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1 **Large carnivore dangerousness affects the reactive spatial response of prey**

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24

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30

31 **Conflict of interest**

32 The authors declare that they have no conflict of interest.

33

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35 The data used in this study is archived and available from a dryad repository.

36

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Authors' contributions

Elise Say-Sallaz: Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Simon Chamaille-Jammes:** Conceptualization (equal); Supervision (supporting); Data curation (equal); Funding acquisition (equal); Project administration (equal); Investigation (equal); Methodology (equal); Writing – review and editing (supporting). **Stéphanie Périquet:** Data curation (equal); Writing – review and editing (supporting). **Andrew J. Loveridge:** Data curation (equal); Funding acquisition (equal); Project administration (equal); Writing – review and editing (supporting). **David W. Macdonald:** Funding acquisition (equal); Writing – review and editing (supporting). **Antony Antonio:** Data curation (equal); Writing – review and editing (supporting). **Hervé Fritz:** Data curation (equal); Funding acquisition (equal); Project administration (equal); Writing – review and editing (supporting). **Marion Valeix:** Conceptualization (equal); Supervision (lead); Methodology (equal); Investigation (equal); Writing – original draft (supporting); Writing – review and editing (equal).

75 **Abstract**

76 Predators differ through different attributes: their body size, sociality, speed, preferred prey
77 size, hunting mode, etc. Altogether these characteristics contribute to shape an overall
78 dangerousness, which is likely to underlie the variations in the nature and strength of a prey
79 anti-predator responses. This link, although somehow intuitive, has been rarely quantified in
80 natural ecosystems.

81 The goal of this study is to compare the antipredator response of a prey to two predators with
82 contrasting dangerousness in large terrestrial mammals, focusing on the less studied reactive
83 spatial response. We assessed if plains zebras' (*Equus quagga*) reactive spatial response
84 differed after an encounter with African lions (*Panthera leo*) or spotted hyaenas (*Crocuta*
85 *crocuta*). We expected lions to be perceived as more dangerous and hence to induce a
86 stronger reactive spatial response than hyaenas.

87 Using data from GPS collars deployed simultaneously on the three species, we studied the
88 reactive spatial responses of zebras after coming into close proximity to either predator.

89 We found that zebras responded differently, and more strongly to lions than to hyaenas.
90 Indeed, zebras were twice more likely to flee after an encounter with a lion than a hyaena and,
91 immediately after an encounter with a lion, zebras moved on average faster and further than
92 after an encounter with a hyaena.

93 The results of this study are consistent with a correlation between the predator dangerousness
94 and the strength of the prey anti-predator response. Future studies covering other pairs of
95 large carnivores are needed to rigorously assess the role of the different predator attributes
96 (body size, speed, preferred prey, and hunting mode).

97

98 **Keywords:** African lion, antipredator response, ecology of fear, plains zebra, predator-prey
99 interactions, spotted hyaena.

100 **Introduction**

101 Most species alter their behaviour in response to changes in predation risk (Lima & Dill,
102 1990). For instance, in ungulates, these responses are as diverse as increased vigilance
103 (Hunter & Skinner 1998), altered grouping strategies (Creel & Winnie, 2005), relocation to
104 safer areas (Fortin et al., 2005), changes in diel activity rhythms (Valeix et al., 2009), and
105 combinations of these (Creel et al., 2014; Courbin et al., 2019). While prey antipredator
106 behavioural responses have been well described for a variety of predator-prey systems and
107 their interactions theoretically investigated (Mitchell & Lima, 2002; Patin et al., 2019), we
108 know very little about the factors underlying the variations in the nature and strength of these
109 responses in natural ecosystems.

110 Not all predatory species are the same and understanding how their characteristics may
111 influence prey anti-predator responses may shade light on some of these variations. Indeed,
112 predators differ through their body size, sociality, speed, preferred prey size, and hunting
113 mode, which all have the potential to play a role in predator-prey interactions, with larger,
114 quicker, social forager, and ambush predators perceived as the most dangerous ones (Thaker
115 et al., 2011; Chamailé-Jammes et al., 2014; Makin et al., 2017; Cuthbert et al., 2020; Hirt et
116 al., 2020). Besides, a response that is efficient toward a predator may not serve as an efficient
117 defence against another one (Leblond et al., 2016). For all these reasons, prey are unlikely to
118 respond the same way to different predators (Relyea, 2001). Studies assessing the effect of
119 several sympatric predators are lacking (Say-Sallaz et al., 2019; Montgomery et al., 2019) and
120 needed if we want to understand the role of predator dangerousness in general, and of
121 predator attributes in particular (e.g., body size, speed, hunting mode), on prey anti-predator
122 behaviour.

