, T., Tittensor, D.P., Emmott, S., Hutton, J., Lyutsarev, V., Smith,

588   M.J., Scharlemann, J.P.W. & Purves, D.W. (2014) Emergent global patterns of ecosystem

589   structure and function from a mechanistic general ecosystem model. *PLOS Biology,* **12(4),**

590   24.

591   Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley,

592   S.E. and Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves.

593   Ecology, 86(8), pp.2135-2144.

594   Jackson, C.R., Power, R.J., Groom, R.J., Masenga, E.H., Mjingo, E.E., Fyumagwa, R.D.,

595   Røskaft, E. and Davies-Mostert, H., 2014. Heading for the hills: risk avoidance drives den site

596   selection in African wild dogs. *PLoS One*, 9(6).

597   Kamau, J.M.Z. & Maloiy, G.M.O. (1985) Thermoregulation and heat balance in the dikdik

598   antelope (*Rhynchotragus kirki*) - a field and laboratory study. *Comparative Biochemistry and*

599   *Physiology a-Physiology,* **81(2),** 335-340.

600   Kingdon, J. & Hoffman, M. (2013) *Mammals of Africa: Volume VI, Hippopotamuses, Pigs,*

601   *Deer, Giraffe and Bovids.* Bloomsbury, London.

602   Levy, O., Dayan, T., Porter, W.P. & Kronfeld-Schor, N. (2018) Time and ecological

603   resilience: can diurnal animals compensate for climate change by shifting to nocturnal

604   activity? *Ecological Monographs*, *89*(1), 01334, doi:10.1002/ecm.1334.

605   Lucas, J.R. (1983) The role of foraging time constraints and variable prey encounter in

606   optimal diet choice. *American Naturalist,* **122(2),** 191-209.

607   Mbizah, M.M., Marino, J. & Groom, R.J. (2012) Diet of four sympatric carnivores in Savé

608   Valley Conservancy, Zimbabwe: implications for conservation of the African wild dog

609   (*Lycaon pictus*). *South African Journal of Wildlife Research,* **42(2),** 94-103.

610   Mills, M.G.L. & Gorman, M.L. (1997) Factors affecting the density and distribution of wild

611   dogs in the Kruger National Park. *Conservation Biology,* **11(6),** 1397-1406.

612   Mole, M.A., Rodrigues DÁraujo, S., van Aarde, R.J., Mitchell, D. & Fuller, A. (2016) Coping

613   with heat: behavioural and physiological responses of savanna elephants in their natural

614   habitat. *Conservation Physiology,* **4(1),** cow044.

615   Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E.A., Amano, T., Bertram, E.,

616   Bradbury, R.B., Bradley, C., Butchart, S.H.M., Doswald, N., Foden, W., Gill, D.J.C., Green, R.E.,

617   Sutherland, W.J., Tanner, E.V.J. & Pearce-Higgins, J.W. (2014) Mechanisms underpinning

618   climatic impacts on natural populations: altered species interactions are more important

619   than direct effects. *Global Change Biology,* **20(7),** 2221-2229.

620   Otieno, T.O. et al., 2019. Human- and risk-mediated browsing pressure by sympatric

621   antelope in an African savanna. *Biological Conservation*, 232, pp.59–65. Available at:

622   https://www.sciencedirect.com/science/article/pii/S0006320718312771

623   Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts

624   across natural systems. *Nature,* **421(6918),** 37-42.

625   Peters, R.H., 1986. *The ecological implications of body size*, Cambridge University Press.

626   Pigeon, K.E., Cardinal, E., Stenhouse, G.B. & Cote, S.D. (2016) Staying cool in a changing

627   landscape: the influence of maximum daily ambient temperature on grizzly bear habitat

628   selection. *Oecologia,* **181(4),** 1101-1116.

629   Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2015) *nlme: Linear and*

630   *Nonlinear Mixed Effects Models. R package version 3.1-119*. http://CRAN.R-

631   project.org/package=nlme.

632   QGIS Development Team (2018) *QGIS Geographic Information System*. Open Source

633   Geospatial Foundation Project, http://qgis.osgeo.org.

634   Quaglietta, L., Mira, A. & Boitani, L. (2018) Extrinsic and intrinsic factors affecting the

635   daily rhythms of a semiaquatic carnivore in a mediterranean environment. *Hystrix-Italian*

636   *Journal of Mammalogy,* **29(4),** 128-136.

637   R Core Team (2015) *R: A language and environment for statistical computing.* R

638   Foundation for Statistical Computing http://www.R-project.org, Vienna, Austria.

639   Rabaiotti, D., Groom, R., McNutt, J.W., Watermeyer, J. & Woodroffe, R. (In Review) High

640   temperatures and human pressures interact to influence mortality in an African carnivore.

641   Rabaiotti, D. & Woodroffe, R. (2019) Coping with climate change: limited behavioural

642   responses to hot weather in a tropical carnivore. *Oecologia,* **189(3),** 587-599.

643   Ricklefs, R.E. & Hainsworth, F.R. (1968) Temperature dependent behavior of cactus

644   wren. *Ecology,* **49(2),** 227-233.

645   Shorrocks, B., Cristescu, B. and Magane, S., 2008. Estimating density of Kirk's dik-dik

646   (*Madoqua kirkii* Günther), impala (*Aepyceros melampus* Lichtenstein) and common zebra

647   (*Equus burchelli* Gray) at Mpala, Laikipia District, Kenya. *African Journal of Ecology*, 46(4),

648   pp.612-619.

