1 **Spatio-temporal factors impacting encounter occurrences between**

2 **leopards and other large African predators**

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Abstract

Encounters between individuals can have implications for a range of processes, including disease transmission, information transfer, and competition. For large carnivores, difficulties in directly observing individuals and historical hardware limitations of GPS collars mean that relatively little is known of the spatio-temporal factors contributing to encounters. The African large predator guild represents one of the few remaining functionally intact guilds of large carnivores on the globe and so represents a unique study system for understanding competitor interactions. We explored the drivers of male leopard (*Panthera pardus*) encounters with lions (*Panthera leo*), African wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) in the context of habitat characteristics and temporal activity overlaps. Using high resolution (five minute GPS fixes) data from 48 large African carnivores from 2012 to 2018, we quantified encounter occurrences between male leopards and other guild species and related these to habitat type (open vs closed), activity overlaps, and moonlight levels. Leopards met wild dogs 4.56 ± 1.15 (standard error), lions 3.11 ± 0.56, and cheetahs 2.27 ± 0.73 times per month. All species instigated encounters, but leopard instigated encounters with dominant competitors appeared to reflect imperfect information on risk, primarily occurring within habitats with limited visibility. Moreover, encounters peaked during periods of high temporal overlap, suggesting that, although previous research indicates temporal activity patterns may not be driven by predator avoidance, temporal overlap has implications for competitor dynamics. Our results show how habitat characteristics and niche overlaps contribute to encounters between competitors and provide an example of how niche shifts within competitor assemblages can impact competition between species.

Introduction

Encounters between individuals of free-ranging species can inform a range of ecological processes, including disease transmission (Craft *et al.*, 2011), information transfer (Berger, Swenson, & Persson, 2001), and competition (Jordan *et al*., 2017). Large carnivore species and the interactions between them can also help to regulate and structure ecosystems (Ripple *et al.*, 2014). Carnivore impacts are context dependent (e.g. depending upon co-occurrence with other carnivores) and exist within a network of interactions that together structure and regulate communities (see Haswell, Kusak & Hayward, 2017). Encounters amongst members of large carnivore assemblages can thus have cascading effects throughout lower trophic levels because encounters can impact species population dynamics, distributions, densities, and behaviours (e.g. Groom, Lannas, & Jackson, 2017). Yet, relatively little is known of direct encounters between species and of the impact that population-level niche partitioning may have on encounter rates and behaviours at a local scale. This is important to understand because species often show a degree of plasticity that allows them to shift their positions along niche-axes in response to changing environmental factors, such as climate, resource distribution, and human activity (Kitchen, Gese & Schauster, 2000; Gaynor *et al.*, 2018; Rabaiotti & Woodroffe, 2019). Such changes in activity, space-use and behaviour could conceivably impact encounter rates and competition dynamics.

Whilst previous studies have investigated spatio-temporal partitioning in the context of intraguild competition (e.g. Edwards, Gange & Wiesel, 2015; Rich *et al.*, 2017), few have quantified and explored the factors predisposing encounters. Encounters between large

70   carnivores have traditionally been difficult to study because these species typically occur

71   at low-densities, are wide-ranging, and move over landscapes that are logistically difficult

72   for researchers to navigate (Gittleman, 2001). To overcome these challenges, GPS collars

73   have historically been used to study large carnivore ecology (Wilmers *et al.*, 2015). These

74   too, however, have been ill-suited in their ability to quantify interactions because

75   hardware limitations, e.g. battery capacity and size, inhibited their ability to collect GPS

76   data at high logging rates, meaning that encounters could go undetected between data

77   points (Du Preez *et al.*, 2015). Thus, much of what we do know of direct large carnivore

78   interactions is typically based on opportunistic sightings from ground-vehicles (e.g. Bailey,

79   2005; Schaller, 1976) and from intensive-monitoring of select areas of interest, such as kill

80   sites, *via* camera traps (e.g. Selva, Jedrzejewska, Jedrzejewski, & Warak, 2003). Whilst

81   useful, such data are often qualitative, captured over short spatio-temporal scales, and

82   can be biased towards landscapes suited to opportunistic sightings, such as the short