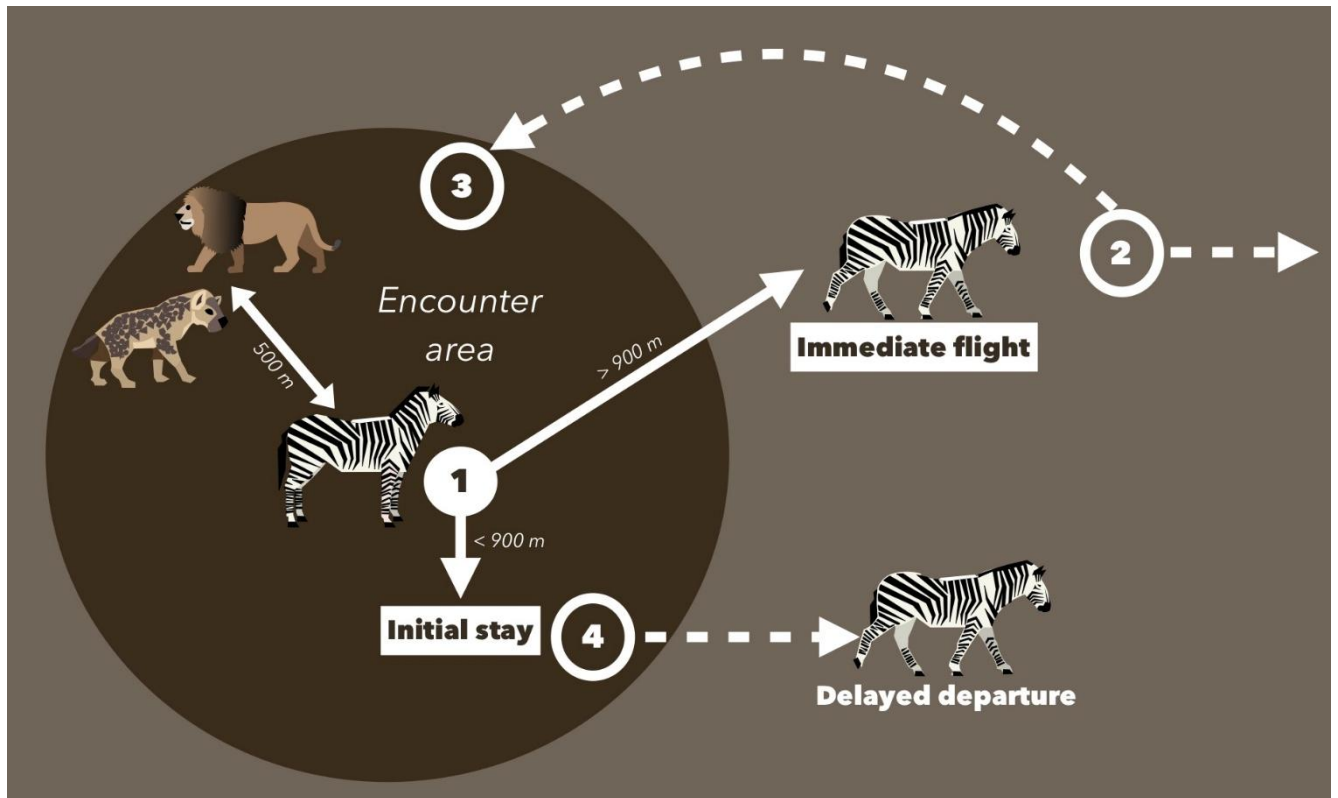
123 Our work contributes to fill this gap. Using GPS data acquired simultaneously on plains
124 zebras *Equus quagga* and their two main predators, lions and spotted hyaenas *Crocuta*

