Dynamic interactions between apex predators reveal contrasting seasonal attraction patterns

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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.

ABSTRACT

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

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

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

INTRODUCTION

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

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

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

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

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

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

MATERIAL AND METHODS

Study area

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

Predator GPS data

From July 2009 to October 2013, nine adult hyaenas (eight females and one male) belonging to 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 ±
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 ≥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

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

Encounter characteristics

Seasonality – Each encounter was attributed to the wet or dry season based on the date when it occurred. We used a Chi^2 test to test for the effects of the presence of a carcass on the seasonality of encounters.

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

Duration - The duration of an encounter in the presence of a carcass was defined as the time elapsed between the first and the last proximal fixes still associated with the given carcass (≤200m), even if they were separated by several hours and interspersed with some non-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 (≤ 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 (≤ 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 ± 10° (case of
259 "strong attraction"); +0.5 if the step of species A was directed toward the step of species
260 B ± 30° - 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 (± 10°) (case of "strong avoidance"); -
262 0.5 when the step of species A was directed opposite the step of species B ± 30° - 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 (≤200 m) before
281 moving away (even if it came back to the carcass at a later stage during the encounter), the

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

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

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

We tested for a significant difference in the speed at which lions and hyaenas moved before 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 ± 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±
319 0.0023 (range=0-0.0107, n=90). The average of the randomly generated proximity index was
320 lower (0.0005±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

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

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

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

Which species provoked the encounter?

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

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

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

Which species was dominant over the encounter?

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

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

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

DISCUSSION

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

Wet season: time for intraguild facilitation

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

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

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

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 kleptoparatism 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

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

Limits and future directions

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

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

Conclusion

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

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685

FIGURES CAPTIONS

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

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

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

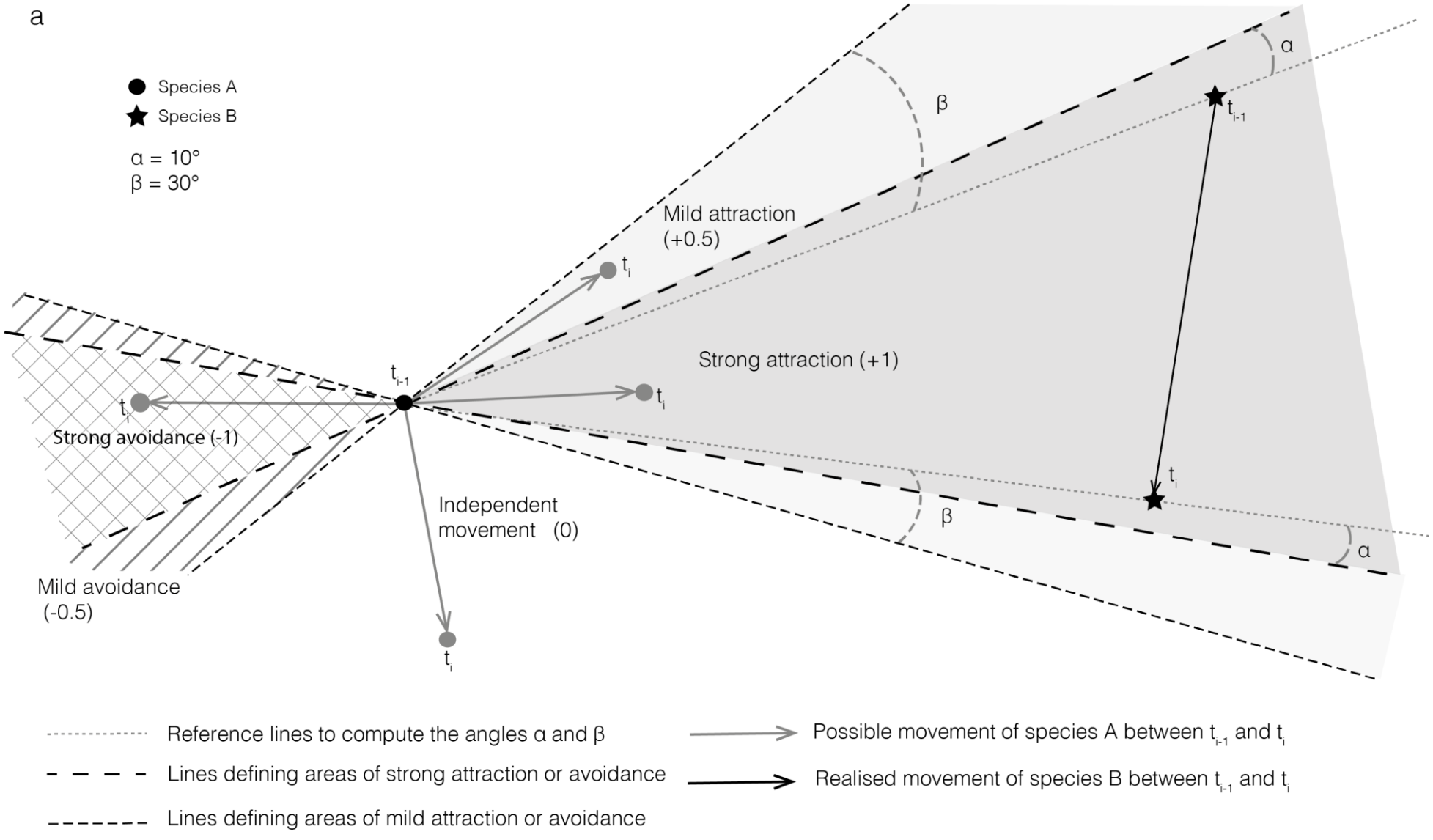
Figure 3: a) Monthly distribution of encounters between hyaenas and lions depending on the presence or absence of a carcass.