83   grasslands of the Serengeti (Schaller, 1976). Recent advances in GPS collar operational

84   times and sampling rates (< five minute GPS fix intervals) offer an opportunity to address

85   these limitations and provide exhaustive GPS monitoring that captures interactions that

86   previously would have been missed (Jordan *et al.*, 2017). However, their application to

87   large carnivore interactions has thus far been limited (but see Broekhuis *et al*., 2019;

88   Elbroch & Quigley, 2017; Jordan *et al*., 2017).

89   In this study, we investigated intraguild encounters involving four members of Africa's

90   large predator guild: lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx*

91   *jubatus*), and African wild dog (*Lycaon pictus*), listed by descending individual body mass

92   (see Kingdon, 2013). These species are members of one of the last intact guilds of large

93   carnivores on the planet and, as such, represent a unique baseline study system to

94   investigate interspecific encounters within a functionally intact group (Dalerum *et al.*,

95   2009). Specifically, we used custom-developed GPS collars to investigate encounters

96   between male leopards and other large predator guild members within northern

97   Botswana. Leopards are a solitary large felid that coexist and compete across much of

98   their sub-Saharan range with other guild species (Jacobson *et al.*, 2016). Within some

99   areas, for example, interspecific competitors are one of the main causes of leopard cub

100 mortality (Balme *et al.*, 2013), and the loss of kills to spotted hyaenas can depress leopard

101 reproductive success (Balme *et al.*, 2017). The numerical advantage and cumulative mass

102 of wild dog packs also mean that wild dog encounters can present risks to leopards (Creel

103 & Creel, 2002). Yet leopards remain, arguably, one of the lesser studied guild species in

104 terms of direct encounters with other guild members. Further, although there is intense

105 interspecific competition within the guild and the population-level outcomes of

106 encounters have been well studied (e.g. Groom *et al.*, 2017; Miller, Pitman, Mann, Fuller,

107 & Balme, 2018), relatively little is known of the factors predisposing direct encounters.

108 We hypothesised that encounters between leopards and other guild members are the

109 result of incomplete information rather than an omniscient knowledge of competitor risk.

110 In particular, we investigated the role habitat structure may play in encounter occurrence

111 because although it can facilitate coexistence between competitors (Janssen *et al.*, 2007),

112 it can also impact the ability to acquire information on the location of other individuals

113 (Boncoraglio & Saino, 2007) and relatively little is known of its impact on decision making.

114 Under this imperfect information hypothesis, we predicted that encounters instigated by

115 the movements of smaller competitors, dependent on the species involved, would occur

116 primarily within closed than within open habitat types. This prediction was made

117 because visual information, the best indicator of an animal's exact location, on

118 competitors is likely to be harder to acquire within closed habitats and so the chances of

119 stumbling into competitors may be greater.

120   We then investigated the temporal circumstances under which encounters occurred. We

121   hypothesised that encounters across the diel cycle would occur most often during periods

122   of high activity overlap between pairs of competitors (hereafter referred to as dyads)

123   because guild members: (i) often compete for similar resources and thus are likely to be

124   attracted to similar areas during periods of movement (Caro & Stoner, 2003) and (ii) may

125   preferentially use the same landscape features (e.g. roads) as travel routes (Abrahms *et*

126   *al.*, 2016). We also predicted that leopard-wild dog and leopard-cheetah nocturnal

127   encounters would peak during periods of high illumination because wild dog and cheetah

128   nocturnal activity levels are positively associated with light availability (Cozzi *et al*., 2012).

129   We predicted that, conversely, leopard-lion encounters would not, since lion activity is

130   unaffected by nocturnal light levels (Cozzi *et al*., 2012).

131   **Methods**

132   Study area

133   This study took place in the Ngamiland region of northern Botswana and covered an area

134   of approximately 2,600 km^2, within which the main habitat types were woodlands

135   dominated by *Acacia* sp. and mopane (*Colophospermum mopane*) (Mendelsohn *et al.*,

136   2010; Cozzi *et al.*, 2013). The study area included community-operated wildlife

137   management areas that were primarily used for wildlife tourism throughout the study

138   period and areas of Moremi Game Reserve (Fig. 1).