125 *Crocuta*, we explored whether the reactive spatial response of zebras is influenced by the
126 predator species encountered. Most studies investigating the role of the predator species on
127 prey responses in large mammals considered proactive responses, i.e., when prey modify their
128 behaviour in response to an a priori assessment of the level of risk based on the cumulative
129 knowledge a prey has of its environment (independently from the actual presence of the
130 predator; e.g., Thaker et al. 2011; Makin et al. 2017). In this work, we assessed the much less
131 studied reactive response, i.e., when prey detect the presence of a predator assimilated to an
132 immediate threat (either an attack, an impending attack, or the mere presence of the predator
133 that may decide to launch an attack an any time). Lions are more than twice the body size of
134 hyaenas, and in general the level of threat posed by lions on zebras can intuitively be
135 considered as higher than the level of threat posed by hyaenas. Further lions are ambush
136 predators, whereas hyaenas are cursorial predators. Following the same logic as the one
137 developed in the existing literature on the role of predator cues for proactive responses
138 (Preisser et al., 2007; Thaker et al., 2011; Miller et al., 2014), we made the assumption that
139 lions, ambush predators, are more likely to stay in a given area than hyaenas, cursorial
140 predators that can chase down their prey over long distances, and hence the detected presence
141 of a lion should be more strongly associated to the probability of presence of this predator in
142 the near future. Consequently, we hypothesized that zebras should display stronger reactive
143 spatial responses to encounters with lions (larger and ambush predators, which are expected to
144 be perceived as more dangerous) than to encounters with hyaenas.

145 To test this hypothesis, we specifically addressed 4 questions corresponding to different steps
146 in the reactive spatial response of zebras (Fig. 1, see “Materials and Methods” for details): (1)
147 Does a zebra leave an area more often after an encounter with a lion than with a hyaena?; (2)
148 When a zebra leaves an encounter area, does it do so at a higher speed and does it go further
149 away after an encounter with a lion than with a hyaena?; (3) For a zebra leaving an encounter

150 area, does it come back to the same area after a longer interval after an encounter with a lion
151 than with a hyaena?; (4) For a zebra that initially stayed in the encounter area, does it stay
152 longer in this area following an encounter with a hyaena than after one with a lion?

153 **Figure 1**



154

155 **Figure 1:** Temporal dynamics of the reactive spatial response of zebras after an encounter
156 with a predator (i.e., zebra and predator simultaneously located less than 500m apart). Once
157 an encounter with a predator has occurred at a specific location, a zebra has two options for its
158 short-term spatial response (<2h) (1): either it leaves the encounter area (defined as the area
159 within 900m of the encounter) or it stays. At a longer time scale, a zebra that left the
160 encounter area can move more or less far from the encounter area (2) and either never return
161 or come back to the encounter area (3). For a zebra that initially stayed in the encounter area,
162 it can either stay for a long period (4) in the encounter area or initiate a delayed departure.

163

164 **Materials & Methods**

165 *Study area*

166 The study area is Hwange National Park, a large unfenced protected area (~15 000 km²)
167 located in western Zimbabwe (19°00'S, 26°30'E). This ecosystem is characterized by a
168 dystrophic (low nutrient soil) semi-arid savanna where the vegetation is dominated by
169 bushlands and woodlands with small patches of grasslands (Arraut et al., 2018). The main
170 woody plant species are *Baikiaea plurijuga*, *Colophospermum mopane*, *Terminalia sericea*,
171 *Acacia* spp. and *Combretum* spp. (Arraut et al., 2018). The long-term mean annual rainfall is
172 600mm (\pm 30% CV), with most rains falling between November and April. The surface water
173 available to animals is found in natural waterholes, which dry up as the dry season progresses,
174 as well as in artificially supplied waterholes pumped throughout the dry season. The study
175 was conducted in the Main Camp region of the Park (~1 200 km²). There, zebra density is
176 estimated to be around 1 indiv./km² (Grange et al., 2015), lion density around 4 indiv./100
177 km² (Loveridge et al., 2016), and hyaena density around 9 indiv./100 km² (Périquet 2014).
178 Zebras are predated by both predators, accounting for 8-9% of lion kill sites (Davidson et al.,
179 2013) and 11% of hyaena scat samples (Périquet et al., 2015). Predation has been suggested
180 as the main ecological process causing low survival in this zebra population (Grange et al.,
181 2015).

182 *Data*

183 Thirty-two female adult zebras from different harems were equipped with GPS collars, which
184 recorded a location every hour or 30 minutes (we used only one location per hour for the
185 analyses) between August 2009 and July 2015. Zebras were equipped for a mean of 387 (\pm
186 256 SD) days. During this 6-year period, in the area used by the studied zebras, 14 lions (from
187 9 different prides/coalitions) and 7 hyaenas (from 3 different clans) were also equipped with

188 GPS collars recording hourly locations. Lions were equipped for a mean of 492 (\pm 580 SD)
189 days, and hyaenas for a mean of 453 (\pm 370 SD) days. The capture and collaring of zebras,
190 lions and hyaenas were performed by qualified personnel, under permits from Zimbabwe
191 Parks and Wildlife Management Authority, using standard protocols for these species (see
192 Ethical notes for details).

