



**HAL**  
open science

## Dynamic interactions between apex predators reveal contrasting seasonal attraction patterns

S. Périquet, H. Fritz, E. Revilla, D. Macdonald, A. Loveridge, G. Mtare,  
Marion Valeix

► **To cite this version:**

S. Périquet, H. Fritz, E. Revilla, D. Macdonald, A. Loveridge, et al.. Dynamic interactions between apex predators reveal contrasting seasonal attraction patterns. *Oecologia*, 2021, 195 (1), pp.51-63. 10.1007/s00442-020-04802-w . hal-03425858

**HAL Id: hal-03425858**

**<https://hal.science/hal-03425858>**

Submitted on 11 Nov 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Dynamic interactions between apex predators reveal contrasting seasonal attraction patterns

2

3 Périquet, S<sup>1,2,3\*</sup>, Fritz, H<sup>1,2,4</sup>, Revilla, E<sup>5</sup>, Macdonald, DW<sup>6</sup>, Loveridge, AJ<sup>6</sup>, Mtare, G<sup>7,8</sup> &

4 Valeix, M<sup>1,2,6</sup>

5

6 <sup>1</sup> Laboratoire de Biométrie et Biologie Evolutive, CNRS UMR 5558, Université Claude Bernard Lyon

7 1, Bât Gregor Mendel, 43 Bd du 11 Novembre 1918, 69622 Villeurbanne cedex, France

8 <sup>2</sup> LTSER France, Zone Atelier “Hwange”, Hwange National Park, Bag 62, Dete, Zimbabwe - CNRS

9 HERD (Hwange Environmental Research Development) program

10 <sup>3</sup> Ongava Research Centre, Private Bag 12041, Suite No. 10, Ausspannplatz, 9000 Windhoek,

11 Namibia

12 <sup>4</sup> REHABS, CNRS - Université Lyon 1 - Nelson Mandela University, International Research

13 Laboratory, George Campus, Madiba Drive, George, South Africa

14 <sup>5</sup> Departamento Biología de la Conservación, Estación Biológica de Doñana (CSIC), Calle Américo

15 Vespucio 26, 41092 Sevilla, Spain

16 <sup>6</sup> Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Reanati-

17 Kaplan Centre, Tubney House, Abingdon Road, Oxfordshire OX13 5QL, United Kingdom

18 <sup>7</sup> Zimbabwe Parks and Wildlife Management Authority, PO Box CY140, Causeway, Harare,

19 Zimbabwe

20 <sup>8</sup> Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA)

21

22 \* Corresponding author: [stephanie.periquet@gmail.com](mailto:stephanie.periquet@gmail.com)

#### **AUTHORS' CONTRIBUTIONS**

SP and MV conceived and designed the study; SP collected the hyeana data and AJL and DWM provided the lion data; SP analysed the data; SP and MV drafted the manuscript. All authors critically contributed to revised versions of the manuscript and gave final approval for publication. The authors declare that they have no conflict of interest.

23 **ABSTRACT**

24 Apex predators play important roles in ecosystem functioning and, where they coexist,  
25 intraguild interactions can have profound effects on trophic relationships. Interactions between  
26 predators range from intraguild predation and competition to facilitation through scavenging  
27 opportunities. Despite the increased availability of fine-scale GPS data, the determinants and  
28 outcomes of encounters between apex predators remain understudied. We used simultaneous  
29 GPS data from collared spotted hyaenas (*Crocuta crocuta*) and African lions (*Panthera leo*) in  
30 Hwange National Park, Zimbabwe, to determine the environmental conditions of the  
31 encounters between the two species, which species provoked the encounter, and which species  
32 dominated the encounter.

33 Our results show that encounters between hyaenas and lions are mostly resource related (over a  
34 carcass or around waterholes). In the wet season, encounters mainly occur at a carcass, with  
35 lions being dominant over its access. In the dry season, encounters mainly occur in the absence  
36 of a carcass and near waterholes. Movements of hyaenas and lions before, during and after  
37 these dry-season encounters suggests two interference scenarios: a passive interference  
38 scenario whereby both predators attracted to waterholes but lions leave a waterhole used by  
39 hyaenas because of prey disturbance, and an active interference scenario whereby hyaenas  
40 would actively chase lions from waterhole areas, which are prime hunting grounds. This study  
41 highlights the seasonal dynamics of predator interactions and illustrates how the relative  
42 importance of negative interactions (interference competition during the dry season) and  
43 positive interactions (scavenging opportunities during the wet season) shifts over the course of  
44 the year.

45

46 **Keywords:** African lion, carnivore intraguild interactions, *Crocuta crocuta*, *Panthera leo*,  
47 spotted hyaena

48

**50 INTRODUCTION**

51 Apex predators, through their effects on the abundance, distribution and behaviour of their prey  
52 and mesopredators, have a profound influence on the functioning of communities and  
53 ecosystems (Ritchie and Johnson 2009; Ripple et al. 2014). In most ecosystems, several  
54 species of apex predators coexist. Understanding the functioning of their guild is key if we  
55 want to grasp the full impact of the changes in the abundance and distribution of apex predator  
56 populations that occur worldwide (Ripple et al. 2014; Chapron et al. 2014). Intraguild  
57 interactions amongst predators are diverse. Negative interactions have been the most studied,  
58 with predators not only competing through depletion of common prey but also posing threats to  
59 each other through kleptoparasitism (Höner et al. 2002; Trinkel and Kastberger 2005) and  
60 direct interference during aggressive interactions with risk of injury (Linnell and Strand 2000)  
61 and intraguild predation (Palomares and Caro 1999). These negative interactions can cause  
62 subordinate species to spatially and/or temporally avoid dominant ones (Durant 2000; Vanak et  
63 al. 2013), similarly to the ecology of fear in predator-prey interactions (Courbin et al. 2013;  
64 Palmer et al. 2017; Kohl et al. 2019). However, this is not always the case, and evidence has  
65 accumulated on the absence of spatial and temporal avoidance between sympatric apex  
66 predators (Cozzi et al. 2012; Miller et al. 2018). This absence of spatio-temporal avoidance  
67 may be due to the fact that (i) avoidance mechanisms occur at very fine spatio-temporal scales  
68 (Broekhuis et al. 2013; du Preez et al. 2015; Swanson et al. 2016) and often go undetected, (ii)  
69 dominance is dynamic with the outcome of an interaction depending on the relative group size  
70 of each of the competing species (Cooper 1991), and (iii) coexisting apex predators also benefit  
71 from positive interactions between them. Positive effects of interactions have been less studied  
72 and underestimated in community ecology (Bruno et al. 2003). They range from scavenging  
73 opportunities (feeding from a carcass, Wilson and Wolkovich 2011) and kleptoparasitism  
74 opportunities (displacing a competitor from its kill, Krofel et al. 2012) to indirect facilitation

75 whereby prey, through anti-predator behavioural adjustments to minimize the risk of predation  
76 by one predator species, become more vulnerable to another predator species. For example, elk  
77 (*Cervus elpahus*) shift to habitats that have a more complex structure to reduce predation risk  
78 from wolves (*Canis lupus*), which significantly increases predation risk from pumas (*Puma*  
79 *concolor*, Atwood et al. 2009).

80 A pair of sympatric apex predators is not characterized by one type of interaction only, and  
81 different, sometimes contrasting, interactions may occur. First, different interactions may  
82 operate at different scales. Sivy et al. (2017) revealed negative responses of several carnivore  
83 species to wolf abundance at the landscape scale (overall lower occupancy probability in  
84 presence of wolves), but positive responses of the same species to localized wolf activity  
85 (increased detection probability of coyote, *Canis latrans*, closer to wolf GPS clusters). Second,  
86 the environmental conditions and the life history traits of the species may also determine the  
87 relative costs and benefits of engaging in one type of interaction, which is illustrated by the  
88 seasonal dynamics of some foraging tactics, such as scavenging (Pereira et al. 2014). Many  
89 studies inferring negative or positive interactions between sympatric apex predators have been  
90 conducted at the large scales of static interactions, focusing on the relative local abundance and  
91 temporal niche of the predators (e.g. Schuette et al. 2013; Swanson et al. 2014; Sivy et al.  
92 2017; Miller et al. 2018; Rasphone et al. 2020). These large-scale studies can only focus on  
93 predictive responses to potential interactions, while fine-scale studies are necessary to  
94 understand the reactive responses to actual encounters between apex predators. Little is known  
95 on the fine-scale dynamics of inter-specific interactions due to the challenges of  
96 simultaneously monitoring large carnivores, but some pioneering research has started (for  
97 prey-predator relationships see Courbin et al. 2016; for apex predators intra-specific  
98 interactions see Jordan et al. 2017; or Broekhuis et al. 2019; for apex predator interspecific  
99 interactions see du Preez et al. 2015). The simultaneous GPS-collaring of sympatric apex  
100 predators can provide information on the direction and speed of a carnivore's movement with

101 respect to the other carnivore involved in the interaction. GPS-tracking has therefore the  
102 potential to reveal which species is attracted to or avoid one another, and under which  
103 circumstances.