649   Speakman, J.R. & Krol, E. (2010) Maximal heat dissipation capacity and hyperthermia

650   risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology,* **79(4),**

651   726-746.

652   Woodroffe, R. (2011a) Demography of a recovering African wild dog (*Lycaon pictus*)

653   population. *Journal of Mammalogy,* **92(2),** 305-315.

654   Woodroffe, R. (2011b) Ranging behaviour of African wild dog packs in a human-

655   dominated landscape. *Journal of Zoology,* **283(2),** 88-97.

656   Woodroffe, R., Groom, R. & McNutt, J.W. (2017) Hot dogs: high ambient temperatures

657   influence reproductive success in a tropical mammal. *Journal of Animal Ecology,* **86(,6)**

658   1329-1338.

659   Woodroffe, R., Lindsey, P.A., Romañach, S.S. & ole Ranah, S.M.K. (2007) African wild dogs

660   (*Lycaon pictus*) can subsist on small prey: implications for conservation. *Journal of*

661   *Mammalogy,* **88(1),** 181-193.

662   Woodroffe, R. & Sillero-Zubiri, C. (2013) *African wild dog Red List Assessment*. IUCN.

663

Table 1 Hypotheses describing how predator behaviour, prey behaviour, and predation risk might vary with ambient temperatures

Hypothesis	Species	Explanation	Implication for predator	Expected dietary change at high temperatures
Hypothesis 1: Restricted foraging time	Wild dogs	Wild dogs are expected to spend less time hunting in daytime when temperatures are high[1].	Predators with limited foraging time are predicted to select more abundant prey even if it contains less energy[2] (in this case dikdiks).	Increased ratio of dikdik to impala
Hypothesis 2: Nocturnal prey selection				
2a: Nocturnal prey concentration	Impala	Impala are predicted to gather in glades at night, as described prior to wild dog recolonisation[3].	Predators find impala more easily at night as they are predictably located in glades[3].	Decreased ratio of dikdik to impala
2b: Increased night time hunting	Wild dogs	Wild dogs are expected to spend more time hunting at night, because daytime foraging is constrained[1].	As a visual hunter active at night, wild dogs may rely on prey which are easily located.	
2c: Night-time habitat selection	Wild dogs	Wild dogs are predicted to hunt in or near glades at night, as impala are predictably located there.	Following hot days, wild dogs spend more time hunting at night, targeting glades where they can easily locate impala.	Decreased ratio of dikdik to impala
Hypothesis 3: Shade seeking	All species	Wild dogs, impala and dikdik are all predicted to move into denser vegetation at high ambient temperatures to avoid overheating.	Wild dogs are able to hunt impala more successfully, as impala are more vulnerable to predation in denser vegetation[4].	Decreased ratio of dikdik to impala
Hypothesis 4: Prey overheating	Impala	When running at high ambient temperatures, larger bodied animals overheat more quickly, and therefore impala slow down more than dikdiks.	Wild dogs are able to capture impala more easily because impala overheat more quickly when running than the smaller-bodied wild dogs[5].	Decreased ratio of dikdik to impala.

[1](Rabaiotti 2019), [4](Lucas 1983), [3](Augustine 2004); [3] (Ford *et al.* 2014); [4](Ford *et al.* 2014),[5](Creel *et al.* 2016).

Table 2 Variables associated with the **<u>duration of hunting periods</u>** of African wild dogs in the morning and evening, and the **<u>occurrence</u>** of night-time hunts. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc < 2) for the duration of hunting periods in the morning and evening (in minutes), 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).

Outcome variable	Explanatory variable	Estimate	Lower 95% CI	Upper 95% CI	Variable Importance (n)
Morning hunt duration (minutes)	Intercept	225.038	206.146	245.931	— (2)
	Denning (Yes)	-76.723	-154.789	1.343	1.00 (2)
	Temperature (°C)	-1.359	-2.035	-0.684	1.00 (2)
	Moonlight night before	0.058	-0.241	0.356	0.72 (1)
	Rainfall (mm)	-2.962	-6.296	0.372	0.72 (1)
	Rainfall:Temperature	0.128	0.004	0.252	0.72 (1)
	Denning:Temperature	5.014	2.834	7.195	0.72 (1)
Evening hunt duration (minutes)	Intercept	226.427	214.182	238.627	— (1)
	Temperature (°C)	-3.005	-3.438	-2.572	1.00 (1)
	Moonlight	-1.846	-2.065	-1.627	1.00 (1)
	Moonrise	-0.005	-0.120	0.110	1.00 (1)
	Denning (Yes)	15.823	13.113	18.534	1.00 (1)
Night-time hunt occurrence	Intercept	-0.414	-0.522	-0.305	— (2)
	Temperature	0.020	0.016	0.023	1.00 (2)
	Moonlight	0.031	0.029	0.033	1.00 (2)
	Denning	-0.069	-0.094	-0.044	0.52 (1)

