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1 **Spatio-temporal factors impacting encounter occurrences between**
2 **leopards and other large African predators**

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17 Running title: Encounters between large African predators

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23 **Abstract**

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

46 **Keywords:** African carnivores, coexistence, competition, interaction dynamics, intraguild
47 encounters, *Panthera pardus*, temporal overlap

48 **Introduction**

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

67 Whilst previous studies have investigated spatio-temporal partitioning in the context of
68 intraguild competition (e.g. Edwards, Gange & Wiesel, 2015; Rich *et al.*, 2017), few have
69 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 km², 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 (\pm 277.80, standard deviation) days
173 for lions, 190.90 (\pm 51.70) days for leopards, 176.89 (\pm 131.47) days for wild dogs, and
174 200.44 (\pm 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 Encounter identification

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 $\frac{1}{2}$ 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 Encounter rates

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
$$ER_i = \frac{E}{T_C} \times \frac{D_{HR} \times T_C}{S_A}$$

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 Classification of habitat types

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 Encounter occurrences

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

264 **Results**

265 Overview and encounter rates

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

272 Encounter occurrences

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

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

285

286 **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

453 behaviour and ecology of species (Wilmers *et al.*, 2013; Dirzo *et al.*, 2014). Understanding
454 the factors driving encounters can help predict the consequences of shifting niches and
455 habitats for wildlife and can, ultimately, facilitate the planning of suitable landscapes for
456 the coexistence of diverse competitor assemblages.

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467 **Author contributions**

468 KR, NJ, and KG conceived the study; KR collected the majority of the leopard data (with
469 other data provided by the BPCT), carried out the analyses, and wrote the manuscript; all
470 authors contributed critically to the drafts and gave final approval for publication.

471

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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