104 In African savannas, African lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) are  
105 the two most common large predators and evidence has accumulated on the richness of their  
106 interactions. These were reviewed by Périquet et al. (2015a) and it was shown that the  
107 coexistence of spotted hyaenas (hyaenas hereafter) and lions is a complex balance between  
108 negative (exploitative competition for prey, kleptoparasitism, aggressive interactions and direct  
109 killing) and positive interactions (scavenging opportunities). Périquet et al. (2015a) highlighted  
110 the need for the study of the spatio-temporal dynamics of these interactions. Here, we used data  
111 from GPS-collars deployed simultaneously on lions and hyaenas to (i) identify the encounters  
112 between the two species based on the proximity of simultaneous GPS locations, (ii) assess  
113 which species provoked the encounter by approaching the other one, (iii) determine which  
114 species was dominant during the encounter and triggered the displacement of the other species,  
115 and (iv) identify when one species attempted to avoid the encounter by moving away from the  
116 other one. We further evaluated the environmental conditions in which encounters occurred.  
117 First, waterholes act as prey hotspots in arid and semi-arid savannas (Valeix et al. 2009; Valeix  
118 2011), so we expected encounters to occur mainly close to waterholes. Second, African arid  
119 and semi-arid savannas are characterized by contrasting (wet and dry) seasons. Large herbivore  
120 body condition is highest in the wet season, when plant productivity peaks, and decreases as  
121 the dry season progresses (Owen-Smith 2002). Hyaenas are cursorial hunters, i.e. chase down  
122 their prey over long distance (Kruuk 1972; Mills 1990), and are therefore more likely to kill  
123 weak individual prey. Their hunting success is thus likely to be lower in the wet season when  
124 prey body condition is high. These seasonal variations in prey vulnerability to predation  
125 provided us with a good opportunity to assess the temporal dynamics of hyaena-lion  
126 interactions.

127 Lions are the main cause of mortality for adult hyaenas and are expected to be dominant at  
128 most encounters, especially when an adult male is present (reviewed in Périquet et al. 2015a).  
129 Hence, we expected hyaenas to generally avoid encounters with lions and flee from an  
130 encounter when it occurs, except in the wet season when prey are scattered through the  
131 landscape and in good condition and therefore more difficult to kill and when hyaenas should  
132 actively search for kleptoparasitism/scavenging opportunities from lion kills.

133

## 134 **MATERIAL AND METHODS**

### 135 *Study area*

136 Hwange National Park (HNP) is located in north-western Zimbabwe (19°00'S, 26°30'E) and  
137 covers an area of approximately 14,600 km<sup>2</sup>. The study area ( $\approx$  1,500 km<sup>2</sup>) is located in the  
138 northern part of HNP, in the Main Camp area (Appendix S1: Fig. S1), and is characterized by  
139 Kalahari sandy soils. The vegetation is primarily bushed woodland and bushland savanna,  
140 interspersed with small patches of grassland (Arraut et al. 2018). HNP is semi-arid (mean  
141 annual rainfall=600 mm, coefficient of variation=25%) with a wet season from November to  
142 April and a dry season from May to October (Chamaillé-Jammes et al. 2006). Availability of  
143 surface water is primarily from rainwater collected in natural depressions. However, most of  
144 these natural depressions do not hold water during the dry season, when water is artificially  
145 pumped in about 50 waterholes spread throughout HNP (Appendix S1: Fig. S1). Hyaena  
146 density in the study area is 11.0 hyaenas/100 km<sup>2</sup> (Unpubl. data) and lion density is 4.3  
147 lions/100 km<sup>2</sup> (Loveridge et al. 2016). Wild dogs (*Lycaon pictus*), cheetahs (*Acinonyx jubatus*)  
148 and leopards (*P. pardus*) are also present in the study area but less abundant.

149

### 150 *Predator GPS data*

151 From July 2009 to October 2013, nine adult hyaenas (eight females and one male) belonging to  
152 four different clans were equipped with GPS collars (see Périquet 2014 for details). Hyaenas

153 spent most of their time foraging alone (Périquet et al. 2015b) and their fission-fusion  
154 dynamics precluded from assessing group sizes during interactions. During the same period, 27  
155 adult lions (20 males and 7 females) were also equipped with GPS collars (see Benhamou et al.  
156 2014 for details). At least one male lion per coalition and one female lion per pride were  
157 collared. As lionesses from the same pride and males from the same coalition spend most of  
158 their time together in the study area (Valeix et al. 2009), we assumed that individual locations  
159 generally represent those of their pride and coalition. Relevant animal care protocols were  
160 followed during capture and collaring of carnivores (Wildlife Drugs Sub-committee of the  
161 Drugs Control Council of Zimbabwe and Zimbabwe Veterinary Association, Wildlife Group,  
162 and licenses to acquire, possess and administer game capture drugs/dangerous drugs), and  
163 permissions were provided by the appropriate agencies (Research Council of Zimbabwe,  
164 Zimbabwe Parks and Wildlife Management Authority). All applicable institutional and/or  
165 national guidelines for the care and use of animals were followed. Collars were programmed to  
166 take hourly fixes during the night (between 6 pm and 6 am). Lion collars were not set up to  
167 record GPS locations at the same time as hyaena collars and the frequency of locations varied  
168 from one location every hour to one location every 2h at night (12 individuals with a collar set  
169 up to record a GPS location every 2h).

170 A prerequisite for two animals to encounter each other is that their space use overlaps. We  
171 preliminarily quantified the static interactions between hyaenas and lions using home range  
172 overlap metrics. Using a 2D measure of home range overlap, we found that on average  $97.9 \pm$   
173  $0.5$  % (range = 85.4-100%) of a given hyaena home range was overlapping with at least one  
174 lion home range (see Appendix S2 for details).

175

### 176 ***Proximity index and encounter definition***

177 Proximal fixes were used to identify and define the encounters between hyaenas and lions. We  
178 defined proximal fixes as simultaneous hyaena and lion GPS locations within 200m of each

179 other. This threshold is conservative compared to other studies (500m in Broekhuis et al. 2019  
180 or Courbin et al. 2016; 800m in Jordan et al. 2017) as we wanted to be sure that both species  
181 were aware of each other's presence. For each hyaena-lion pair with overlapping home ranges,  
182 we computed the proximity index as the proportion of the number of proximal fixes over the  
183 total number of simultaneous fixes for the pair (Long et al. 2014). This proximity index is a  
184 measure of how often hyaenas encounter lions in the landscape. In order to quantify if hyaena  
185 and lions encountered each other more often than expected by chance, we generated proximity  
186 indices by randomly creating new GPS locations for hyaenas but keeping the lion locations  
187 unchanged. These random locations were generated in a similar way as in a Step Selection  
188 Function framework (Fortin et al. 2005). Each hyaena used location was set as the starting  
189 point from which we created 100 steps (a step is the straight line movement between two  
190 successive GPS locations) by randomly drawing step length and turning angle from their  
191 respective empirical distributions obtained by pooling step data from all other hyaenas, as  
192 recommended by Fortin *et al.* (2005). In case of a hyaena GPS location falling within 200 m of  
193 several lion GPS locations, we used the distance to the closest lion location.

194 Movement of the given hyaena-lion pair during each night containing at least one pair of  
195 proximal fixes was plotted and visually examined. We categorized whether an encounter  
196 occurred at a large prey carcass (> 120 kg) that could provide scavenging opportunities. We  
197 thus defined encounters occurring in the presence of a carcass when proximal fixes were  
198 located near a known carcass (found in the field during systematic hyaena GPS cluster searches  
199 or opportunistically) or near a large and clearly defined lion cluster (>5h within a 200 m  
200 radius). Previous work using GPS clusters to investigate potential lion kill sites used cluster of  
201  $\geq 2$  GPS locations within 100m of each other (e.g. Tambling and Belton 2009; Tambling et al.  
202 2012; Davidson et al. 2013), but since we did not investigate these clusters in the field and  
203 lions hardly ever rest for more than 5h in the same location at night (Schaller 1972) we feel  
204 confident that clusters identified using our definition represent carcasses. When there was no

205 clear GPS cluster near the proximal fixes, we assumed that the encounter occurred in the  
206 absence of a carcass. While we acknowledge that with this classification, small carcasses  
207 would be missed, these are unlikely to provide scavenging opportunities. In the presence of  
208 small and loose clusters (multiple GPS locations not tightly grouped together and scattered  
209 within a radius of ~100 m), we classified the encounter as undefined in terms of carcass  
210 presence. Depending on the situation, multiple pairs of proximal fixes could be assigned to the  
211 same encounter (for instance, proximal fixes occurring in the vicinity of a given carcass).

212

### 213 *Encounter characteristics*

214 *Seasonality* – Each encounter was attributed to the wet or dry season based on the date when it  
215 occurred. We used a Chi<sup>2</sup> test to test for the effects of the presence of a carcass on the  
216 seasonality of encounters.

217 *Distance to water* - Because waterholes play an important role in the spatial ecology of both  
218 lions (Valeix et al. 2010) and hyaenas (Périquet 2014) in HNP, we computed the distance  
219 between the first proximal fixes and the nearest pumped waterhole (distance to water hereafter)  
220 for each encounter. We tested the effect of distance to water on the probability of encounter  
221 using Generalized Linear Models (GLMs) with a binomial error structure with encounter  
222 (coded 0/1) as the dependent variable and distance to water as an explanatory variable. We  
223 used separated models for encounter in the presence and absence of a carcass, irrespective of  
224 the season. For each model, 500 locations with no encounter were drawn randomly from the  
225 hyaena GPS dataset only including nights during which no encounter between hyaenas and  
226 lions was identified.