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

Outcome variable	Explanatory variable	Estimate	Lower 95% CI	Upper 95% CI	Variable importance (n)
impala - morning	Intercept	0.0465	0.0352	0.0578	(1)
	Temperature	0.0019	0.0003	0.0022	1.00 (1)
impala - midday	Intercept	0.0762	0.0640	0.0884	(1)
	Temperature	0.0014	0.0011	0.0018	1.00 (1)
impala - evening	Intercept	0.0948	0.0878	0.1018	(1)
	Wet *vs* dry phase	-0.0021	-0.0035	-0.0006	1.00 (1)
impala - night	Intercept	0.0574	0.0531	0.0616	(1)
	Rainfall	0.0003	0.0002	0.0004	1.00 (1)
dikdik – morning and evening	Intercept	0.1211	0.1011	0.1412	(1)
	Wet *vs* dry phase	0.0055	-0.0003	0.0114	1.00 (1)
dikdik - midday	Intercept	0.1288	0.1102	0.1474	(1)
	Wet *vs* dry phase	-0.0002	-0.0063	0.0059	1.00 (1)
dikdik - night	Intercept	0.1313	0.1075	0.1551	(2)
	Moonlight	-0.0225	-0.0283	-0.0168	0.70 (1)
	Wet *vs* dry phase	0.0234	0.0170	0.0298	0.30 (1)
wild dog – morning and evening	Intercept	0.1666	0.1506	0.1827	- (1)
	Denning vs not	-0.0356	-0.0465	-0.0247	1.00 (1)
wild dog - night	Intercept	0.1480	0.1216	0.1745	- (1)
	Denning *vs* not	-0.1205	-0.1481	-0.0993	1.00 (1)

Table 4 Relationship between time of day (day or night) and **<u>use of glades</u>** by wild dogs, impala, and dikdiks.

Outcome variable		Estimate	Lower 95% CI	Upper 95% CI	p
impala – probability of being in a glade	Intercept	0.0586	0.0401	0.0772	
	Night *vs* day	0.1878	0.1832	0.1923	<0.0001
dikdik – probability of being in a glade	Intercept	0.0126	0.0016	0.0237	
	Night *vs* day	0.0219	0.0091	0.0349	0.09
wild dog - distance to glade	Intercept	0.0041	0.0037	0.0043	
	Night *vs* day	0.0002	0.0001	0.0003	0.001

			Lower 95% CI	Upper 95% CI	

Table 5 Variables associated with **<u>African wild dog consumption of impala</u>**. The table presents estimated effects of explanatory variables included in the top model sets (ΔAICc<2) for African wild dog consumption of impala. The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n).