139   GPS collars

140   From 2012-2018, we used GPS collars fitted with GPS-linked inertial measurement units

141   (GPS-IMU) that were developed by the Royal Veterinary College, University of London

142   (Wilson *et al*., 2013). To conserve battery life and maximise collar deployment, collars

143   switched between different sampling regimes based on GPS collar loaded configurations

144   and GPS-IMU activity-derived behaviour classifications (see Wilson *et al*., 2013). These

145   sampling regimes typically ranged from five minute GPS fixes during periods of

146   locomotion to hourly fixes during periods of inactivity. In addition, when high fix-rate

147   configurations were loaded onto collars, during periods of high acceleration, five fixes per

148   second were recorded (Wilson *et al*., 2013). When high fix-rate configurations were not

149   loaded onto collars, the five minute fix-rate was the highest resolution of data collected.

150   Data were stored on GPS collars and available to download *via* radio link to a hand held

151   base station. Further details on collar development and specifications can be found in the

152   supplementary material of Wilson *et al*., 2013.

153   To fit collars, immobilisations were carried out by a Botswana-registered veterinarian

154   after animals were located through spoor tracking, opportunistic sightings, and/or the use

155   of baited capture sites. Immobilisation cocktails were typically delivered *via* an air-

156   pressure powered dart gun (Telinject USA; Dan-Inject, USA; or Pneu-Dart, USA) with drug

157   combinations and quantities varying with species and individual mass and determined by

158   the veterinarian (see Hubel *et al*., 2016; Wilson *et al*., 2018, 2013). Collar weights for

159   lions (~970g), leopards (~550g), wild dogs, and cheetahs (~340g) represented < 2% of

160   estimated collared animal body masses. Collars were typically fitted with bio-degradable

161   or electronic (Sirtrack Ltd, New Zealand) drop-off units. Collars with no drop-off unit

162   were manually removed from animals following the completion of the study or upon

163   collar expiry. Carnivore vital signs were monitored throughout immobilisations, and we

164   prioritised collar attachment over body measurement and biological sample collection.

165   Most immobilisations were concluded within 60 minutes after darting and reversal drugs

166   were administered intramuscularly. Animals were then monitored from a ground-vehicle

167   until animal movements and coordination returned to pre-immobilisation levels, based

168   on researcher knowledge of the study species. In total, we immobilised and GPS collared

169   8 leopards, 14 lions (from 4 prides and 3 male coalitions), 21 African wild dogs (from 11

170   packs), and 5 cheetahs. For lions, wild dogs, and cheetahs, we GPS collared individuals of

171   both sexes, and for leopards, only males were collared to minimise the collar to animal

172   weight ratio. Mean collar deployments were 356.67 (± 277.80, standard deviation) days

173   for lions, 190.90 (± 51.70) days for leopards, 176.89 (± 131.47) days for wild dogs, and

174   200.44 (± 111.76) days for cheetahs. Further details on collar deployments, including

175   specific timings and durations, can be found in the supplemental material. Animals were

176   visited at least every two to three weeks to download GPS collar data and check welfare.

177   We noticed no ill-effects of GPS collar deployments.

178   All work was reviewed and approved by Liverpool John Moores University's ethical

179   committee (reference number: CM_KR/2016-7) and Botswana's Department of Wildlife

180   and National Parks (permit number: EWT 8 / 36 / 4 xxxv (31)).

181   <u>Encounter identification</u>

182   Raw datasets were resampled to create regular trajectories of fixes at one minute

183   intervals through a combination of linear interpolation and down sampling of high-

184   resolution GPS data. For example, this meant that during periods of low-acceleration

185   movement (e.g. walking), the known locations of individuals, occurring at five minute

186   intervals, were linearly interpolated with inferred locations, occurring at one minute

187   intervals. Interpolation was carried out within the R environment for statistical computing

188   (R Core Team, 2018). GPS collars were not programmed to record fixes at precise times,

189   and so interpolation compensated for differences in GPS timestamps. To filter erroneous

190   GPS locations from our dataset, prior to interpolation, we removed GPS fixes with > 10 m

191   horizontal accuracy and removed fixes that required individuals to have travelled at

192 speeds exceeding 15 m/s between locations > five minutes apart. Although large African

193 predators can reach maximum speeds that exceed these values, these speeds typically

194 occur over short distances and are unlikely to have been sustained over five minute step

195 lengths (Hubel, Golabek, Rafiq, McNutt, & Wilson, 2018; Wilson *et al*., 2013).