193 *Ethical note*

194 The collaring exercises on the three species were part of three separate long-term monitoring
195 projects. Animals from different species were captured neither at the same location nor at the same
196 time. Permissions were provided by the appropriate agencies (Zimbabwe Parks and Wildlife
197 Management Authority, Wildlife Drugs Sub-committee of the Drugs Control Council of Zimbabwe
198 and Zimbabwe Veterinary Association, Wildlife Group, and licenses to acquire, possess and
199 administer game capture drugs/dangerous drugs) and permits were issued for each monitoring protocol
200 (lions' monitoring permits: REF:DM/Gen/(T) 23(1)(c)(ii):713/12/01, 03/2002, 07/2003, 20/2004,
201 01/2005, 01/2007, 03/2008, 03/2009, 25/2010, 06/2011, 12/2012, 08/2013, 51/2014, 10/2015; Spotted
202 hyaenas' monitoring permit: [ZPWMA, 23(1)(c)(ii)15/2012-2013]); zebras' monitoring permit:
203 REF:DM/Gen/(T) 23(1) (c)(ii): 03/2009, 01/2010, 25/2010, 05/2011, 06/2011, 12/2012, 15/2012,
204 08/2013). Relevant animal care protocols were followed during capture and collaring of all the
205 animals, which were under chemical immobilization/anesthesia during the collaring. Drugs were
206 administered by trained project personnel who attended and successfully passed the Zimbabwe
207 wildlife capture and handling course, and who held a dangerous drug license (renewed annually
208 through the Wildlife Veterinary Association and administered by Medicines Control Authority,
209 Zimbabwe). Also, animal capture and collaring followed the ASAB/ABS guidelines for the Use of
210 Animals in Research.

211 Lions were equipped with GPS collars from Televilt/Followit Positioning (AB, Lindesberg,
212 Sweden, or African Wildlife Tracking, Pretoria, South Africa) or Sirtrack Ltd. (Havelock North, New
213 Zealand), the GPS collars weighed between 600 and 900 g, which represent 0.6 and 0.9%,

214 respectively, of the smallest individual captured (100 kg). Spotted hyaenas were equipped with GPS
215 radio-collars with UHF download and VHF transmitter from African Wildlife Tracking (model: UHF
216 407). The GPS collars fitted weighed 1kg, which represents 1.2%, of adult female hyaena body weight
217 (60kg). Zebras were equipped with GPS radio-collars with UHF download and VHF transmitter from
218 Africa Wildlife Tracking or Vectronics (Vectronics Aerospace GmbH, Berlin, Germany). Fitted
219 collars always weighted less than 1kg, which would be less than 0.5% of the body weight of a 200kg
220 adult female zebra.

221 All the animals were immobilized by chemicals, they were darted from the ground using Dan
222 Inject J.M.SP.25 CO₂ powered dart guns, hence drugs were administered by intramuscular injection
223 (shoulder or rump) and were species specific. For lions and hyaenas, a bait was used to attract the
224 targeted individuals and to be in a position to dart them, hence there was no pursuit of the animal
225 before the immobilization. Zebras were darted once sighted from a vehicle. Lions received the
226 dissociative anaesthetic Zoletil; dosage: 0.83-0.32 (range 0.53e1.38) mg/kg; manufacturer: Virbac
227 RSA, Halfway house, South Africa, and sedative (Medetomidine (Zalopine/Domitor); dosage 1/4 0.05
228 0.01 (range 0.04e0.06); manufacturer: Novartis, Isando, South Africa or Orion Pharma, Turku,
229 Finland), Hyaenas received a standard mix of 500 mg Ketamine (Kyron laboratories Pvt. Ltd, Ben-
230 rose, RSA) and 200 mg Xylazine (Rompun; Bayer, Leverkusen, Germany) or of 80 mg Zoletil (Virbac
231 RSA, Halfway House, RSA) and 4 mg Medetomidine (Zalopine, Wildlife Pharmaceuticals, Karino,
232 RSA). Zebras received a standard mix of 6mg of Etorphine (Captivon®, Wildlife pharmaceuticals
233 (Pty) Ltd., Mpumalanga, South Africa) and 48 mg of Azaperone (Wildlife pharmaceuticals (Pty) Ltd.,
234 Mpumalanga, South Africa). It took about 7-8 minutes for the animals to be immobilized after the
235 drugs were administered, then the eyes were covered and ear plugs fitted to reduce stimuli and stress
236 and the collars were fitted. For lions, an additional safety measure was taken by using a light leg
237 restraint in case of unexpected arousal of the animal. While animals were immobilized, blood and hair
238 samples were collected for hyaenas and lions (not for the purpose of this specific study but to optimize
239 the immobilization and prevent the need for other animals to be captured to answer different scientific
240 questions). Scat sample (when possible) were collected on hyaenas. The complete procedure could