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

Figure 1 Daily movement patterns of African wild dogs (A) activity measured by collar-mounted accelerometers fitted to 18 wild dogs; blue bands denote the start and stop times used to classify morning and evening hunts (B) Mean maximum temperature throughout the day at the study site
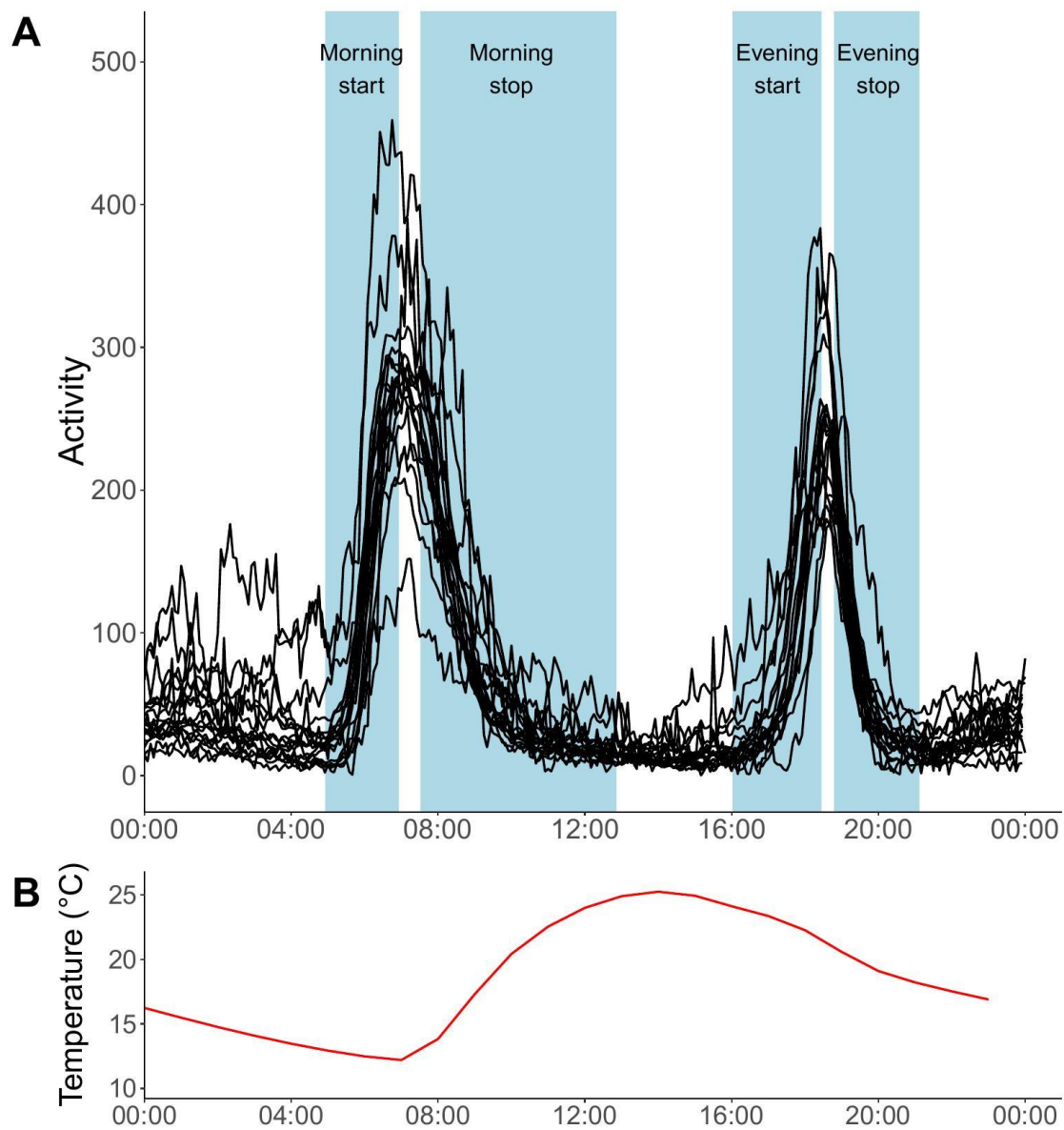
Figure 2 Percentage of hunts and total activity which fall in Morning, Midday, Evening and Night periods, and the percentage of bouts and total activity which spanned multiple time periods, and were therefore determined not to be hunts.