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

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

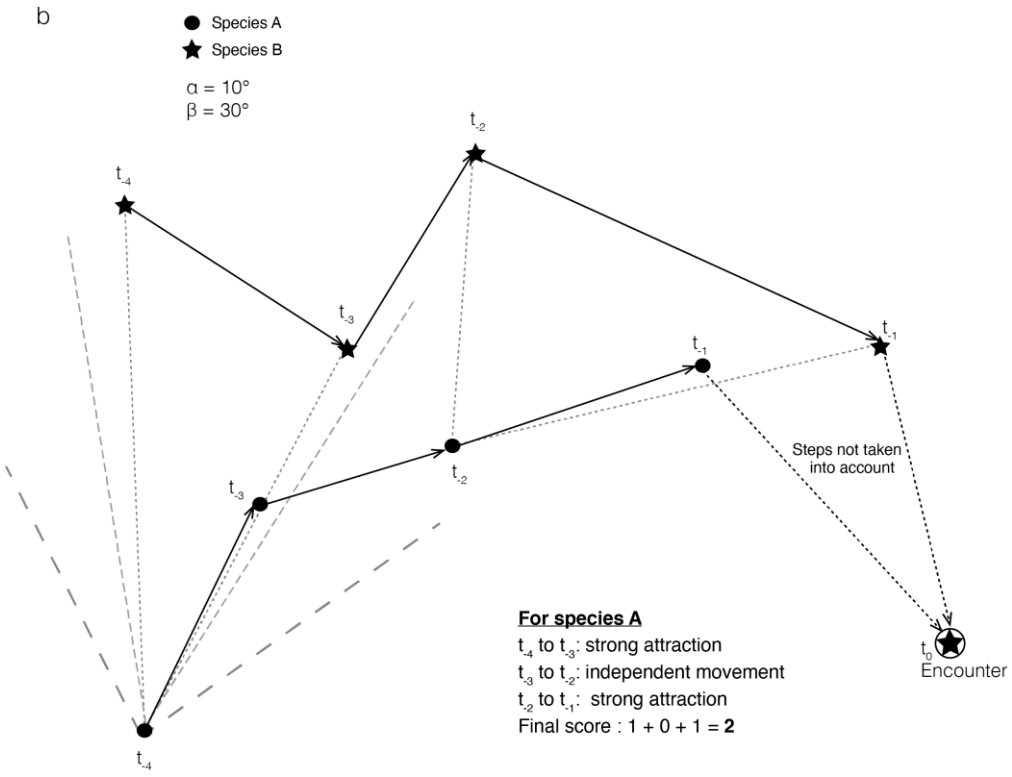
Figure 4: Creation and outcome of encounters occurring in the presence versus absence of a carcass between hyaenas and lions.