227 *Duration* - The duration of an encounter in the presence of a carcass was defined as the time  
228 elapsed between the first and the last proximal fixes still associated with the given carcass  
229 ( $\leq 200\text{m}$ ), even if they were separated by several hours and interspersed with some non-  
230 proximal fixes (it is indeed common for carnivores to visit a carcass over several consecutive

231 days, Cozzi et al. 2015). We extracted the GPS data of the two species from the night of the  
232 first proximal fixes to the night of the last proximal fixes for subsequent analyses. The duration  
233 of an encounter in the absence of a carcass was calculated from the first to the last pair of  
234 consecutive proximal fixes. Since all encounters away from carcasses were restricted to one  
235 night, we extracted the GPS data of the two species for the night when the encounter occurred  
236 for subsequent analyses. Because of high heterogeneity in the duration between encounter in  
237 the presence and absence of a carcass, we used a Wilcoxon rank sum test to determine the  
238 effect of carcass presence on encounter duration.

239

#### 240 ***Which species provoked the encounter?***

241 For all encounters (presence and absence of a carcass), we computed the speed (in m/h) of  
242 movement during the hour preceding the start of the encounter for both species. Speed was  
243 only computed if the last GPS location was taken a maximum of 2 h before the start of the  
244 encounter.

245 For encounters in the presence of a carcass, we further performed a visual examination of the  
246 movement of the two species before the start of the encounter (GPS locations preceding the  
247 first pair of proximal fixes but belonging to the same night) to identify which species was the  
248 first at the carcass ( $\leq 200$  m). It is noteworthy that the species arriving first at a carcass did not  
249 necessarily kill the prey. For encounters in the absence of a carcass, we also visually examined  
250 the movement of each species before the encounter and defined two situations: (1) one species  
251 was in the vicinity ( $\leq 200$  m) of the encounter location while the other one moved towards the  
252 encounter location, in which case the species moving towards the encounter location was  
253 considered as attracted to the location of the other species, or (2) both species showed clear  
254 movement before the encounter. In this case, we calculated, for each species, an attraction  
255 score for each step of the 4 hours preceding the encounter.

256 The attraction score was based on the direction of the step compared to the simultaneous step  
257 made by the other species (see Fig. 1a for details). The attraction score for a step could take 5  
258 values: +1 if the step of species A was directed toward the step of species B  $\pm 10^\circ$  (case of  
259 “strong attraction”); +0.5 if the step of species A was directed toward the step of species  
260 B  $\pm 30^\circ$  - but excluding cases of strong attraction - (case of “mild attraction”); -1 when the step  
261 of species A was directed opposite the step of species B ( $\pm 10^\circ$ ) (case of “strong avoidance”); -  
262 0.5 when the step of species A was directed opposite the step of species B  $\pm 30^\circ$  - but  
263 excluding cases of strong avoidance – (case of “mild avoidance”); and 0 in any other case  
264 (“independent movement”). Finally, we summed the scores of the steps of the 4 hours  
265 preceding the encounter to calculate an overall attraction score for each species (see Fig. 1b for  
266 an example). Based on these overall scores, we established if one species was clearly attracted  
267 to the location of the other species and therefore likely to provoke the encounter (positive  
268 overall score while the other species had a null or negative overall score) or avoiding the  
269 location of the other species (negative overall score while the other species had a null or  
270 positive overall score). Only GPS locations separated by a maximum of 2 h and only  
271 encounters before which at least two steps could be computed were taken into account. In  
272 addition, to be sure that hyaenas and lions could have detected each other’s presence, we only  
273 considered steps for which both starting and ending points were located within 2 km of the  
274 other species.

275

### 276 ***Which species was dominant over the encounter?***

277 For encounters in the presence of a carcass, if the species present at the carcass moved away  
278 (further than 200 m from the carcass) in the 2 hours following the arrival of the second species,  
279 the latter was considered dominant. However, if the species at the carcass was not displaced,  
280 and the arriving species spent less than 2h in the vicinity of the carcass ( $\leq 200$  m) before  
281 moving away (even if it came back to the carcass at a later stage during the encounter), the

282 former was considered as dominant. Staying at the carcass after the end of the encounter (if the  
283 first arriving species was not displaced) was not considered as an indication of dominance.  
284 Indeed, while a carcass can initially provide a lot of food (assuming it was killed or discovered  
285 in good condition), its profitability decreases with time. Thus, a species leaving the carcass  
286 might do so when it is not profitable enough to stay longer. For each encounter, we established  
287 whether at least one adult male lion was present as the presence of a male lion has often been  
288 reported as the determinant of the outcome of aggressive interactions between lions and  
289 hyaenas (Cooper 1991; Höner et al. 2002). At the time of the study, all male coalitions had at  
290 least one individual collared in the study area. We further computed the speed of movement  
291 during the hour following the end of the encounter for both species. Speed was only computed  
292 if the first GPS location was taken maximum 2h after the end of the encounter.

293 To test for differences in speed and distance to the carcass between the two species, we used  
294 linear mixed effect models including speed or distance to the carcass as the dependent variable,  
295 species as the explanatory variable, and carcass identity as a random intercept. Both speed and  
296 distance to carcass were log transformed to meet normality assumptions.

297 For encounters in the absence of a carcass, we used the attraction score approach described  
298 above for the 4h following the end of the encounter, to assess which species avoided the other  
299 one after the encounter. When there were insufficient data to characterize the movement of the  
300 two species for 4h after an encounter, we used speed during the hour immediately following  
301 the encounter to determine if one species was clearly moving away from the other one. In this  
302 case, we considered a ratio of hyaena speed to lion speed above 2 to be indicative of a  
303 behaviour of lion avoidance by hyaenas and of less than 0.5 to be indicative of a behaviour of  
304 hyaena avoidance by lions.

305 We tested for a significant difference in the speed at which lions and hyaenas moved before  
306 and after an encounter depending on the presence of a carcass using a linear model including

307 the interaction between species and carcass presence (coded as 0/1) as explanatory variables  
308 and speed as dependent variable. Speed was log transformed to meet the model assumptions.

309  
310 All data extraction and analyses were conducted using the R software (R Core Team 2020,  
311 version 3.5.2) with the packages *adehabitaHR* (version 0.4.15), *adehabitatLT* (version 0.3.23,  
312 Calenge 2006), *lmer* (version 3.0-1, Bates 2010). Values are provided as the mean  $\pm$  standard  
313 error (SE) unless mentioned otherwise.

314

## 315 **RESULTS**

### 316 *Proximity index and encounter definition*

317 *Proximity index* - We found a total of 108 proximal fixes out of 170,120 simultaneous fixes in  
318 our dataset, which resulted in an average proximity index for a given hyaena of  $0.0011 \pm$   
319  $0.0023$  (range=0-0.0107, n=90). The average of the randomly generated proximity index was  
320 lower ( $0.0005 \pm 0.00001$ , range=0-0.0076, Fig. 2) suggesting that hyaenas and lions came into  
321 contact more often than expected by chance.

322 *Encounter definition* - Based on visual examination of hyaena and lion movements around  
323 proximal fixes, we defined 70 encounters between the two predators. Twenty-eight of them  
324 occurred in the presence of a carcass and 35 occurred in the absence of a carcass. For seven  
325 encounters, the presence or absence of a carcass could not be established with certainty and  
326 their characteristics are not discussed hereafter (see Appendix S3 for a complete list of  
327 encounters and their characteristics).

328

### 329 *Encounter characteristics*

330 *Seasonality* – More than half of the encounters in the presence of a carcass occurred during the  
331 wet season (57.1%, n=12; [Fig. 3a](#), [Appendix S3](#)). Most encounters in the absence of a carcass  
332 occurred during the dry season (77.1%, n=27; [Fig. 3a](#), [Appendix S3](#)). Encounters in the

333 presence of a carcass were significantly more likely to occur during the wet season ( $\chi^2=6.4$ ,  
334  $p=0.01$ ).

335 *Distance to water* – In the presence of a carcass, we found no effect of the distance to water on  
336 the probability of encounter ( $p=0.64$ ), suggesting that these were evenly distributed in the  
337 landscape. However, encounters in the absence of a carcass were more likely to occur as the  
338 distance to water decreased ( $z$  value= $-0.36$ ,  $p=0.0003$ ), see distribution of the encounters  
339 depending on the distance to water in Fig. 3b).

340 *Duration* - Excluding the six encounters characterized by one pair of proximal fixes only (i.e.  
341 for which we could not estimate duration), encounters in the presence of a carcass lasted on  
342 average  $40\pm 9$ h ranging from 1 to 162h (nearly seven days, Fig. 3c, see also Appendix S4: Fig.  
343 S2 for examples of encounters). For encounters in the absence of a carcass, 80 % of the 35  
344 encounters were characterized by only one pair of proximal fixes (Fig. 3c, see also Appendix  
345 S4: Fig. S4 for examples of encounters) and they were significantly shorter than encounters in  
346 the presence of a carcass ( $1.4\pm 0.2$ h, range: 1-6h,  $W=2088$ ,  $p=0.004$ ).

347

#### 348 ***Which species provoked the encounter?***

349 *Encounters in the presence of a carcass* - Of the 28 encounters at a carcass, lions were the first  
350 at the carcass in 71% of the cases ( $n=20$ , Fig. 4). The few cases ( $n=7$ ) when hyaenas arrived  
351 first corresponded to situations with only lionesses present. In the hour preceding the  
352 encounter, hyaenas moved significantly faster ( $1,011\pm 230$ m/h,  $n=27$ ) than lions ( $580\pm 200$  m/h,  
353  $n=27$ ,  $t=3.12$ ,  $p=0.002$ , Appendix S4: Fig. S1).