241 take up to one hour maximum for all species. Then, immobilization drugs were reversed, for lions
242 drugs were reversed with Atipamezole (dosage 1/4 0.18 0.07 (range 0.01e0.28) mg/kg; manufacturer:
243 Farnos, Orion Corp., Finland or Novartis, Isando, South Africa), for hyaenas drugs were reversed
244 with 16 mg of Yohimbine (Rx drug, Kyron Labs, Benrose, RSA), and for zebras drugs were reversed
245 using 18mg of Diprenorphine (Wildlife pharmaceuticals (Pty) Ltd., Mpumalanga, South Africa). Once
246 drugs reversal were injected animals were monitored until their full recovery (meaning walking away
247 normally and joining back their group especially their harem for zebras), it took on average 20 minutes
248 post drug reversal injections for the individuals to fully recover, zebras were even standing up within
249 seconds after the drug reversal injections. No adverse effect has been recorded for any of the three
250 species. For all the species, fully grown adult were preferentially collared and when subadults were
251 collared, sufficient space was allowed to ensure that the collar did not become tight as the neck grew.
252 Non-pregnant females were preferably collared, early-stage pregnancy cannot be determined visually
253 but the immobilization drugs used have no known effect on unborn fetuses, are extremely safe and
254 widely used on wildlife.

255 All the collared individuals were monitored by being tracked from a vehicle. Collared lions
256 were located weekly to bimonthly from a vehicle or microlight aircraft. Positional data from the GPS
257 radio-collars were downloaded, and observations made of group composition. Collared hyaenas and
258 zebras were tracked from a vehicle using a four-element yagi antenna and VHF (Very High
259 Frequency) receiver (Icom IC-R20). Data from GPS collars were downloaded using a downloading
260 console and a USB UHF modem on a monthly basis whenever possible, either directly by the observer
261 or retrieved from automatic downloading stations (African Wildlife Tracking, range of download:
262 ~300 m) located at waterholes.

263 Collars were removed when batteries were flat, when collars were malfunctioning, or
264 deteriorations happened to ensure the safety of animals. For one zebra, the collar had slipped over the
265 ears of the animals and so was removed the day after the observation. Also, sometimes collars would
266 fall off due to the deterioration. If the collar did not fall off by itself (or with the help of a drop-off

267 systems that were controlled using UHF signals for certain zebras' collars) collars were removed using
268 the same immobilization procedure as described before.

269

270 *Analyses*

271 *Definition of encounters* - We assumed that a zebra encountered a predator when they were
272 simultaneously located less than 500m apart (as in Courbin et al., 2016; this distance
273 threshold appears a good balance between a biologically meaningful threshold for this work
274 and a cut-off point that allows reasonable sample sizes; we preliminarily checked that the
275 results of this work were qualitatively robust if we would have used a shorter distance, and
276 that there was no effect of the distance between the zebra and its predator on the results). For
277 consecutive pairs of simultaneous locations less than 500m apart, the first pair was considered
278 as the encounter. We only considered night encounters (between 6pm and 6am) since this is
279 when lions and hyaenas are active and likely to be hunting (Hayward & Slotow, 2009). In the
280 subsequent analyses, we included only individual zebras that encountered both predators
281 during the period they were tracked. This was the case for 15 zebras. We identified 68
282 encounters between a zebra and a lion, and 90 encounters between a zebra and a hyaena.

283 *Definition of controls* - For each encounter between a zebra and a predator, we randomly
284 selected 10 locations of the same zebra that occurred at the same time but at a different date.
285 We made sure that these randomly selected locations were not from a night during which an
286 encounter with another GPS-collared predator occurred. The effect of undetected predators
287 should mainly reduce our capacity to detect differences in zebra spatial response between
288 encounters and controls.