196 Leopard-competitor (i.e. lion, wild dog, or cheetah) dyads that showed temporal overlap

197 in collar deployments were then cross-referenced to find encounters using the R package

198 *wildlifeDI* (Long, 2014). Putative encounters were defined as occurring when

199 simultaneous fixes from dyad members were within 200 m of one another. The range at

200 which species may detect one another is likely dependent on a range of factors, including

201 habitat density, vigilance levels, and the species involved (e.g. Gorini *et al.*, 2012). We

202 chose the 200 m threshold distance to define encounters because a pilot study suggested

203 this as a conservative measure of the distance leopards may visually detect competitors

204 within woodland habitats (Rafiq, 2016) and the value followed previous guidelines for

205 defining interactions in solitary carnivores (Elbroch & Quigley, 2017). Further, for lion and

206 wild dog encounters, since collared individuals can travel in prides and packs and the

207 group's location was based on a single individual's location, it is possible that other

208 individuals within the group were closer to leopards than GPS data suggested. Following

209 Long (2014), the temporal threshold for defining fixes as simultaneous was set at ½ of the

210 iterated sampling intensity, i.e. fixes within 30 seconds of one another were defined as

211 simultaneous. The encounter location and encounter time were defined as the mid-point

212 between the encountering individuals' GPS locations, when species were at their closest,

213 and the time that this occurred. The encounter area was defined by a 100 m radius

214 around the encounter location. New encounters could not occur until dyad members had

215 vacated the encounter area and had been separated by > 200 m for at least 24 hours

216 since their last encounter (Elbroch & Quigley, 2017).

217 <u>Encounter rates</u>

218 We used a subset of our data, from 2012 to 2016, to calculate encounter rates because

219 this is when we had the most leopard-competitor GPS collars deployed at the same times

220 that overlapped spatially (Figure S1). We calculated an adjusted measure of encounter

221 rates for each leopard using the following equation:

222 $$ER_i = \frac{E}{T_C} \ \text{x} \ \frac{D_{HR} \ x \ T_C}{S_A}$$

223 Where ER_i is the encounter rate for leopard *i*; E is the total number of leopard-species

224 encounters; T_C is the number of months the leopard was GPS collared; D_{HR} is the

225 estimated number of individuals of the competitor species within the leopard's home

226 range, using density estimates for the study area from Rich *et al.*, (2019) for lion and wild

227 dog, and Broekhuis (2012) for cheetah; and S_A is the total number of months that leopard

228 *i* overlapped with GPS collared individuals of the species. For example, if leopard *i*

229 overlapped with two individuals of the species for three and five months each, the S_A was

230 eight. Leopard home ranges were defined as 95% utilisation distributions created using

231 Brownian Bridge Movement Models (Horne *et al.*, 2007), with the location error

232 parameter defined as 10 m, based on GPS error in Wilson *et al.,* (2013). By considering

233 competitor density, this equation provided an estimate of leopard-competitor encounters

234 that accounted for the fact that not all individuals of the competitor species were GPS

235 collared. Since wild dogs travel in packs (Creel & Creel, 2002), leopard-wild dog

236 encounter rates were calculated for packs.

237 <u>Classification of habitat types</u>

238 Encounters were manually classified into open and closed habitat types based on canopy

239 cover at each encounter location using Google satellite imagery from the OpenLayers

240   plugin (Kalberer & Walker, 2018) within QGIS (QGIS Development Team, 2018).

241   Specifically, a 100 metre circular buffer was applied to the encounter location and

242   encounters were classified into open habitats, with little to no canopy cover, and closed

243   habitats, with at least 50 % of the area covered by canopies separated by less than 5 m.

244   <u>Encounter occurrences</u>

245   To investigate encounter occurrences, we used our full 2012 to 2018 data set. For each

246   encounter, we recorded the timings that dyad members arrived into the encounter area.