354 *Encounters in the absence of a carcass* - A male lion was present in 34% ( $n=12$ ) of the  
355 encounter in the absence of a carcass. When movement could be characterized before the  
356 encounter ( $n=26$ ), hyaenas appeared to be attracted to lions (42% of the encounters) or to  
357 ignore them, but they never seemed to avoid them (Fig. 4, Appendix S3: Table S2). In contrast,  
358 lions showed movement characteristics of avoidance before the encounter in 11.5% of

359 encounters (Fig 4, Appendix S3: Table S2) and of attraction in 15% of encounters. In the hour  
360 preceding the encounter, hyaenas moved on averaged at  $1,045 \pm 195$  m/h ( $n=34$ ), which was not  
361 significantly different from the lion speed of  $766 \pm 136$  m/h ( $n=31$ ,  $t=0.47$ ,  $p=0.64$ , Appendix  
362 S4: Fig S3).

363

#### 364 ***Which species was dominant over the encounter?***

365 *Encounters in the presence of a carcass* - We found that lions were dominant over access to the  
366 carcass in 18 out of the 20 encounters where dominance could be clearly established (Fig. 4,  
367 Appendix S3: Table S1, see Appendix S4: Fig. S2 for examples of encounters). Hyaenas were  
368 dominant only once. During the 22 encounters that were characterized by more than one pair of  
369 proximal fixes, hyaenas moved on average  $739 \pm 47$  m/h (range= $1-5,600$ m/h,  $n=479$  steps)  
370 which was significantly more than lions ( $115 \pm 13$ m/h, range = $0-1900$ m/h,  $n=409$  steps,  $t=15.98$ ,  
371  $p<0.0001$ ). Hyaenas were also found significantly further away from the carcass than lions  
372 (hyaena:  $1,614\text{m} \pm 127\text{m}$ , range= $4-15,400\text{m}$ ,  $n=544$  locations; lion:  $250 \pm 2\text{m}$ , range= $0-1,900\text{m}$ ,  
373  $n=483$  locations;  $t=20.48$ ,  $p<0.0001$ ). In the hour following the end of the encounter, hyaenas  
374 moved at  $527 \pm 129$ m/h ( $n=28$ ), which was significantly more than lions ( $60 \pm 32$ m/h,  $n=27$ ,  
375  $t=5.49$ ,  $p<0.0001$ , Appendix S4: Fig. S1).

376 *Encounters in the absence of a carcass* - When movement could be characterized after the  
377 encounter ( $n=33$ ), hyaenas seemed to move away from lions in only 18% of the cases (Fig. 4,  
378 Appendix S3: Table S2), whereas lions moved away from hyaenas in 58% of the cases (Fig. 4,  
379 Appendix S3: Table S2). In the hour following the end of the encounter, hyaenas moved at  
380  $578 \pm 146$ m/h ( $n=33$ ) and lions at  $658 \pm 118$ m/h ( $n=30$ , Fig. S3) and the difference was not  
381 significant ( $t=1.07$ ,  $p=0.28$ ). After an encounter, we found a significant effect of the interaction  
382 between species and the presence of a carcass ( $F=14.48$ ,  $p=0.002$ ) with lions moving faster in  
383 the absence of a carcass compared to when a carcass was present ( $t=6.73$ ,  $p<0.0001$ ). We found

384 no effect of the presence of a carcass on hyaena movement speed after an encounter ( $t=0.11$ ,  
385  $p=0.90$ , Appendix S4: Fig. S1 and S3).

386

## 387 **DISCUSSION**

388 The analysis of simultaneous GPS locations of hyaenas and lions showed that these two apex  
389 predator species did not avoid encountering each other. Rather, they encountered each other  
390 more often than expected by chance. Encounters between lions and hyaenas may occur through  
391 either active mechanisms of attraction between the two predators or passive mechanisms  
392 whereby the two predators are attracted to the same locations in the landscape.

393

### 394 *Wet season: time for intraguild facilitation*

395 During the wet season, lions and hyaenas encountered each other mainly at carcasses and  
396 throughout the landscape (i.e. independently of water sources). As we expected, hyaenas  
397 arrived at carcasses after the lions, and travelled far and fast to reach the carcasses. Lions  
398 killing prey and feeding on a carcass are indeed likely to be heard (noises of high-speed chase,  
399 struggle, and prey distress call) and smelt (blood and stomach content odour) by hyaenas from  
400 quite a distance, and hyaena intraspecific communication may also play a role resulting in  
401 hyaena moving up to 5 km in the hour preceding its arrival to a carcass that had just been killed  
402 by lions. Further, lions were dominant over the access to carcasses, and hyaenas did not stay  
403 near the carcasses while the lions were present (Appendix S5). However, hyaenas came back  
404 regularly to the carcasses for up to one week after their first arrival. This suggests that hyaenas  
405 regularly checked whether lions were still at the carcass and fed on the carcass only after the  
406 lions had gone. Hyaenas are particularly well-equipped to make use of carcass parts usually  
407 disregarded by other species (Kruuk 1972), and are therefore able to benefit from whatever was  
408 left by lions. Our results showed that hyaenas hardly ever displaced lions from a carcass. This  
409 is consistent with result from an experiment conducted in South Africa showing that

410 interactions occur at large carcasses over which lions maintain preferential access (Amorós et  
411 al. 2020). Previous studies showed that the likelihood of hyaenas winning an encounter with  
412 lions depends on the group sizes of the two species (with hyaenas likely to take over a kill  
413 when they outnumber lions by a factor of 4 – Cooper 1991) and the presence of an adult male  
414 lion (Kruuk 1972; Cooper 1991; Trinkel and Kastberger 2005). We do not know the number of  
415 hyaenas and lions involved in the encounters mentioned in this study. However, male lions  
416 were present during most of these interactions. As the population of adult male lions increased  
417 after a moratorium on trophy hunting around HNP in 2005-2008 (Loveridge et al. 2016), male  
418 lions are now more likely to be present and thus hyaenas less likely to win their encounters  
419 with lions. In our study, even though we cannot infer if the prey was killed or found dead by  
420 lions, we suggest that lions producing/finding a carcass provide extra scavenging opportunities  
421 for hyaenas by making the given carcass more easily located.

422 Carcasses are widely used resources across ecosystems, which have been overlooked for  
423 terrestrial mammals, and their ecological importance, along with that of scavenging, has  
424 recently gained increased recognition in community ecology (Wilson & Wolkovich 2011,  
425 Pereira et al. 2014). For instance, wolverine (*Gulo gulo*) take advantage of prey killed by wolf  
426 (*Canis lupus*) and lynx (*Lynx lynx*, van Dijk et al. 2008) and access to these carcasses,  
427 especially during winter, has a stabilizing effect on wolverine populations as well as on the  
428 whole food web (Wilson and Wolkovich 2011). Altogether, our results illustrate that intra-  
429 guild facilitation (through scavenging opportunities) may be an important process to explain  
430 the coexistence between lions and hyaenas. As expected based on the hunting mode of  
431 hyaenas, our results further suggest that hyaena scavenging from lion kills mainly occurs in the  
432 wet season. Seasonal variations in the prevalence of scavenging have already been highlighted  
433 Pereira *et al.* (2014).

434

435 ***Dry season: time for interference competition?***

436 We revealed a significant number of encounters between lions and hyaenas in the dry season.  
437 They encountered each other mainly in the absence of a carcass. In the dry season, hyaenas are  
438 likely to be more efficient killers than during the wet season and more carcasses from  
439 herbivore natural mortality are likely to be available in the landscape, which will increase the  
440 chance of locating a carcass from which lions are absent. Altogether, this may explain the  
441 lower number of interactions at carcasses between hyaenas and lions in the dry season.  
442 Interestingly, during the dry season, lions and hyaenas encountered each other mainly close to  
443 waterholes.  
444 In arid and semi-arid savannas, large herbivores tend to aggregate around scarce water sources  
445 in the dry season (Thrash et al. 1995; Redfern et al. 2003). This is the case in HNP (Valeix et  
446 al. 2009; Valeix 2011) where waterholes can be considered as prey hotspots during the dry  
447 season. Both predators are attracted to these areas (Valeix et al. 2010; Périquet 2014), and are  
448 therefore more likely to encounter each other there. Our results suggest that management  
449 decisions to artificially provide water throughout the year may influence apex predator  
450 interactions by creating, maintaining and strengthening prey hotspots.  
451 Encounters in the absence of a carcass were very short and usually limited to a single contact  
452 point with one or both species moving away immediately afterwards. This suggests that in the  
453 absence of food, predators avoid spending time near each other. Hyaenas did not avoid these  
454 encounters, and even appeared to provoke many of them. Surprisingly, lions seemed to avoid  
455 the encounter on a few occasions. Additionally, hyaenas did not appear to flee after an  
456 encounter, while lions quickly moved away on more than half of the encounters. Altogether,  
457 these results are quite counterintuitive and suggest that hyaenas were not scared of proximity to  
458 lions and were even attracted to them. These observations could result from hyaenas following  
459 lions to assess kleptoparasitism and scavenging opportunities, as foxes have been observed to  
460 follow striped hyaenas (*Hyena hyena*, Macdonald 1978). Yet, we found that hyaenas hardly  
461 ever displace lions from carcasses and that very few encounters at carcasses occur in the dry

462 season, making this scenario unlikely. The observed patterns could result from two scenarios: a  
463 passive interference scenario whereby the two predators actively select for areas rich in prey  
464 and lions leave a patch due to prey disturbance following hyaena arrival, or an active  
465 interference scenario whereby hyaenas actively seek to encounter lions near waterholes to  
466 displace them from these prime hunting grounds. In the two scenarios, our results would  
467 suggest an interference competition between the two species, with potential negative effects  
468 from hyaenas on lions, which would challenge the widely accepted view that lions are  
469 dominant over hyaenas. While many studies (including this one) found lions to be dominant  
470 over hyaenas in terms of food access (Cooper 1991; Höner et al. 2002; Trinkel and Kastberger  
471 2005), to our knowledge, this is the first time that interactions between the two species away  
472 from food resources are studied.