289 *Description of environmental variables* - For each encounter and control location, we
290 extracted:

291 (1) the distance to the closest waterhole. Waterhole areas are considered hotspots of
292 predator-prey interactions in the Hwange ecosystem (Valeix et al., 2009; Périquet 2014;). We
293 were interested in contrasting zebra responses in the vicinity or away from waterholes, and
294 thus used a simple dichotomy for the variable ‘distance to water’ (referred as ‘water’ in the
295 equations below): ‘close’ (≤ 1 km from a waterhole) vs “distant” (> 1 km from a waterhole).

296 (2) the vegetation type (referred as ‘vegetation’ in the equations). Based on the
297 vegetation structure map by Arraut et al. (2018), we contrasted two types of vegetation: ‘open
298 vegetation’ (corresponding to the class ‘grassland’ in the original map) and ‘dense vegetation’
299 (corresponding to the classes ‘bushed grassland’, ‘bushland’, ‘woodland’, ‘mopane
300 woodland’, and ‘woodland evergreen’ in the original map).

301 (3) the period of the night (referred as ‘night’ in the equations), classified as either the
302 ‘beginning’ (between 6pm and midnight) or ‘end’ (between midnight and 6am) of the night.
303 At the ‘beginning’ of the night, prey, if not responding, will have to cope with the presence of
304 the predator for most of the night. In contrast, at the ‘end’ of the night prey only have to deal
305 with the presence of the predator for a few hours before it becomes much less dangerous after
306 dawn, as both predators are mainly active at night (Hayward & Slotow, 2009). We therefore
307 predicted that prey would be more likely to leave an encounter area at the ‘beginning’ of the
308 night than at the ‘end’.

309 We preliminarily assessed if encounters occurred in a specific subset of circumstances
310 (environmental conditions or time), compared to those generally experienced by zebras during
311 the night in order to assess if characteristics of the encounters varied between the two
312 predators. We detected no major difference. Details on the analyses and the results are
313 available in Appendix A.

314 *Describing the variability of the reactive spatial response* - For each encounter with a
315 predator (a lion or a hyaena) and for each control, we calculated the distance between these
316 locations and each zebra's location during the next 24h. Plotting the data revealed a high
317 variability of how zebras moved away from the locations with time (Appendix B), which led
318 us to decompose the spatial response of zebras to understand this variability (Fig. 1). Building
319 upon Courbin et al. (2016), who performed an unsupervised model-based clustering analysis
320 to classify the immediate response of zebras after an encounter with lions and found that the
321 best model was a two-cluster model (superior to the model with only one model), we first
322 identified two types of immediate spatial responses depending on whether zebras were further
323 than 900m from the encounter location 2 hours after the encounter ('immediate flight') or not
324 ('initial stay'). This 900m threshold distance defines the 'encounter area' hereafter, and was
325 the distance that best discriminated the two types of immediate responses in Courbin et al.
326 (2016). To assess whether the choice of the 2-hour time window affected the results, we ran
327 the subsequent analyses with a 1-hour and a 3-hour time window to preliminarily check that
328 the results were qualitatively the same. As this was the case, we present the results for the 2-
329 hour window only. This corresponds to step (1) in Fig. 1. We assessed whether this immediate
330 response was influenced by the predator species and the environmental variables. We then
331 investigated whether there were longer-term spatial responses. We specifically calculated, for
332 zebras that left the encounter area, the speed with which they left the area and at which
333 distance they moved away over 24 hours (step (2) in Fig. 1), and compared whether this
334 dynamic of the flight was influenced by the predator species. We further assessed how long it
335 took zebras that initially displayed a flight response to come back to an encounter area (step
336 (3) in Fig. 1). For zebras that initially stayed in the encounter area, we assessed whether
337 predator species or environmental variables influenced the time zebras spent ultimately in the
338 encounter area after the encounter (step (4) in Fig. 1).