709 **FIGURE 1A**



710

711 **FIGURE 1B**



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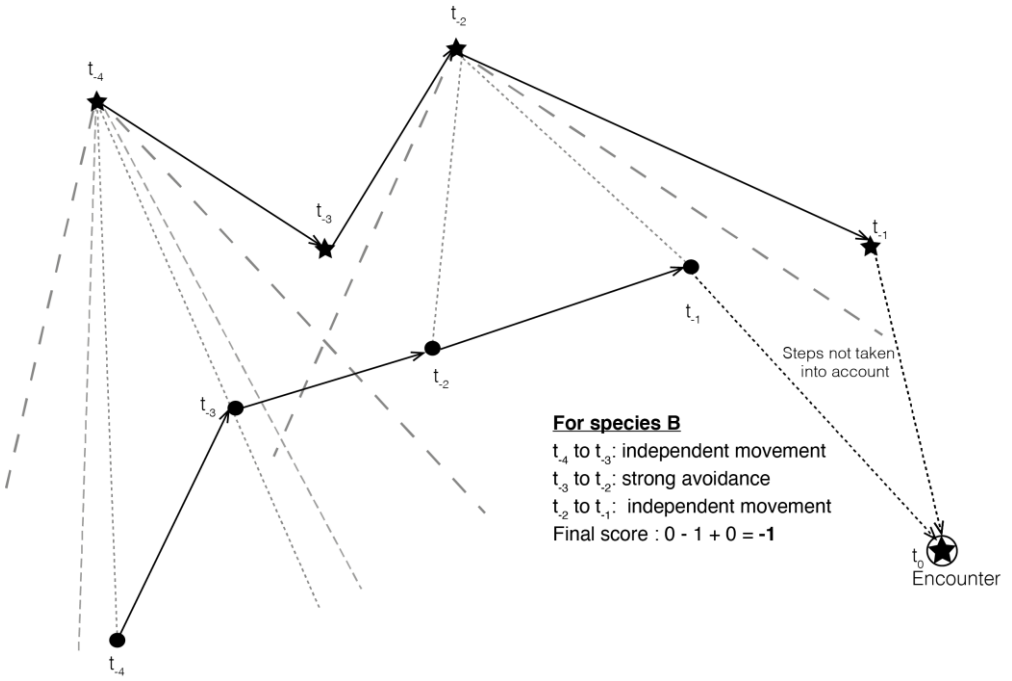

713 **FIGURE 2**

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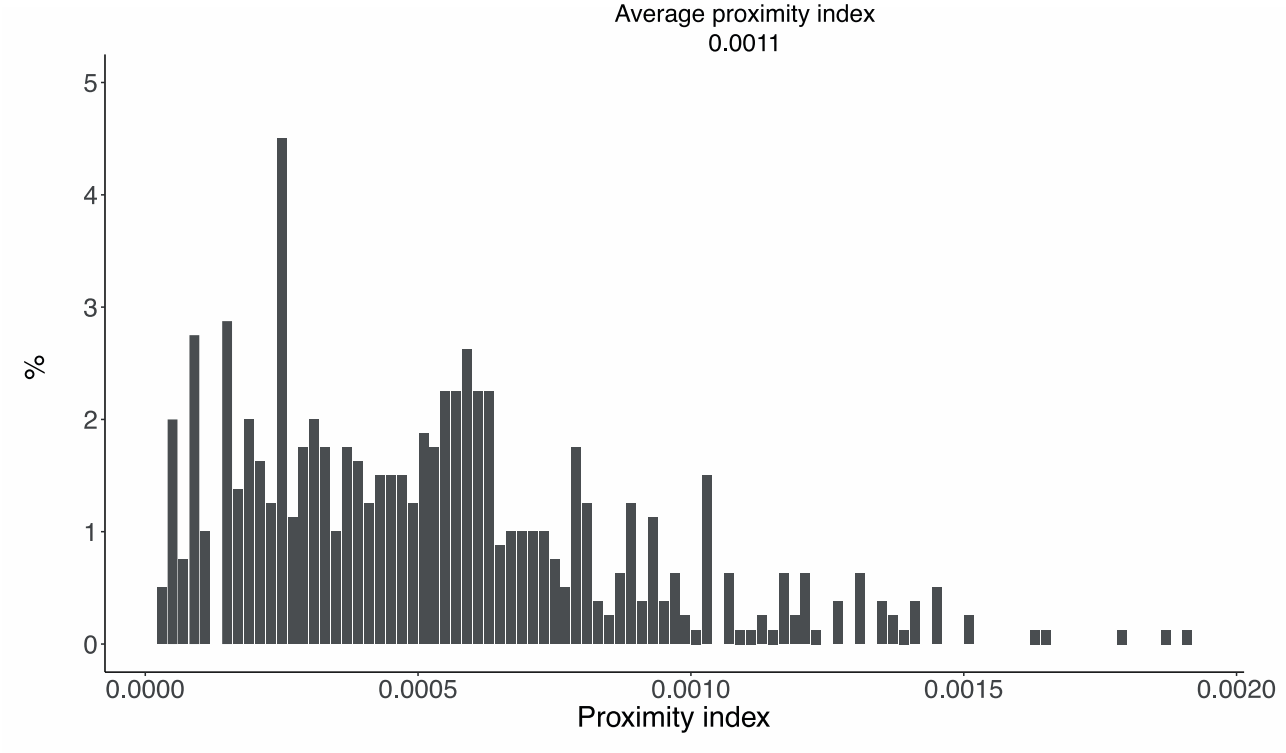
715