473

#### 474 *Limits and future directions*

475 Our results show the great potential of GPS data loggers to provide extensive information on  
476 interactions between species. It is however important to note that the frequency of encounters  
477 was underestimated as the proximity index was calculated from GPS locations separated by  
478 one hour at least, and short encounters that occurred between consecutive 1h locations may  
479 have been undetected. Additionally, we could not quantify the encounters involving a collared  
480 animal and a non-collared one. Significant improvements in battery life should soon allow the  
481 use of this technology with high frequency of GPS fixes acquisition that would provide a much  
482 finer spatiotemporal scale to study interactions between apex predators. This would allow  
483 testing the scenarios sketched above about the underlying mechanisms of the interactions. We  
484 also encourage the development of methods to quantify attraction and avoidance from  
485 simultaneous movement data (as started by Jordan et al. 2017 and Chisholm et al. 2019).  
486 Additionally, only one individual (at best two) per predator group was radio-collared, and since  
487 hyaena groups are characterized by a highly dynamic fission-fusion (Kruuk 1972; Smith et al.

488 2008), we cannot say with certainty whether some hyaenas arrived before or stayed after the  
489 collared one. Hyaenas also behave differently depending on their social rank (Smith et al.  
490 2008) and they have marked personality which could influence the outcome of interactions  
491 with lions (Watts et al. 2010).

492

### 493 *Conclusion*

494 While interference competition occurs between lions and hyaenas, as it is widely accepted  
495 between apex predators (e.g. Broekhuis et al. 2013; Vanak et al. 2013; du Preez et al. 2015),  
496 the extent of facilitation through scavenging opportunities should not be ignored (van Dijk et  
497 al. 2008; Mattisson et al. 2011; Pereira et al. 2014; Sivy et al. 2017). Our results show that the  
498 balance between intraguild competition and facilitation is likely to be affected by  
499 environmental conditions and at least in semi-arid savanna ecosystems is most probably driven  
500 by water availability and seasonality.

501

### 502 **ACKNOWLEDGEMENTS**

503 The Zimbabwe Research Council and the Zimbabwe Parks and Wildlife Management  
504 Authority are kindly acknowledged for providing the opportunity to carry out this research. We  
505 deeply thank Nicholas Elliot, Jane Hunt and Brent Stapelkamp for the collection of lion GPS  
506 data. This study was supported by the HERD project (Hwange Environmental Research  
507 Development), funded by the ANR FEAR (ANR-08-BLAN-0022), the CNRS, the RP-PCP  
508 platform and by the Hwange Lion Project supported by grants from The Darwin Initiative for  
509 Biodiversity Grant 162/09/015, The Eppley Foundation, Disney Foundation, Marwell  
510 Preservation Trust, Regina B. Frankenburg Foundation, The Rufford Maurice Laing  
511 Foundation, Panthera Foundation, and the generosity of Joan and Riv Winant. SP salary was  
512 provided by the ENS of Lyon and UCBL Lyon1. ER was supported by the Spanish Ministry of  
513 Science and Innovation co-funded by FEDER (projects CGL2009-07301/BOS, CGL2012-

514 35931/BOS and CGL2017- 83045-R). This work was performed using the computing facilities  
515 of the CC LBBE/PRABI. This work benefited from ideas developed in the framework of the  
516 ANR project FUTURE-PRED (ANR-18-CE02-0005-01). We thank two anonymous reviewers  
517 for their helpful comments on a previous version of the manuscript.

518

519

## 520 REFERENCES

- 521 Amorós M, Gil-Sánchez JM, de las N López-Pastor B, Moleón M (2020) Hyaenas and lions:  
522 how the largest African carnivores interact at carcasses. *Oikos* 1–36.  
523 <https://doi.org/10.1111/oik.06846>
- 524 Arraut EM, Loveridge AJ, Chamaillé-Jammes S, et al (2018) The 2013–2014 vegetation  
525 structure map of Hwange National Park, Zimbabwe, produced using free satellite  
526 images and software. *Koedoe* 60:a1497. <https://doi.org/10.4102/koedoe.v60i1.1497>
- 527 Atwood TC, Gese EM, Kunkel KE (2009) Spatial partitioning of predation risk in a multiple  
528 predator–multiple prey system. *J Wildl Manage* 73:876–884.  
529 <https://doi.org/10.2193/2008-325>
- 530 Bates DM (2010) *lme4: Mixed-effects modeling with R*
- 531 Benhamou S, Valeix M, Chamaillé-Jammes S, et al (2014) Movement-based analysis of  
532 interactions in African lions. *Anim Behav* 90:171–180
- 533 Broekhuis F, Cozzi G, Valeix M, et al (2013) Risk avoidance in sympatric large carnivores:  
534 reactive or predictive? *J Anim Ecol* 82:1098–1105
- 535 Broekhuis F, Madsen EK, Keiwua K, Macdonald DW (2019) Using GPS collars to investigate  
536 the frequency and behavioural outcomes of intraspecific interactions among carnivores:  
537 A case study of male cheetahs in the Maasai Mara, Kenya. *PLoS ONE* 14:e0213910-  
538 16. <https://doi.org/10.1371/journal.pone.0213910>
- 539 Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory.  
540 *Trends Ecol Evol* 18:119–125
- 541 Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space  
542 and habitat use by animals. *Ecological Modelling* 197:516–519.  
543 <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- 544 Chamaillé-Jammes S, Fritz H, Murindagomo F (2006) Spatial patterns of the NDVI–rainfall  
545 relationship at the seasonal and interannual time scales in an African savanna.  
546 *International Journal of Remote Sensing* 27:5185–5200

- 547 Chapron G, Kaczensky P, Linnell JD, et al (2014) Recovery of large carnivores in Europe's  
548 modern human-dominated landscapes. *Science* 346:1514–1517.  
549 <https://doi.org/10.1126/science.1256620>
- 550 Chisholm S, Stein AB, Jordan NR, et al (2019) Parsimonious test of dynamic interaction. *Ecol*  
551 *Evol* 90:171–11. <https://doi.org/10.1002/ece3.4805>
- 552 Cooper SM (1991) Optimal hunting group size: the need for lions to defend their kills against  
553 loss to spotted hyaenas. *African Journal of Ecology* 29:130–136
- 554 Courbin N, Fortin D, Dussault C, et al (2013) Multi-trophic resource selection function  
555 enlightens the behavioural game between wolves and their prey. *J Anim Ecol* 82:1062–  
556 1071. <https://doi.org/10.1111/1365-2656.12093>
- 557 Courbin N, Loveridge AJ, Macdonald DW, et al (2016) Reactive responses of zebras to lion  
558 encounters shape their predator–prey space game at large scale. *Oikos* 125:829–838.  
559 <https://doi.org/10.1111/oik.02555>
- 560 Cozzi G, Börger L, Hutter P, et al (2015) Effects of Trophy Hunting Leftovers on the Ranging  
561 Behaviour of Large Carnivores: A Case Study on Spotted Hyenas. *PLoS ONE*  
562 10:e0121471
- 563 Cozzi G, Broekhuis F, McNutt JW, et al (2012) Fear of the dark or dinner by moonlight?  
564 Reduced temporal partitioning among Africa's large carnivores. *Ecology* 93:2590–2599
- 565 Davidson Z, Valeix M, Van Kesteren F, et al (2013) Seasonal Diet and Prey Preference of the  
566 African Lion in a Waterhole-Driven Semi-Arid Savanna. *PLoS ONE* 8:e55182.  
567 <https://doi.org/10.1371/journal.pone.0055182.t003>
- 568 du Preez B, Hart T, Loveridge AJ, Macdonald DW (2015) Impact of risk on animal behaviour  
569 and habitat transition probabilities. *Animal Behaviour* 100:22–37.  
570 <https://doi.org/10.1016/j.anbehav.2014.10.025>
- 571 Durant SM (2000) Living with the enemy: avoidance of hyenas and lions by cheetahs in the  
572 Serengeti. *Behavioral Ecology* 11:624–632. <https://doi.org/10.1093/beheco/11.6.624>
- 573 Fortin D, Beyer HL, Boyce MS, et al (2005) Wolves influence elk movements: behavior  
574 shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330
- 575 Höner OP, Wachter B, East ML, Hofer H (2002) The response of spotted hyaenas to long-term  
576 changes in prey populations: functional response and interspecific kleptoparasitism.  
577 *Journal of Animal Ecology* 71:236–246. [https://doi.org/10.1046/j.1365-  
578 2656.2002.00596.x](https://doi.org/10.1046/j.1365-2656.2002.00596.x)
- 579 Jordan NR, Buse C, Wilson AM, et al (2017) Dynamics of direct inter-pack encounters in  
580 endangered African wild dogs. *Behav Ecol Sociobiol* 71:1–12.  
581 <https://doi.org/10.1007/s00265-017-2338-9>
- 582 Kohl MT, Ruth T, Metz MC, et al (2019) Do prey select for vacant hunting domains to  
583 minimize a multi-predator threat? *Ecol Lett* 73:876–10.  
584 <https://doi.org/10.1111/ele.13319>