247   If members arrived within 30 seconds of one another, they were assumed to have arrived

248   simultaneously. Otherwise, we assumed that the second species arriving into the

249   encounter area instigated the encounter, i.e. their movement was responsible for setting

250   the encounter into motion, irrespective of whether encounters were intended. We then

251   used a series of Fisher's exact tests to investigate counts of leopard and competitor

252   instigated encounters across competitor species and habitat types. We used the R

253   package *suncalc* (Agafonkin & Thieurmel, 2018) to derive moonlight illumination levels

254   and lunar phases for the day of each encounter, and we used a series of Kuiper's one

255   sample tests for uniformity of circular data (Jammalamadaka & Sengupta, 2011) to assess

256   whether leopard and competitor instigated encounters were equally distributed across

257   diel and lunar cycles. We also used graphical displays to make descriptive inferences of

258   the impact of moonlight illumination on encounter onsets. When considering

259   distributions of encounters across lunar cycles and moonlight illumination levels, we used

260   a subset of our data that contained only encounters occurring during the night, which we

261   defined as the period after the day's end of evening civil twilight and before the start of

262   the following day's morning nautical twilight.

263

Results

Overview and encounter rates

In total, we recorded 115 leopard-competitor encounters. Specifically, male leopards encountered GPS collared lions 64 times, wild dogs 43 times and cheetahs 8 times (Fig. 1). For each competitor species, after adjusting for only a portion of their populations being GPS collared, this translated to 4.56 ± 1.15 leopard-wild dog pack, 3.11 ± 0.56 leopard-lion, and 2.27 ± 0.73 leopard-cheetah encounters per leopard per month (mean $\pm$ standard error).

Encounter occurrences

There were only two instances where species arrived into encounter areas at the same time, which may represent random encounters when dyad members were both moving. Overall, all species were as likely to instigate encounters by approaching leopards first, with or without intent, as leopards were to instigate encounters with them (Fisher's-exact test, $p = 0.555$) (Table 1).

Leopards were less likely to instigate lion encounters within open habitats than within closed habitats (Fisher's exact test, $p = 0.037$). In contrast, leopard-wild dog (Fisher's exact test, $p = 0.060$) and leopard-cheetah (Fisher's exact test, $p = 1.00$) encounters were instigated equally by both dyad member species within both habitat types. All five leopard-wild dog encounters within open habitats were, however, instigated by wild dogs, suggesting that rejection of the alternate hypothesis may be due to low samples sizes rather than lack of an effect (Table 1).

Table 1: Summary of leopard and competitor instigated encounters across open and closed habitats

Dyad	Open habitat		Closed habitat		Total
	Leopard instigated	Competitor instigated	Leopard instigated	Competitor instigated	
Leopard-lion	1	9	25	28	63
Leopard- wild dog	0	5	18	19	42
Leopard-cheetah	1	1	4	2	8
Total	2	15	47	49	113

287

288 Overall, leopard-lion encounters were non-uniformly distributed across the diel cycle,

289 with encounters typically occurring during the night (68% of encounters; n = 63, Kuiper

290 test statistic (k) = 3.056, p < 0.01). This was also the case when considering lion (70% of

291 encounters; n = 37, k = 2.385, p < 0.01) and leopard (65% of encounters; n = 26, k = 2.321,

292 p < 0.01) instigated encounters separately (Fig. 2). Across the lunar cycle, overall,

293 leopard-lion encounters were uniformly distributed (n = 43, k = 0.864, p > 0.15), as were

294 those encounters specifically instigated by lions (n = 26, k = 0.707, p > 0.15) and those

295 instigated by leopards (n = 17, k = 1.306, p > 0.15). Encounters did, however, appear non-

296 random in respect to nocturnal light levels and, independent of the instigating species,

297 peaked during periods of high moonlight. Interestingly, lion instigated encounters also

298 showed an additional peak during periods of low moonlight (Fig. 2).

299 Leopard-wild dog encounters, overall, peaked during early evening and morning hours

300 (65% of encounters; n = 42, k = 2.124, p < 0.01) (Fig. 2). For leopard instigated wild dog

301 encounters, there was no significant difference in the distribution of encounters across

302 the diel cycle (n = 18, k = 1.586, p > 0.10); in contrast, wild dog instigated encounters

303 peaked in the morning hours (63% of encounters; n = 24, k = 2.722, p < 0.01) (Fig. 2).