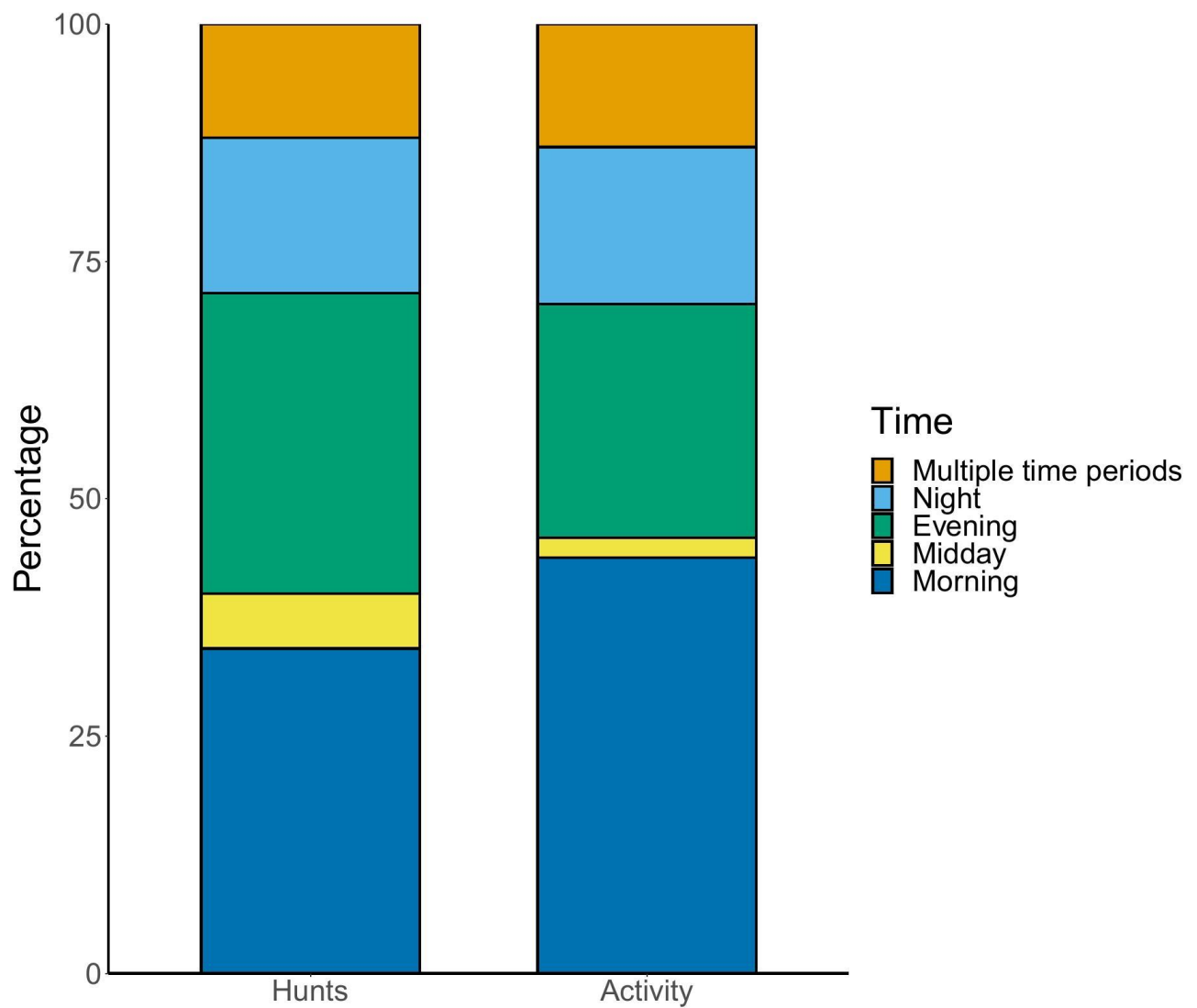
Figure 3 Diel variation in habitat selection by African wild dogs, dikdiks, and impala a) Mean woody cover use by impala, dikdiks and wild dogs across time periods. b) Mean wild dog distance to glades, in km, across time periods. c) Probability of glade use by impala and dikdiks across time periods. Bars represent standard error.
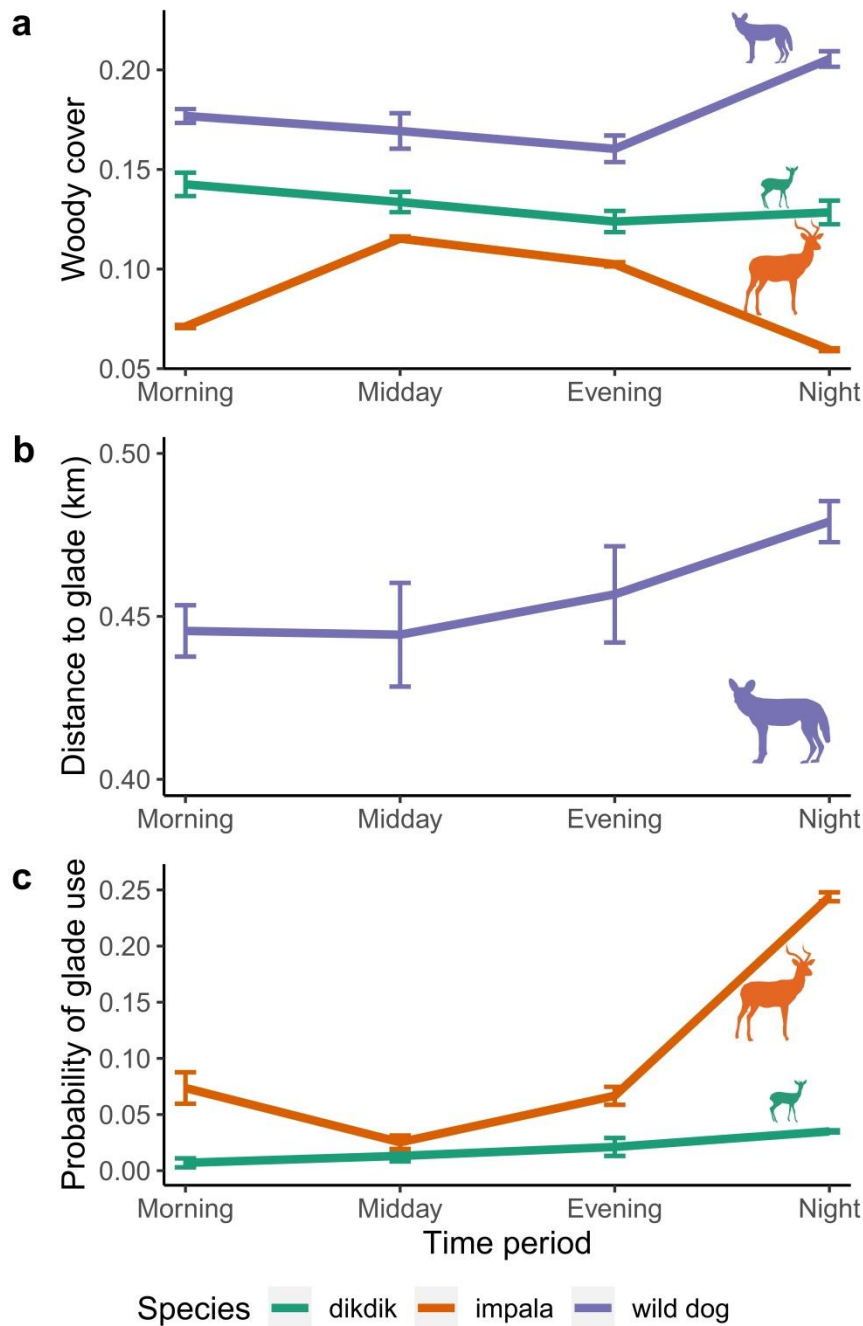