339 *Statistical analyses*

340 *1. Short-term spatial response of zebras after a predator encounter* - We used a mixed
341 logistic regression to assess the probability that an encounter led to an ‘immediate flight’
342 response (coded 1) vs. an ‘initial stay’ response (coded 0) and if this probability was affected
343 by the predator species and the environmental variables (step (1) in Fig. 1):

$$P_{ij} = \frac{\exp(\beta_0 + \beta_p \text{predator}_{ij} + \beta_w \text{water}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij} + \gamma_{0j})}{1 + \exp(\beta_0 + \beta_p \text{predator}_{ij} + \beta_w \text{water}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij} + \gamma_{0j})}$$

344 (1)

345 Where P_{ij} is the probability of an ‘immediate flight’, i being the i^{th} observation and j the j^{th}
346 zebra. β_0 is the intercept, β_p is the estimated coefficient for the explanatory variable ‘predator
347 species encountered’ (abbreviated ‘predator’; a categorical variable with three levels: hyaena,
348 lion, and control), the others β are the estimated fixed regression coefficients for the
349 environmental variables, and γ_{0j} is the random effect on the intercept β_0 for zebra j .

350 *2. Temporal dynamics of the spatial response for zebras that performed an ‘immediate flight’*

351 – For ‘immediate flight’ responses (n=19 after an encounter with a hyaena and n=31 after an
352 encounter with a lion), we assessed if the predator species encountered influenced (i) the
353 speed with which the zebra left the encounter area, and (ii) how far the zebra went following
354 the ‘immediate flight’ response (step (2) in Fig. 1). The controls included in this analysis (and
355 the next one) are controls when zebras moved further than 900m in 2 hours, i.e., comparable
356 to an “immediate flight”. For each encounter or control location, we calculated, for each
357 hourly interval from 5h before to 24h after the location, the speed (meters/hour) of the zebra.
358 To assess how far zebras moved after a predator encounter, we calculated the net
359 displacement from the encounter or control location for each location over the same period
360 (5h before to 24h after the encounter or control location). We then compared the mean

361 difference of speed over each hourly interval (for all the encounters) and the mean difference
362 of net displacement between situations corresponding to encounters with a lion, encounters
363 with a hyaena and controls by using multiple means comparisons (Herberich et al., 2010).
364 Including data 5 hours before the encounter allowed comparing zebras' trajectories before and
365 after the encounter.

366 *3. Avoidance of the encounter area by zebras that performed an 'immediate flight' – For*
367 'immediate flight' responses, we calculated the time elapsed before coming back to the
368 encounter area (Appendix C, step (3) in Fig. 1). We chose to study this response only within a
369 72h-window following the encounter, to ensure that we were studying the actual prey
370 antipredator response. Indeed, the larger the time gap since the encounter is, the less likely it
371 is that zebras' trajectories are influenced by the predator encounter. For returns within 72
372 hours (which happened for 92% of the 'immediate flight' responses, Appendix C), we further
373 studied the drivers of this temporal dynamics of avoidance of the encounter area by using a
374 Poisson regression:

$$T_{ij} = \exp(\beta_0 + \beta_p \text{predator}_{ij} + \beta_w \text{water}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij})$$

375 (2)

376 *4. Time spent in the encounter area for zebras that initially stayed – For 'initial stay'*
377 responses (n=71 after an encounter with a hyaena and n=36 after an encounter with a lion, one
378 lion encounter was removed from the analysis as it was lethal), and for controls where zebras
379 initially stayed in the encounter area, we calculated the time spent in the encounter area
380 (Appendix D; step (4) in Fig. 1) and investigated if some factors influenced it using a mixed
381 negative binomial regression as it fitted the data better than the Poisson regression model:

$$S_{ij} = \exp(\beta_0 + \beta_p \text{predator}_{ij} + \beta_w \text{water}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij})$$

382 (3)

383 The goodness of fit of every model was assessed using the Hosmer-Lemeshow test (Hosmer
 384 & Lemeshow, 2000; see gof p-value in the results). All the statistical analyses were performed
 385 with the R software (version 3.6.1, Team, R core, 2021). We considered explanatory variables
 386 with p-value lower than 0.05 statistically significant.