304 Overall, leopard-wild dog encounters were uniformly distributed across lunar phases (n =

305 13, k = 1.222, p > 0.15) and so were those encounters specifically instigated by leopards (n

306 = 7, k = 0.959, p > 0.15). Wild dog instigated encounters were non-uniformly distributed

307   across lunar phase (n = 5; k = 1.904, p < 0.025), with four out of five encounters occurring

308   between moon phases of 0.48 and 0.61, i.e. encompassing the waxing and waning

309   periods closest to the full moon. In respect to nocturnal light levels, leopard-wild dog

310   encounters peaked during periods of high moonlight, regardless of which species

311   instigated the encounter. There was also a second smaller peak in encounters during

312   periods of low moonlight when considering leopard and wild dog instigated encounters

313   together (Fig. 2).

314   Leopard-cheetah encounters occurred most frequently at night (75% of encounters; n = 8,

315   k = 1.973 p < 0.025). Encounters were uniformly distributed across lunar phases (n = 6, k

316   = 1.243 p > 0.15), but did appear to peak during periods of intermediate nocturnal light

317   availability (Fig. 2). Due to a limited leopard-cheetah night encounters sample size (n = 6),

318   we did not investigate leopard and cheetah instigated encounters separately.

319   **Discussion**

320   Our study showed that overlap of activity patterns (see Rafiq, 2019) contributes to

321   increased contacts between African predators. Across the diel cycle, encounters with

322   guild members peaked during periods of shared temporal activity (Cozzi *et al*., 2012),

323   suggesting that activity overlaps increase competitor contact rates and that the costs of

324   these overlaps are not fully offset by partitioning along other niche axes. Animal activity

325   patterns often show behavioural plasticity to changing environments (e.g. Frey *et al.*,

326   2017; Gaynor *et al.*, 2018; Rabaiotti & Woodroffe, 2019), and our results suggest that

327   within competitor assemblages, changes to species activity patterns that increase activity

328   overlap could increase the strength of interference competition. For example, activity

329   patterns are commonly thought to be driven by bottom-up forces (Kronfeld-Schor &

330   Dayan, 2003), and so simplification of prey resources (Creel *et al.,* 2018) could

331 conceivably lead to increased niche overlap across multiple axes (e.g. dietary, spatial, and

332 temporal) within assemblages. Such shifts could lead to greater levels of top-down

333 suppression of subordinate competitors, potentially inhibiting population growth and

334 increasing a population's susceptibility to localised extinctions through stochastic events

335 (Carbone, Toit, & Gordon, 1997).

336 Our results also suggest that encounters between African large predator guild members

337 reflect imperfect information within heterogeneous environments, and to our knowledge

338 our study is the first to look at encounters between large carnivores within this context.

339 Male leopards within our study area instigated encounters with lions within closed

340 habitats as often as lions did, but they rarely instigated encounters within open habitats.

341 This suggests that: (i) habitats with reduced visibility limit the leopard's ability to

342 accurately assess immediate competitor risk; and (ii) habitat structure plays a role in

343 mediating encounter occurrences between competitors (Janssen *et al.*, 2007). It is

344 possible that some encounters within our distance threshold were 'near-misses', where

345 individuals remained unaware of one another's presence. However, by definition, and

346 given that few leopard instigated encounters occurred within open habitats, this is most

347 likely to have occurred within closed habitats and thus also supports the role of habitat

348 structure in mediating encounters (Janssen *et al*., 2007). These findings align with

349 previous work in which leopard avoidance behaviours to lions were greatest within open

350 than within closed areas (e.g. Du Preez *et al.*, 2015), suggesting that the costs and

351 benefits of encounters, and likely detectability, vary across habitats.

352 In open habitats, long-range detection of competitors may have allowed leopards to

353 adapt movement directions to maintain spatial distances over the encounter threshold,

354 whereas in closed habitats, detection may have been limited to short-distances.