Figure 4 Associations between ambient temperature and African wild dog hunting behaviour a) Duration of African wild dog morning and evening hunts at different daily maximum temperatures (°C). Points represent the means for each 1°C interval, vertical bars indicate the standard error b) Probability of the presence of impala in wild dog scat at different daily maximum temperatures (°C). Lines represent conditional mean, and shaded areas represent the 95% confidence interval.
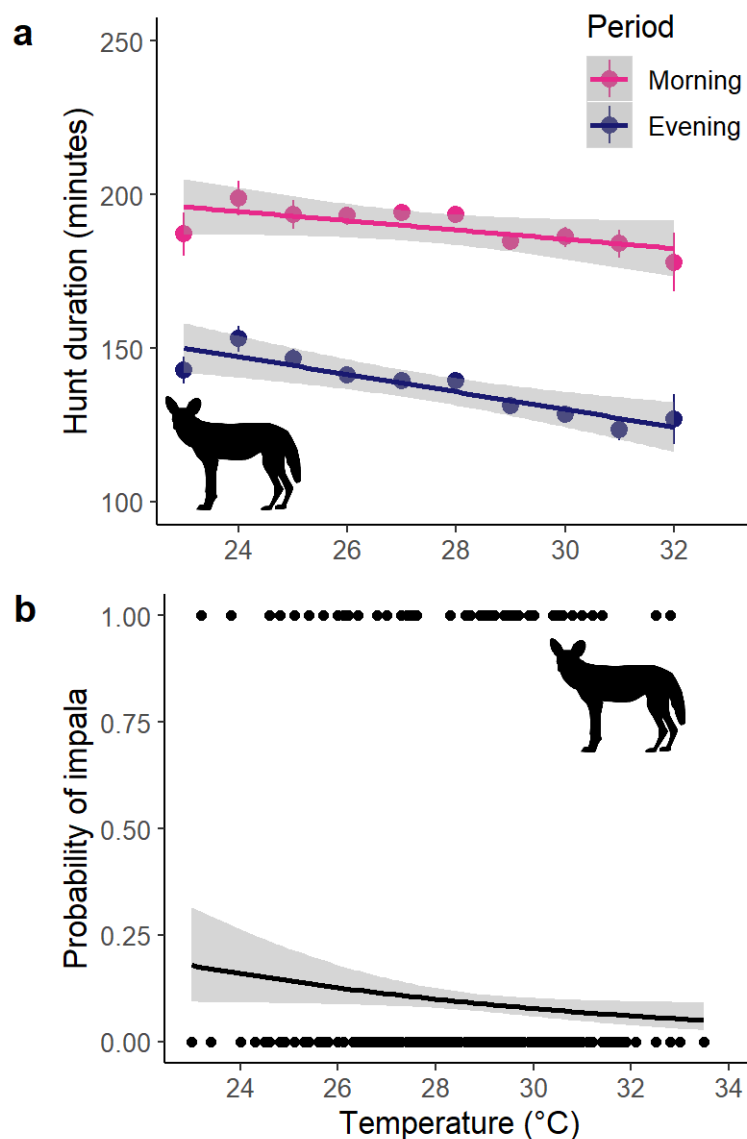
Temperature affects predator-prey interactions in an African savanna