- 585 Krofel M, Kos I, Jerina K (2012) The noble cats and the big bad scavengers: effects of  
586 dominant scavengers on solitary predators. *Behav Ecol Sociobiol* 66:1297–1304.  
587 <https://doi.org/10.1007/s00265-012-1384-6>
- 588 Kruuk H (1972) *The Spotted Hyena: A Study of Predation and Social Behavior*. University of  
589 Chicago Press, Chicago
- 590 Linnell JD, Strand O (2000) Interference interactions, co-existence and conservation of  
591 mammalian carnivores. *Div Distrib* 6:169–176
- 592 Long JA, Nelson TA, Webb SL, Gee KL (2014) A critical examination of indices of dynamic  
593 interaction for wildlife telemetry studies. *J Anim Ecol* 83:1216–1233.  
594 <https://doi.org/10.1111/1365-2656.12198>
- 595 Loveridge AJ, Valeix M, Chapron G, et al (2016) Conservation of large predator populations:  
596 Demographic and spatial responses of African lions to the intensity of trophy hunting.  
597 *Biol Conserv* 204:247–254. <https://doi.org/10.1016/j.biocon.2016.10.024>
- 598 Macdonald DW (1978) Observations on the behaviour and ecology of the striped hyena, *Hyena*  
599 *hyena* in Israel. *Israel Journal of Zoology* 27:189–198
- 600 Mattisson J, Andrén H, Persson J, Segerström P (2011) Influence of intraguild interactions on  
601 resource use by wolverines and Eurasian lynx. *J Mamm* 92:1321–1330.  
602 <https://doi.org/10.1644/11-MAMM-A-099.1>
- 603 Miller JRB, Pitman RT, Mann GKH, et al (2018) Lions and leopards coexist without spatial,  
604 temporal or demographic effects of interspecific competition. *J Appl Ecol* 87:1709–  
605 1726. <https://doi.org/10.1111/1365-2656.12883>
- 606 Mills MGL (1990) *Kalahari hyaenas: Comparative behavioural ecology of two species*. The  
607 Blackburn Press, Caldwell NJ, USA
- 608 Owen-Smith RN (2002) *Adaptive Herbivore Ecology*. Cambridge University Press, Cambridge
- 609 Palmer MS, Fieberg J, Swanson A, et al (2017) A ‘dynamic’ landscape of fear: prey responses  
610 to spatiotemporal variations in predation risk across the lunar cycle. *Ecol Lett* 20:1364–  
611 1373. <https://doi.org/10.1111/ele.12832>
- 612 Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. *The*  
613 *American Naturalist* 153:492–508
- 614 Pereira LM, Owen-Smith N, Moleón M (2014) Facultative predation and scavenging by  
615 mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Rev*  
616 44:44–55. <https://doi.org/10.1111/mam.12005>
- 617 Périquet S (2014) *Sharing the top: How do Spotted hyaenas cope with Lions? Apex predator*  
618 *coexistence in a wooded savanna*. PhD, Université Claude Bernard, Lyon 1
- 619 Périquet S, Fritz H, Revilla E (2015a) The Lion King and the Hyaena Queen: large carnivore  
620 interactions and coexistence. *Biol Rev* 90:1197–1214.  
621 <https://doi.org/10.1111/brv.12152>

- 622 Périquet S, Valeix M, Claypole J, et al (2015b) Spotted hyaenas switch their foraging strategy  
623 as a response to changes in intraguild interactions with lions. *J Zool* 297:245–254.  
624 <https://doi.org/10.1111/jzo.12275>
- 625 R Core Team (2020) R: A language and environment for statistical computing. R Foundation  
626 for Statistical Computing. Version 4.0.2. Vienna, Austria
- 627 Rasphone A, Kamler JF, Macdonald DW (2020) Temporal partitioning by felids, dholes and  
628 their potential prey in northern Laos. *Mamm Res* 40:36–11.  
629 <https://doi.org/10.1007/s13364-020-00524-9>
- 630 Redfern JV, Grant R, Biggs HC, Getz WM (2003) Surface-water constraints on herbivore  
631 foraging in the Kruger National Park, South Africa. *Ecology* 84:2092–2107.  
632 <https://doi.org/10.1890/01-0625>
- 633 Ripple WJ, Estes JA, Beschta RL, et al (2014) Status and Ecological Effects of the World’s  
634 Largest Carnivores. *Science* 343:1241484–1241484.  
635 <https://doi.org/10.1126/science.1241484>
- 636 Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity  
637 conservation. *Ecology Letters* 12:982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- 639 Schaller GB (1972) *The Serengeti lion- A Study of Predator-Prey Relations*. University of  
640 Chicago Press, Chicago
- 641 Schuette P, Wagner AP, Wagner ME, Creel S (2013) Occupancy patterns and niche  
642 partitioning within a diverse carnivore community exposed to anthropogenic pressures.  
643 *Biol Conserv* 158:301–312. <https://doi.org/10.1016/j.biocon.2012.08.008>
- 644 Sivy KJ, Pozzanghera CB, Grace JB, Prugh LR (2017) Fatal Attraction? Intraguild Facilitation  
645 and Suppression among Predators. *Am Nat* 190:663–679.  
646 <https://doi.org/10.5061/dryad.tj590>
- 647 Smith JE, Kolowski JM, Graham K, et al (2008) Social and ecological determinants of fission–  
648 fusion dynamics in the spotted hyaena. *Anim Behav* 76:619–636.  
649 <https://doi.org/10.1016/j.anbehav.2008.05.001>
- 650 Swanson A, Arnold T, Kosmala M, et al (2016) In the absence of a “landscape of fear”: How  
651 lions, hyenas, and cheetahs coexist. *Ecol Evol* 1–12. <https://doi.org/10.1002/ece3.2569>
- 652 Swanson A, Caro TM, Davies-Mostert HT (2014) Cheetahs and wild dogs show contrasting  
653 patterns of suppression by lions. *Journal of Animal Ecology* 83:1418–1427
- 654 Tambling CJ, Belton LE (2009) Feasibility of using proximity tags to locate female lion  
655 *Panthera leo* kills. *Wildlife Biol* 15:435–441. <https://doi.org/10.2981/09-029>
- 656 Tambling CJ, Laurence SD, Bellan SE, et al (2012) Estimating carnivoran diets using a  
657 combination of carcass observations and scats from GPS clusters. *J Zool* 286:102–109.  
658 <https://doi.org/10.1111/j.1469-7998.2011.00856.x>

- 659 Thrash I, Theron GK, du P Bothma J (1995) Dry season herbivore densities around drinking  
660 troughs in the Kruger National Park. *Journal of Arid Environments* 29:213–219.  
661 [https://doi.org/10.1016/s0140-1963\(05\)80091-6](https://doi.org/10.1016/s0140-1963(05)80091-6)
- 662 Trinkel M, Kastberger G (2005) Competitive interactions between spotted hyenas and lions in  
663 the Etosha National Park, Namibia. *Afr J Ecol* 43:220–224
- 664 Valeix M (2011) Temporal dynamics of dry-season water-hole use by large African herbivores  
665 in two years of contrasting rainfall in Hwange National Park, Zimbabwe. *J Trop Ecol*  
666 27:163–170. <https://doi.org/10.1017/S0266467410000647>
- 667 Valeix M, Loveridge AJ, Chamaillé-Jammes S, et al (2009) Behavioral adjustments of African  
668 herbivores to predation risk by lions: Spatiotemporal variations influence habitat use.  
669 *Ecology* 90:23–30. <https://doi.org/10.1890/08-0606.1>
- 670 Valeix M, Loveridge AJ, Davidson Z, et al (2010) How key habitat features influence large  
671 terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of  
672 north-western Zimbabwe. *Landscape Ecology* 25:337–351.  
673 <https://doi.org/10.1007/s10980-009-9425-x>
- 674 van Dijk J, Gustavsen L, Mysterud A, et al (2008) Diet shift of a facultative scavenger, the  
675 wolverine, following recolonization of wolves. *J Anim Ecol* 77:1183–1190.  
676 <https://doi.org/10.1111/j.1365-2656.2008.01445.x>
- 677 Vanak AT, Fortin D, Thaker M, et al (2013) Moving to stay in place: behavioral mechanisms  
678 for coexistence of African large carnivores. *Ecology* 94:2619–2631.  
679 <https://doi.org/10.1890/13-0217.1>
- 680 Watts HE, Blankenship LM, Dawes SE, Holekamp KE (2010) Responses of Spotted Hyenas to  
681 Lions Reflect Individual Differences in Behavior. *Ethology* 116:1199–1209.  
682 <https://doi.org/10.1111/j.1439-0310.2010.01833.x>
- 683 Wilson EE, Wolkovich EM (2011) Scavenging: how carnivores and carrion structure  
684 communities. *Trends Ecol Evol* 26:129–135. <https://doi.org/10.1016/j.tree.2010.12.011>
- 685

686 **FIGURES CAPTIONS**

687 **Figure 1: a)** Rules for attributing attraction scores to simultaneous steps of hyaenas and lions  
688 before and after an encounter. The figure presents an example of movement of species A  
689 (circles) and B (stars) 4h before their encounter. Darker grey areas characterize strong  
690 attraction (score +1) of species A to species B (or to location of species B) while light grey  
691 show mild attraction (score +0.5). Squared hashed areas show strong avoidance (score -1) of  
692 species B (or of location of species B) by species A and grey hashed areas represent areas of  
693 mild avoidance (score -0.5). Areas of strong and mild attraction/avoidance are based on  
694 threshold angles of  $\alpha=10^\circ$  and  $\beta=30^\circ$  respectively. In any other case, species A was considered  
695 as moving independently from species B.