355   Interestingly, Vanak *et al.*, (2013) found that leopards avoided areas recently occupied by

356   lions during the dry season but not during the wet season. This may reflect the difficulties

357   in assessing competitor risk during seasons with increased vegetation cover, e.g. when

358   increased rainfall during wet seasons results in increased vegetation densities. Our

359   leopard instigated lion encounters may thus have been a consequence of leopards

360   approaching areas of interest (e.g. potential carcasses) without being aware of

361   competitor presence or of opportunistic encounters arising from inadvertently occupying

362   the same areas in close proximity to competitors. Our results suggest that, similar to prey

363   detection, visual cues appear to be the primary sensory mechanism used in immediate

364   risk assessment, whilst olfactory and auditory information appears to play a limited role,

365   perhaps because such signals are not always available (Sunquist & Sunquist, 2002).

366   Olfactory cues, for example, require suitable environmental conditions (e.g. wind

367   direction) for detection, and the information they provide can depend on a range of

368   factors, including olfactory signal location and time since deposition (Parsons *et al.*, 2018).

369   Leopard instigated encounters within closed habitats could also have occurred if leopards

370   were aware of lion presence but still chose to approach. Such instances could have

371   occurred because of the potential to acquire resources (e.g. prey), curiosity, or the

372   ability to move quickly to a safe tree if attacked (Bailey, 2005). Whilst closed habitats can

373   allow leopards to take refuge in trees, considering the increased ambush risks associated

374   with these areas and mortality risks associated with encountering lions (Bailey, 2005;

375   Hopcraft, Sinclair & Packer, 2005), we find the chance that they approach with intent

376   unlikely. Instead, we suggest that such encounters within closed habitats likely reflect (i)

377   the shared occupancy of these areas, perhaps occurring as a result of similar resource

378   acquisition strategies (Balme *et al.*, 2017b), and (ii) the difficulties of detecting

379   competitors within these areas.

380   Excluding cheetah encounters, for which we had a limited sample size to discuss

381   inferences, encounters peaked for all dyads during periods of high moonlight illumination.

382   Given that not all guild species' activity levels are influenced by moonlight availability

383   (Cozzi *et al.*, 2012), this may reflect the lower risks associated with approaching

384   potentially contested resources during periods of high illumination, e.g. reduced lion

385   ambush risks because of greater visibility (Funston, Mills & Biggs, 2001). Alternatively,

386   encounter peaks across moonlight levels may have been driven by periodicity in the use

387   of shared areas of home ranges, which in turn, may have been driven by periodicity in

388   resource distributions (Riotte-Lambert, Benhamou & Chamaillé-Jammes, 2013). For

389   example, impala (*Aepyceros melampus*), a favoured prey species of leopards (Hayward *et*

390   *al.*, 2006), can show periodicity in the use of some open habitats within their home range,

391   with use declining during full moon periods (Riotte-Lambert *et al.*, 2013). If similar

392   patterns of periodicity drive the space use of other prey species and/or cause prey to

393   congregate into similar habitat patches, e.g. to reduce predation risk through mixed herd

394   benefits (Schmitt, Stears & Shrader, 2016), then increased encounters during high

395   moonlight illumination may reflect the attraction of competitors to habitat patches with

396   high periodic resource availability.

397   Interestingly, leopard-lion and leopard-wild dog encounters also showed secondary peaks

398   during periods of low light availability. This may simply reflect the impacts of low light

399   levels on species detectability (Funston *et al.*, 2001). In other words, encounters may

400   have increased during these periods because species were able to travel closer to other

401   guild members, with or without intent, without being detected and species remained

402   unaware of one another's presence. However, since leopard instigated lion encounters

403   did not also show a peak during low moonlight periods, we speculate that leopards were

404   still able to detect and avoid instigating lion encounters and that the other species'

405   encounter peaks may have thus been species approaching guild members with purpose.