D. Rabaiotti[1,2], Adam T. Ford[3], Ben Chapple[2], Sophie Morrill[2],

Jacob Goheen[4] and Rosie Woodroffe[1]

Supplementary Material

Figure S1 Frequency distribution of (A) start times and (B) stop times of African wild dog hunting periods, identified using collar-mounted accelerometers.
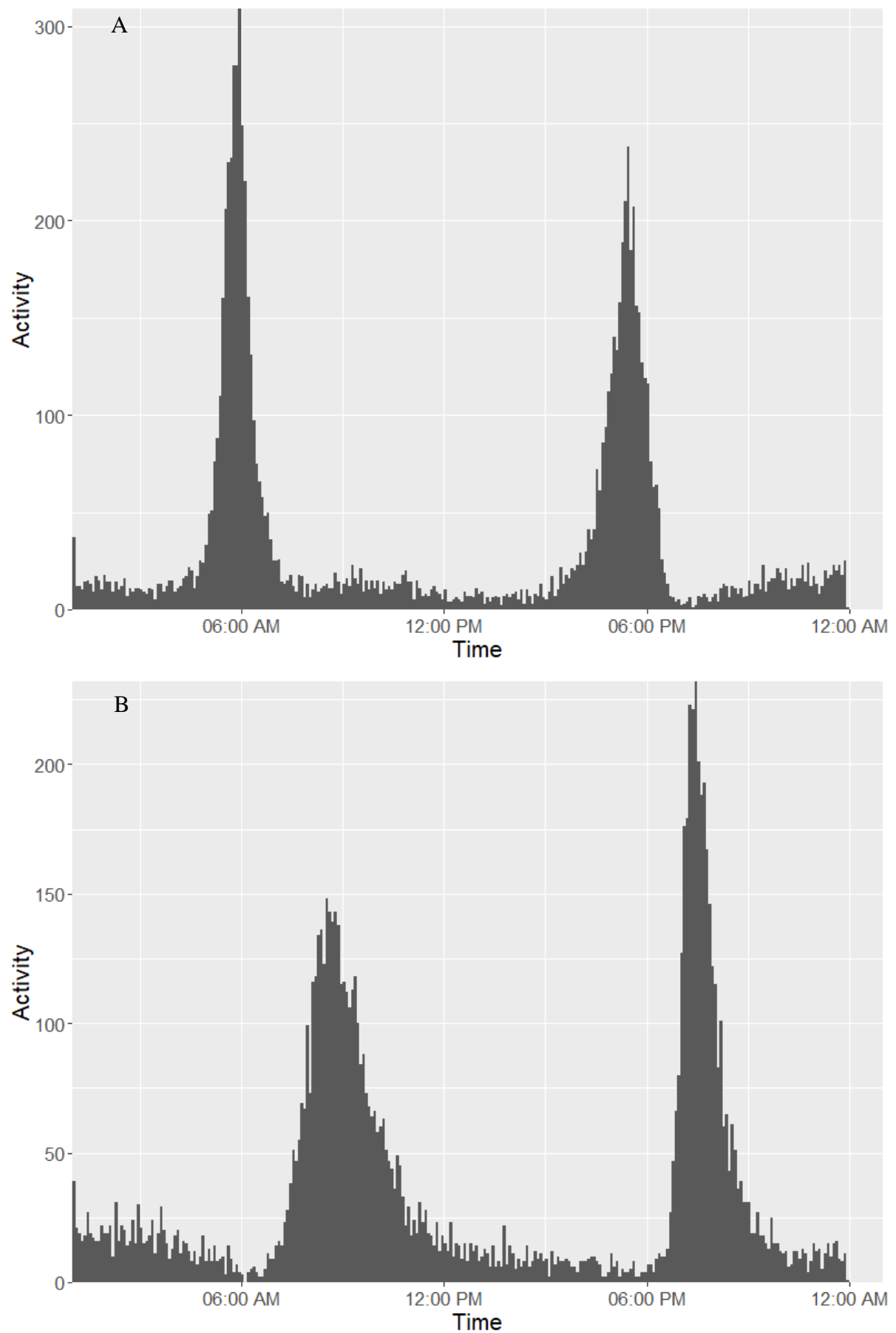
Figure S2 Distance to glades for wild dogs, impala and dikdiks during morning, day, evening and night time periods. Note that, as dikdik ranges are very small, their distance to glades will be influenced by the locations of home ranges where dikdiks were captured.
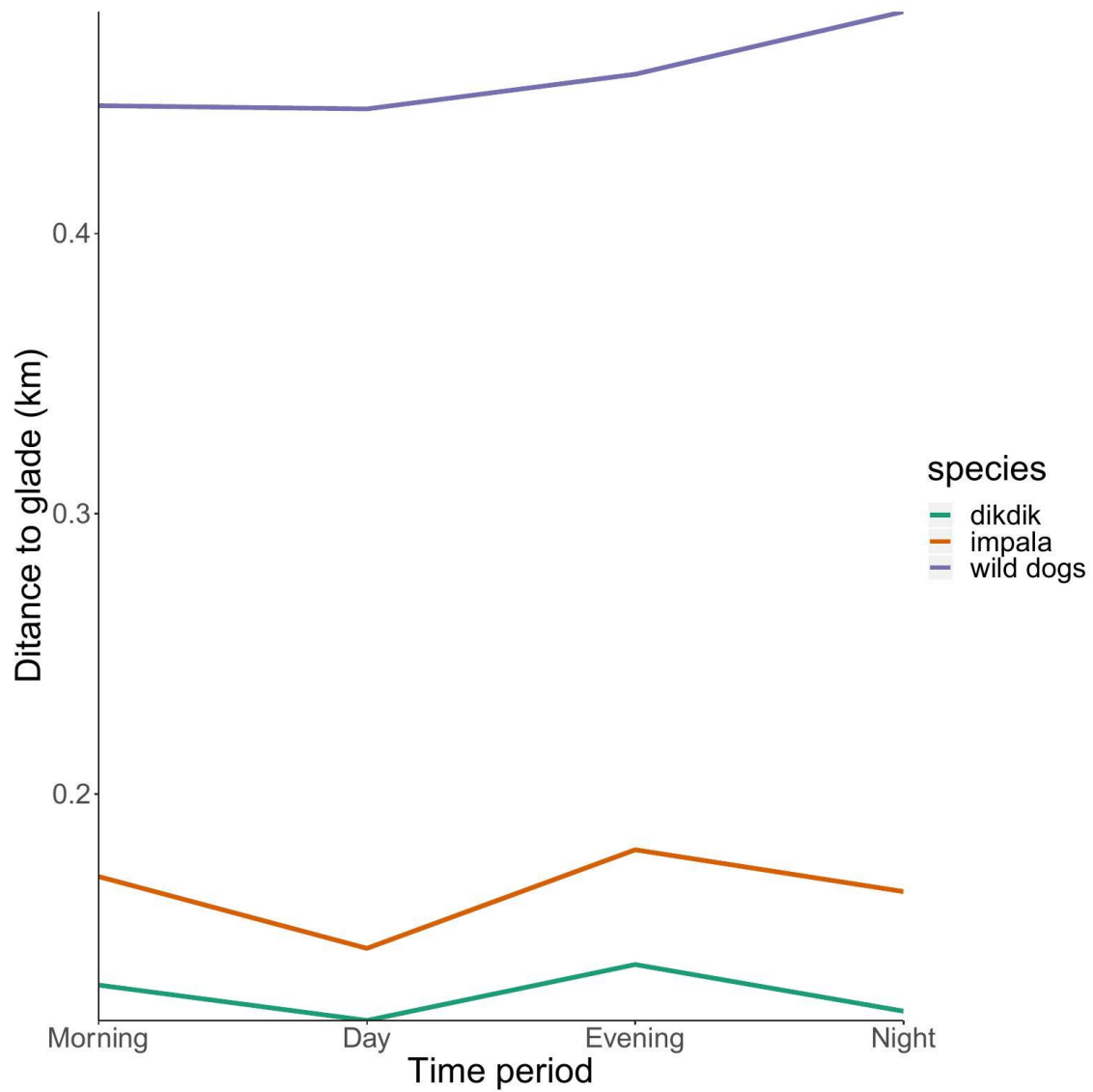
Table S1 Annual temperature and rainfall values at Mpala Research Centre throughout the period of the study.

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

Table S2 Start and stop times of hunting periods allocated to each time period within the analysis.

Type of Bout	Earliest start time	Latest start time	Earliest stop time	Latest stop time
Morning	04:55:39	06:56:04	07:30:41	12:51:33
Midday	06:56:05	16:01:54	12:51:34	18:47:02
Evening	16:01:55	18:26:52	18:47:03	21:06:56
Night	18:26:53	04:55:38	21:06:57	07:30:40

Table S3 Explanatory variables, other than temperature, included in models of wild dog hunts, and justification for their inclusion.