696 b) Example of movement paths of species A (circles) and species B (stars) leading to an  
697 encounter with overall attraction computed for the 4 hours preceding the encounter as the sum  
698 scores of all steps from both species.

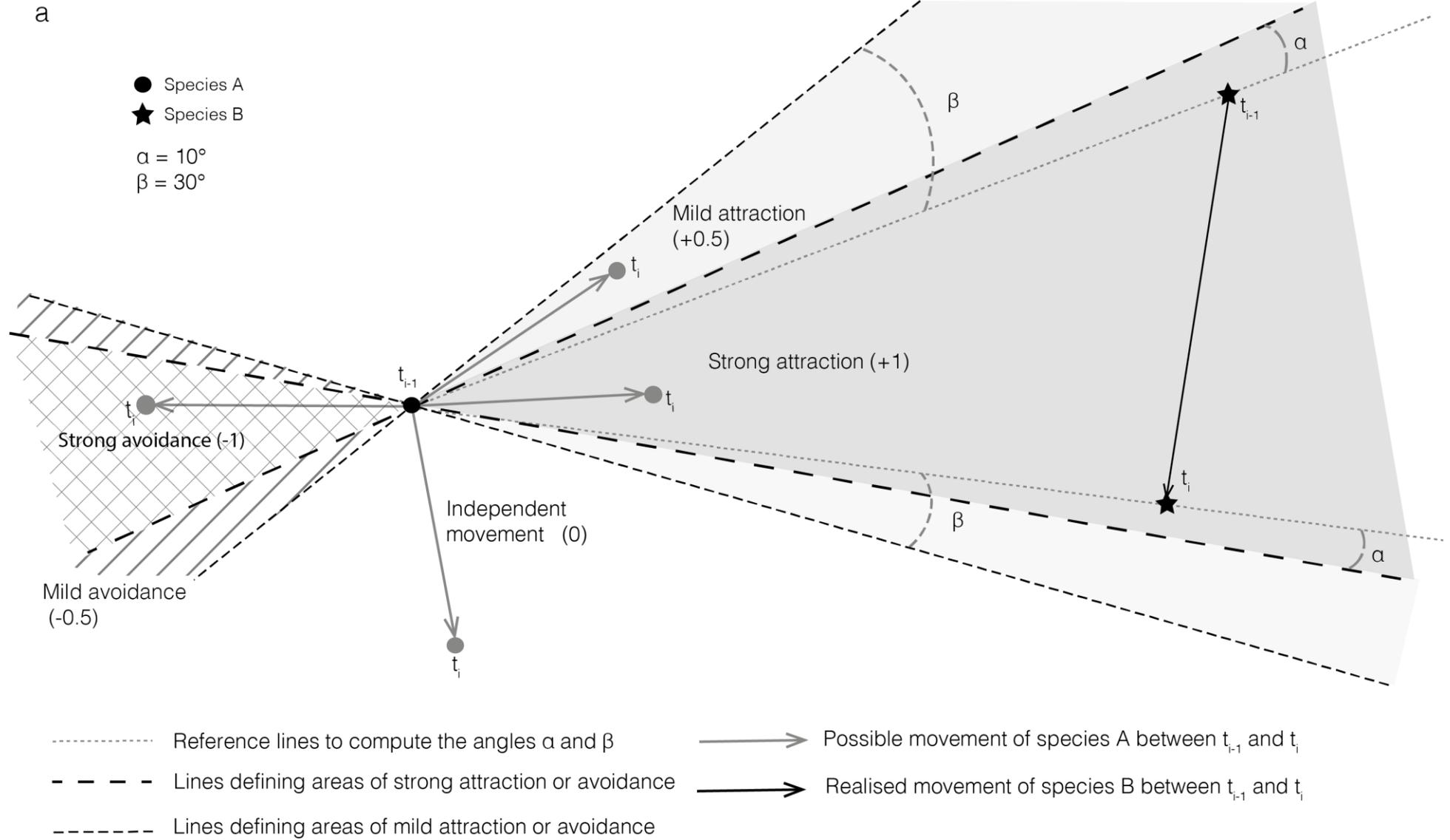
699 **Figure 2:** Distribution of the 100 proximity indices randomly generated compared to the  
700 proximity index computed from actual GPS data (black vertical line).

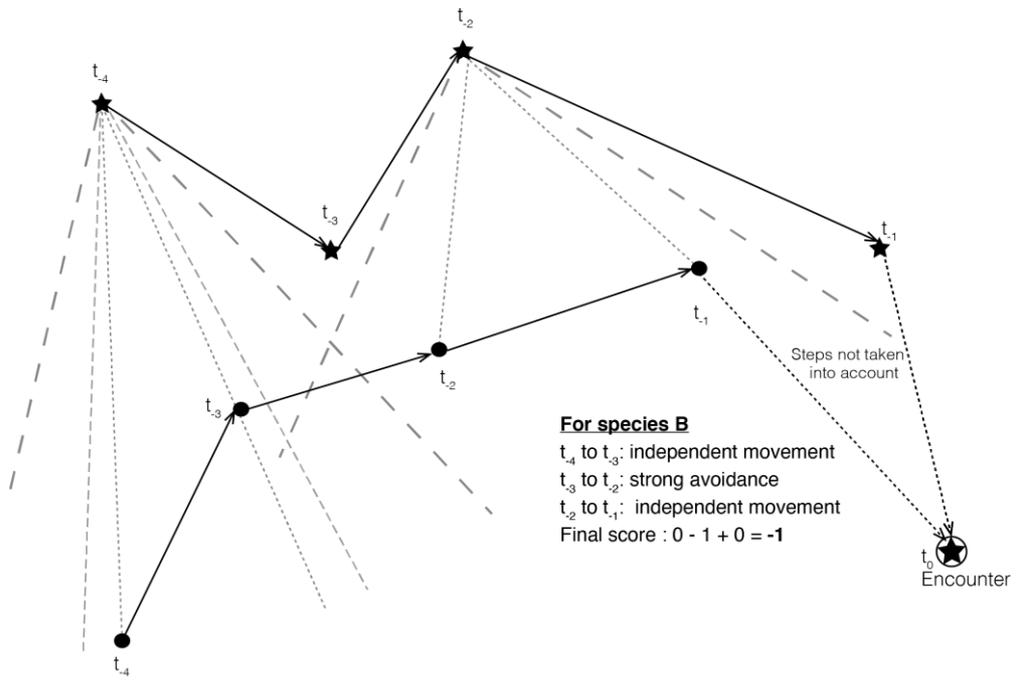
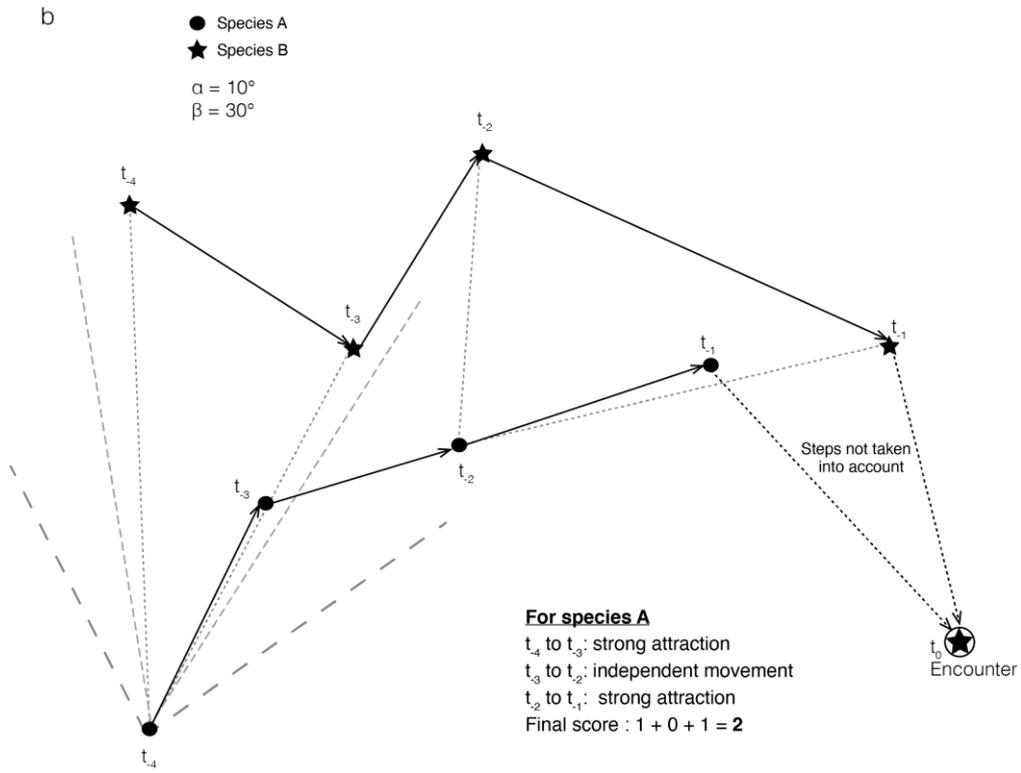
701 **Figure 3:** a) Monthly distribution of encounters between hyaenas and lions depending on the  
702 presence or absence of a carcass.