406   The scale of interspecific competition can vary across landscapes (Ripple *et al.*, 2014), and

407   we provide leopard-competitor encounter frequencies as a measure of the potential for

408   interference competition. However, some caveats apply. Cheetah densities used to

409   estimate encounter rates were based on whole counts from Broekhuis (2012), which may

410   be unreliable since they do not account for detection probability (Hayward & Marlow,

411   2014). Yet they are the best measure of cheetah density within our study area, and so

412   our cheetah encounter frequencies are presented tentatively. Further, within our study

413   area, species densities vary across habitat types (Rich *et al.*, 2019). As a result, it is likely

414   that encounter rates also vary with habitat. Habitat-specific encounter rates were,

415   however, not calculated because of the unavailability of accurate vegetation maps for our

416   study area at the time of the study. The creation of high-resolution vegetation maps is

417   ongoing, but non trivial (see Oeser *et al.*, 2019). Paired with recent advances in analysing

418   animal movement on continuous scales (Wang *et al.*, 2019), we anticipate such maps will

419   provide greater insights into the processes mediating encounters.

420   This was one of the few studies to directly investigate the drivers of direct encounters

421   between large carnivores. Yet much remains to be done, and below we identify

422   limitations to our approach and areas warranting further enquiry. Specifically, the

423   complexity of our study system combined with the limited number of detected

424   encounters prevented the inclusion of all potential factors impacting meeting

425   occurrences. Resource distribution, for example, may also be a potential driver of

426   encounters (e.g. Parsons *et al.*, 2019), yet subsampling of encounters by additional factors

427   would have reduced effective sample sizes to unworkable levels. Unfortunately, due to

428   the logistical challenges of working within such systems (Gittleman, 2001), with current

429   technologies, these outcomes are near inevitable. Further, our analyses were restricted

430   to data collected exclusively from male leopards. Female leopards were ~50% lighter

431   than males in our study area (unpublished data), and the decision to collar only male

432   leopards was made to minimise the ratio between the leopard collar weight and the

433   weight of the animal. It is possible, however, that responses to competitors differ

434   between the sexes, particularly during life-history phases when the reproductive costs of

435   encounters are greater for females, e.g. during cub rearing (Balme *et al.*, 2013). As such,

436   further work on the responses of females is warranted. Spotted hyaenas were also

437   absent from our study, due to no individuals being GPS collared over the study period.

438   However, spotted hyaenas can have significant impacts on leopard fitness through

439   kleptoparasitism (Balme *et al.*, 2017a) and spatial capture-recapture studies suggest

440   hyaenas actively track leopards (Balme *et al.*, 2019). Further work on the factors

441   predisposing leopard-hyaena encounters is thus warranted. Finally, we were unable to

442   validate the presence of prey carcasses at encounter locations due to logistical challenges

443   in visiting encounter sites to identify kills. However, work is underway to remotely

444   identify carcasses by using behavioural classifications from GPS collar accelerometer data.

445   In summary, we have shown that habitat characteristics and temporal overlap in activity

446   patterns impact encounter occurrences between members of the African large predator

447   guild. Our results suggest that encounters between competitors are influenced by factors

448   which increase the difficulty in acquiring information on competitor risk and/or which

449   increase niche axes overlaps. For example, changes in species' activity patterns that

450   increase the level of temporal overlap between competitors may also increase encounter

451   frequencies between them. This is particularly relevant given that we live in an era of

452   rapid anthropogenic landscape modification, where human activities can alter the

behaviour and ecology of species (Wilmers *et al.*, 2013; Dirzo *et al.*, 2014). Understanding

the factors driving encounters can help predict the consequences of shifting niches and

habitats for wildlife and can, ultimately, facilitate the planning of suitable landscapes for

the coexistence of diverse competitor assemblages.

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Author contributions

KR, NJ, and KG conceived the study; KR collected the majority of the leopard data (with

other data provided by the BPCT), carried out the analyses, and wrote the manuscript; all

authors contributed critically to the drafts and gave final approval for publication.

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629

630   **Fig. 1: Map of the core study area showing its location within Botswana and Africa and showing locations**

631   **of leopard encounters with lions (triangle), wild dogs (pentagon), and cheetah (circle). Black lines on the**

632   **satellite map represent roads. Community-owned wildlife management areas are grouped and shown as**

633   **the dark shaded contiguous area covering most of the map. Moremi Game Reserve is shown as the light**

634   **shaded area. The core study area map was created using Google satellite imagery obtained within the**

635   **QGIS OpenLayers Plugin (Kalberer and Walker 2018).**

636

637   **Fig. 2: Leopard-competitor encounter peaks across diel cycles and moon illumination levels.**

638