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

Table S4 Explanatory variables, other than temperature, included in models of wild dog, impala and dikdik woody cover use and justification for their inclusion.

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

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

Outcome variable	Explanatory variable	Estimate	Lower 95% CI	Upper 95% CI	Variable importance (n)
Occurrence	Intercept	0.8005	0.7698	0.8312	— (1)
	Moonlight before	-0.0097	-0.0115	-0.0079	1.00 (1)
Duration (minutes)	Intercept	225.038	206.146	245.931	— (2)
	Denning *vs* not	-76.723	-154.789	1.343	1.00 (2)
	Temperature (°C)	-1.359	-2.035	-0.684	1.00 (2)
	Moonlight before	0.058	-0.241	0.356	0.72 (1)
	Rainfall (mm)	-2.962	-6.296	0.372	0.72 (1)
	Rainfall:Temperature	0.128	0.004	0.252	0.72 (1)
	Denning:Temperature	5.014	2.834	7.195	0.72 (1)
Intensity	Intercept	50.9285	46.4112	55.4459	— (2)
	Denning *vs* not	1.5610	0.7941	2.3279	1.00 (1)
	Temperature (°C)	-0.2552	-0.3743	-0.1362	0.52 (2)
Start time	Intercept	06:31:41	06:24:07	06:39:14	(1)
	Denning *vs* not	-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 *vs* not	00:13:25	00:09:37	00:17:14	0.57(2)

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

Outcome variable	Explanatory variable	Estimate	Lower 95% CI	Upper 95% CI	Variable importance (n)
Occurrence	Intercept	1.2315	1.1211	1.3419	— (1)
	Moonlight	-0.0098	-0.0118	-0.0079	1.00 (1)
	Temperature (°C)	-0.0167	-0.0206	-0.0129	0.97 (1)
Duration (minutes)	Intercept	226.427	214.182	238.627	— (1)
	Temperature (°C)	-3.005	-3.438	-2.572	1.00 (1)
	Moonlight	-1.846	-2.065	-1.627	1.00 (1)
	Moonrise	-0.005	-0.120	0.110	1.00 (1)
	Denning *vs* not	15.823	13.113	18.534	1.00 (1)
Intensity	Intercept	62.7066	59.0173	66.3959	— (2)
	Temperature (°C)	-0.8203	-0.9451	-0.6954	1.00 (4)
	Denning *vs* not	6.4783	5.6993	7.2573	1.00 (2)
	Moonlight	-0.2122	-0.2744	-0.1499	0.36 (1)
	Moonrise	-0.0043	-0.0369	0.0283	0.36 (1)
Start time	Intercept	15:43:55	15:34:49	15:53:01	(1)
	Temperature (°C)	00:03:30	00:03:11	00:03:49	1.00 (1)
	Denning *vs* not	-00:10:49	-00:08:52	-00:09:18	1.00 (1)
	Moonlight	00:01:01	00:00:52	00:01:10	1.00 (1)
	Moonrise	-00:00:01	-00:00:05	00:00:05	1.00 (1)
Stop time	Intercept	19:42:14	19:38:50	19:45:39	(2)
	Denning *vs* not	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 S7 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 < 2) for each outcome variable. The relative importance of each variable is shown along with the number of models in the top model set in which it was included (n).

Outcome variable	Explanatory variable	Estimate	Lower 95% CI	Upper 95% CI	Variable importance (n)
Occurrence	Intercept	-0.414	-0.522	-0.305	— (2)
	Temperature	0.020	0.016	0.023	1.00 (2)
	Moonlight	0.031	0.029	0.033	1.00 (2)
	Denning	-0.069	-0.094	-0.044	0.52 (1)
Duration (minutes)	Intercept	80.2071	47.2221	113.1922	— (3)
	Moonlight	5.5885	4.9986	6.1783	1.00 (3)
	Moonrise	0.8356	0.4175	1.2537	1.00 (3)
	Denning *vs* not	106.6300	-50.2589	263.5188	1.00 (3)
	Temperature (°C)	0.7343	-0.5236	1.9921	0.79 (2)
	Rainfall (mm)	-0.5488	-7.7647	6.6672	0.52 (1)
	Rainfall:Temperature	0.0042	-0.2645	0.2729	0.52 (1)
	Denning:Temperature	-7.4281	-13.7490	-1.1071	0.52 (1)
Intensity	Intercept	28.2814	20.3200	36.2428	— (2)
	Moonlight	0.8649	0.7477	0.9822	1.00 (2)
	Moonrise	-0.0111	-0.0942	0.0720	1.00 (2)
	Denning *vs* not	2.1092	-0.0491	4.2676	1.00 (2)
	Temperature (°C)	0.4325	0.1926	0.6724	0.52 (1)
Start time	Intercept	15:52:55	09:34:32	22:11:08	(1)
	Moonrise	00:24:22	00:20:30	00:24:22	1.00 (1)
	Moonlight	-00:05:15	-00:10:38	00:00:08	1.00 (1)
Stop time	Intercept	09:14:33	06:28:31	12:00:35	(1)
	Moonlight	-00:24:17	-00:20:20	-00:28:14	1.00 (1)
	Moonrise	00:03:22	00:00:31	00:06:12	1.00 (1)