716 **FIGURE 3**

717

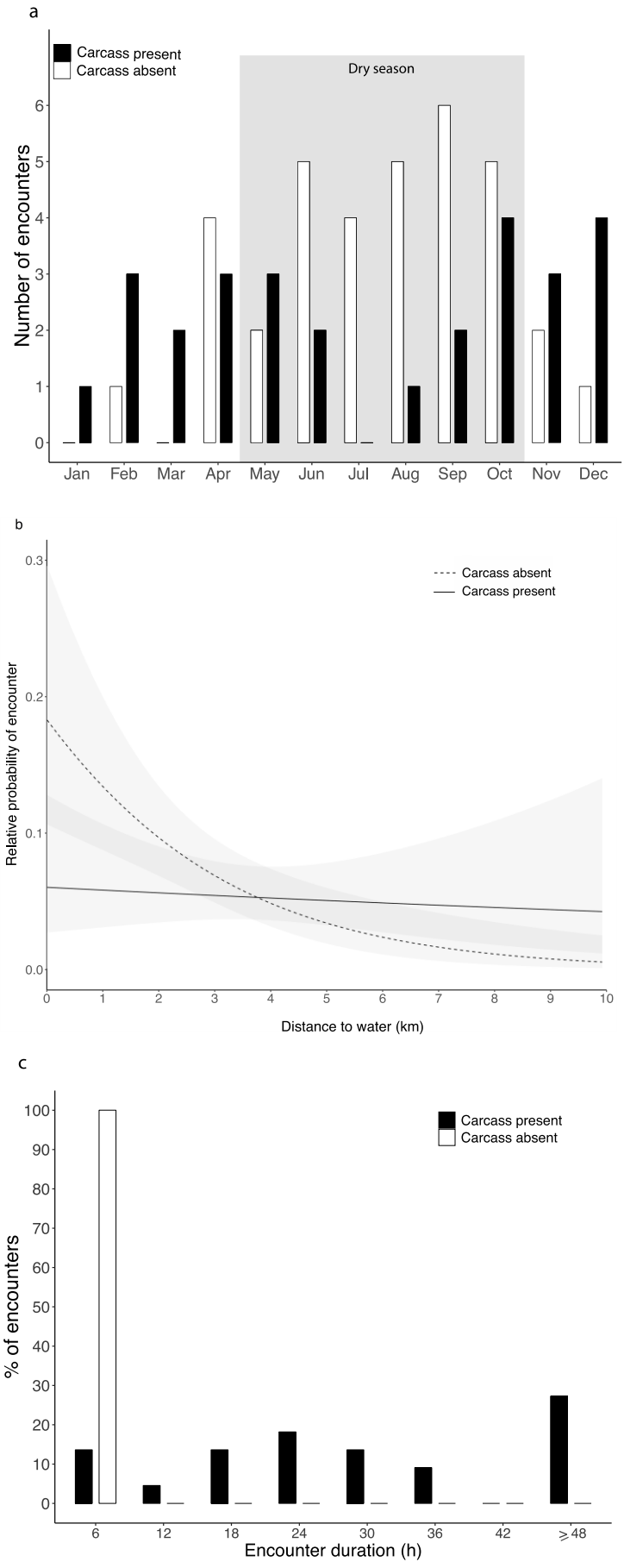
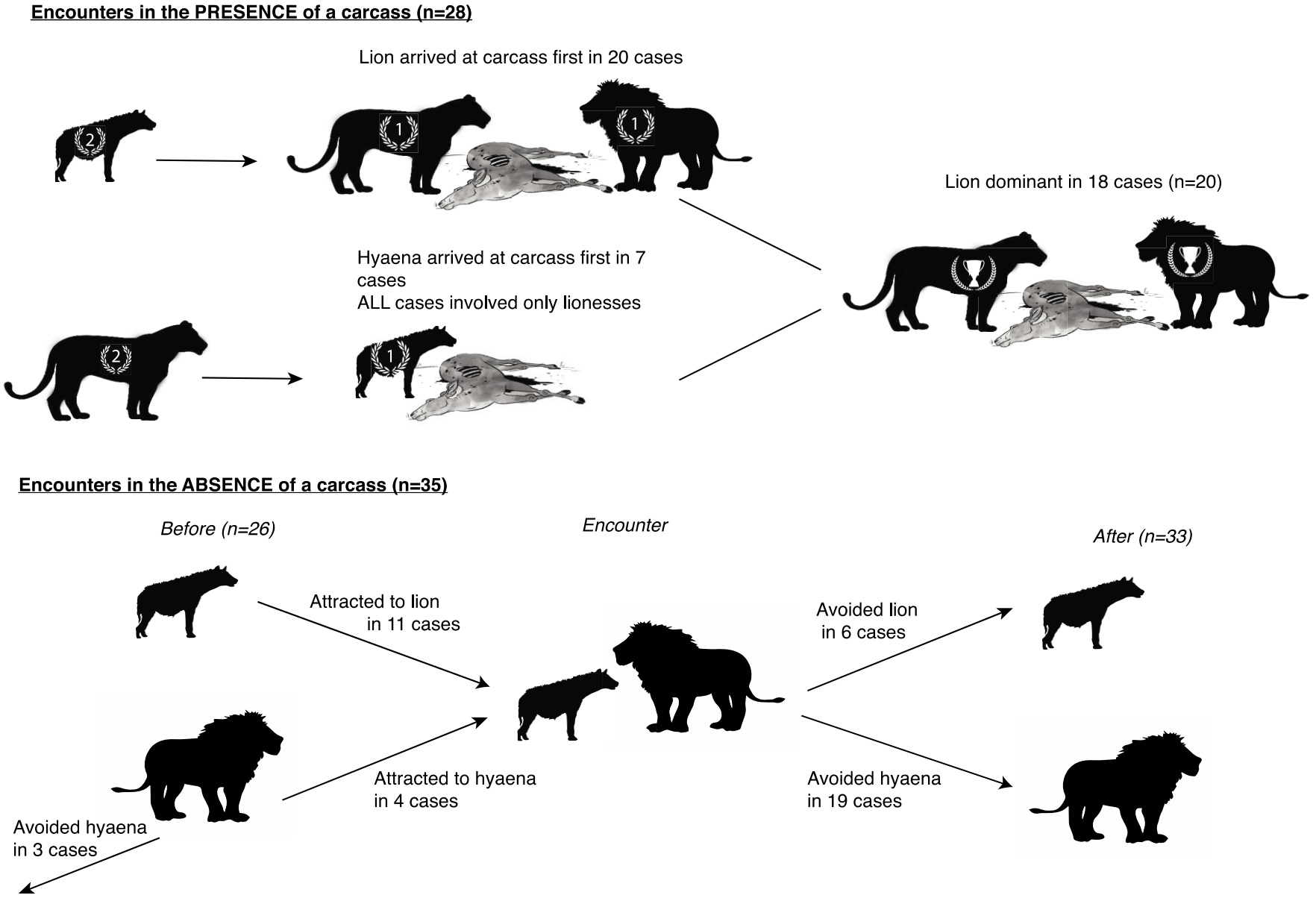


FIGURE 4


Encounters in the PRESENCE of a carcass (n=28)
Lion arrived at carcass first in 20 cases
Hyaena arrived at carcass first in 7 cases
ALL cases involved only lionesses
Lion dominant in 18 cases (n=20)
Encounters in the ABSENCE of a carcass (n=35)
Before (n=26)
Encounter
After (n=33)
Attracted to lion in 11 cases
Attracted to hyaena in 4 cases
Avoided hyaena in 3 cases
Avoided lion in 6 cases
Avoided hyaena in 19 cases