703 b) Effect of distance to water of the probability of encounter in the presence and absence of a  
704 carcass.

705 c) Duration of encounters between hyaenas and lions depending on the presence or absence of  
706 a carcass.

707 **Figure 4:** Creation and outcome of encounters occurring in the presence versus absence of a  
708 carcass between hyaenas and lions.

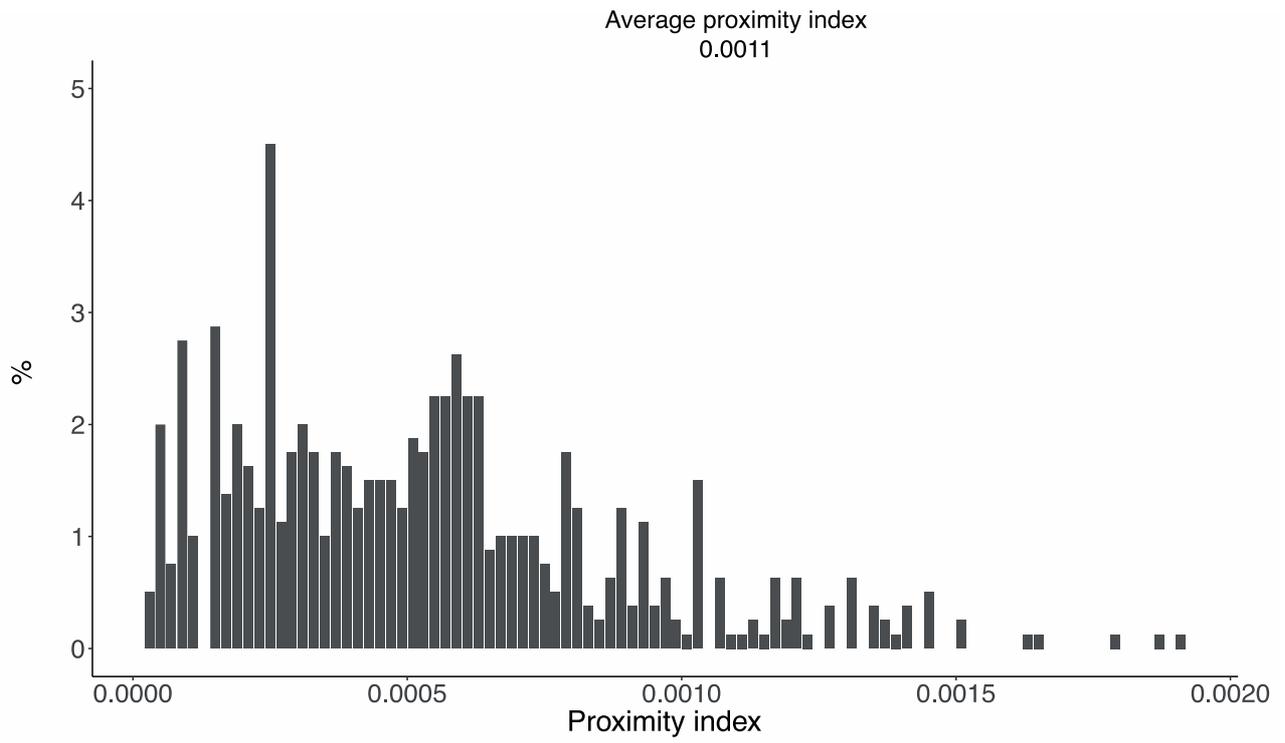


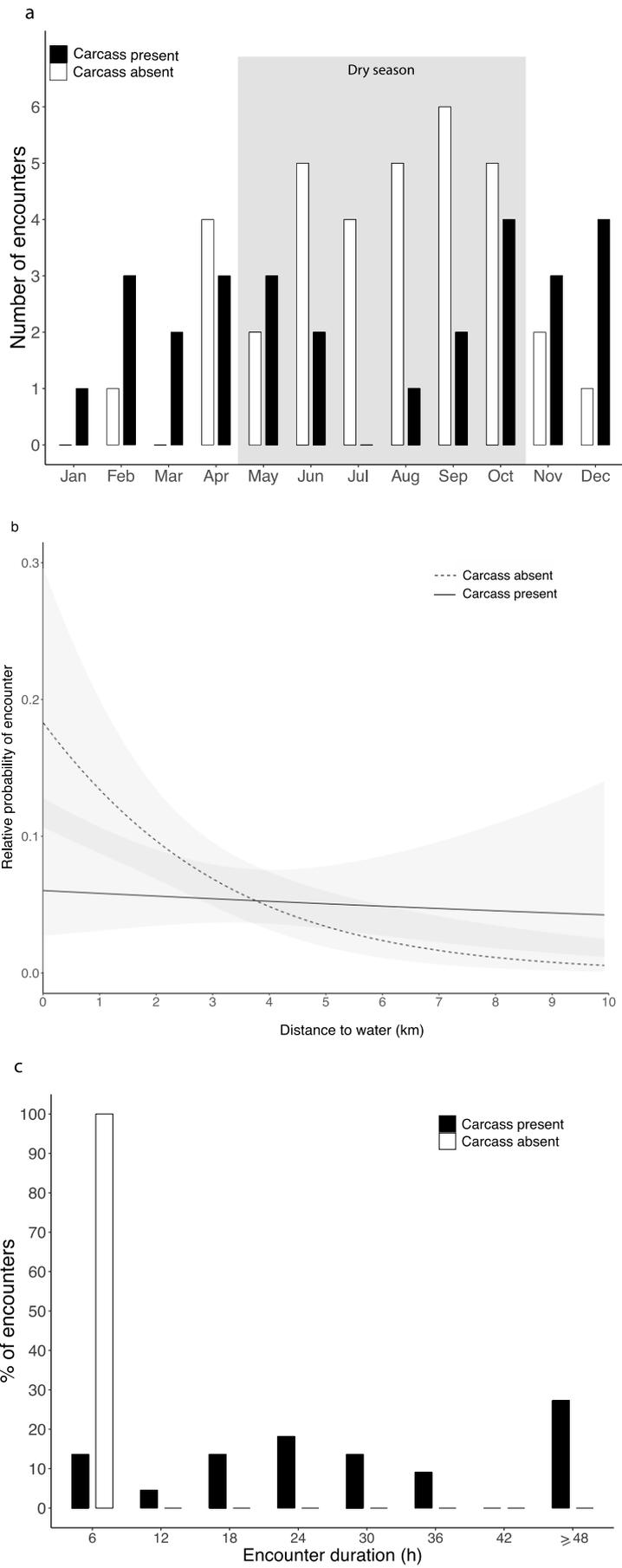


713 **FIGURE 2**

714

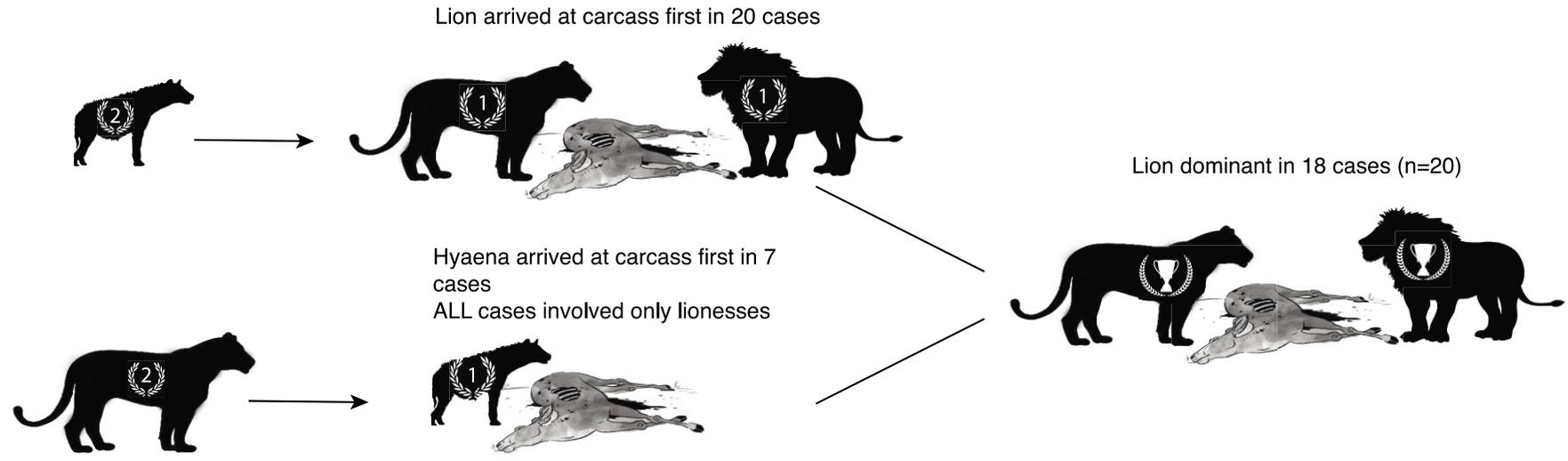
715





**FIGURE 4**

**Encounters in the PRESENCE of a carcass (n=28)**



**Encounters in the ABSENCE of a carcass (n=35)**