387

388 **Results**

389 *1. Short-term spatial response of zebras after a predator encounter*

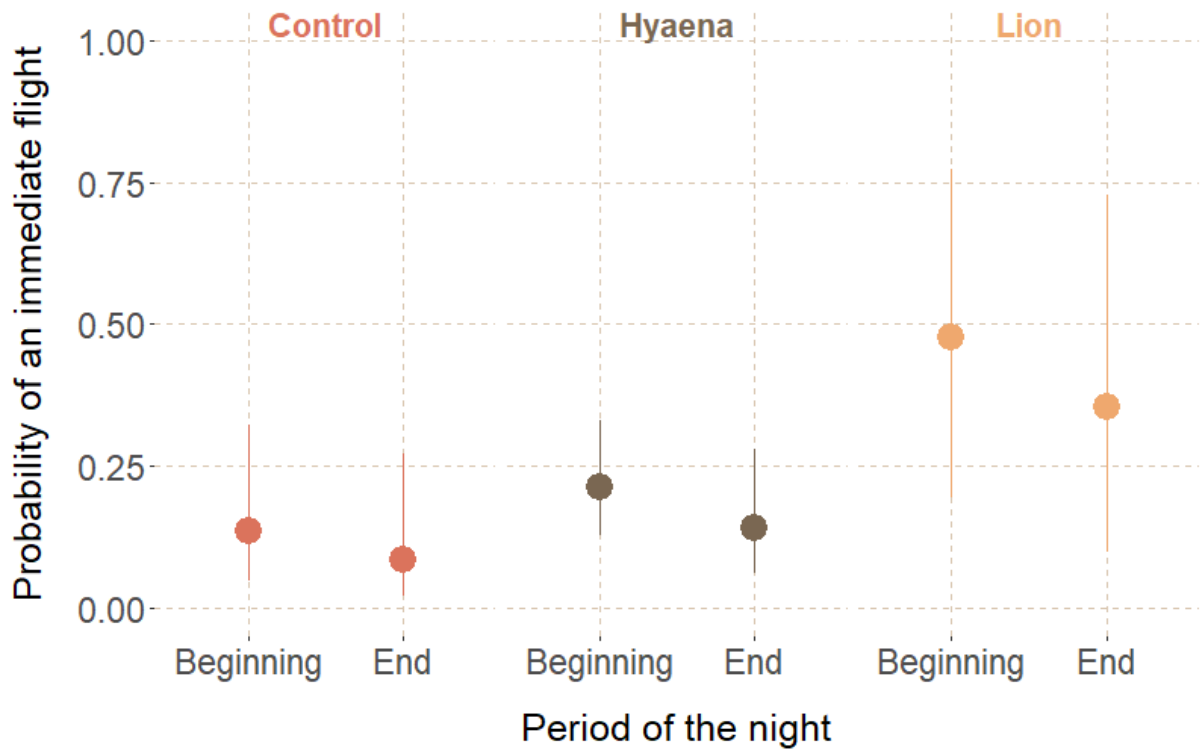
390 The probability of observing an “immediate flight” response was higher after an encounter
 391 with a lion (0.48 on average) than after an encounter with a hyaena (0.21 on average), both
 392 being higher than for control situations (0.14 on average, Table 1, Fig. 2). After an encounter
 393 with a predator, zebras went mostly in the direction opposite from the predator location during
 394 the encounter (Appendix E). The probability of an ‘immediate flight’ response was lower at
 395 the end of the night (Table 1, Fig. 2), but was not significantly affected by distance to water or
 396 the vegetation type where the encounter occurred (Table 1, gof p-value = 0.07).

397 Table 1: Estimates of the variables explaining the probability for a zebra to engage in an
 398 ‘immediate flight’ response within the 2 hours following an encounter with a predator (hyaena
 399 being the reference level for the predator variable). Significant values are in bold.

| | Estimates | Std. Error | z | pr(> z) | Confidence Interval | |
|-----------------------------|--------------|-------------|--------------|-----------------|---------------------|--------------|
| | | | | | 2.5% | 97.5% |
| Intercept | -1.30 | 0.31 | -4.18 | 2.95e-05 | -1.93 | -0.71 |
| Control (predator) | -0.55 | 0.27 | -2.04 | 0.0410 | -1.07 | -0.03 |
| Lion (predator) | 1.21 | 0.36 | 3.36 | 7.79e-04 | 0.51 | 1.93 |
| End (night period) | -0.51 | 0.14 | -3.68 | 2.30e-04 | -0.79 | -0.24 |
| Open (vegetation type) | 0.21 | 0.21 | 1.00 | 0.318 | -0.21 | 0.61 |
| Distant (distance to water) | 0.27 | 0.19 | 1.38 | 0.168 | -0.10 | 0.66 |

400

401 **Figure 2**



403

404

405 **Figure 2:** Probability (calculated from the model estimates, with error bars representing the
 406 95% confidence intervals) for a zebra to leave the encounter area in the 2 hours following an
 407 encounter with a predator ('immediate flight') according to the period of the night
 408 ('Beginning' or 'End'). Probabilities were calculated for the default values of the other
 409 variables (i.e., when close to water and in a dense vegetation)

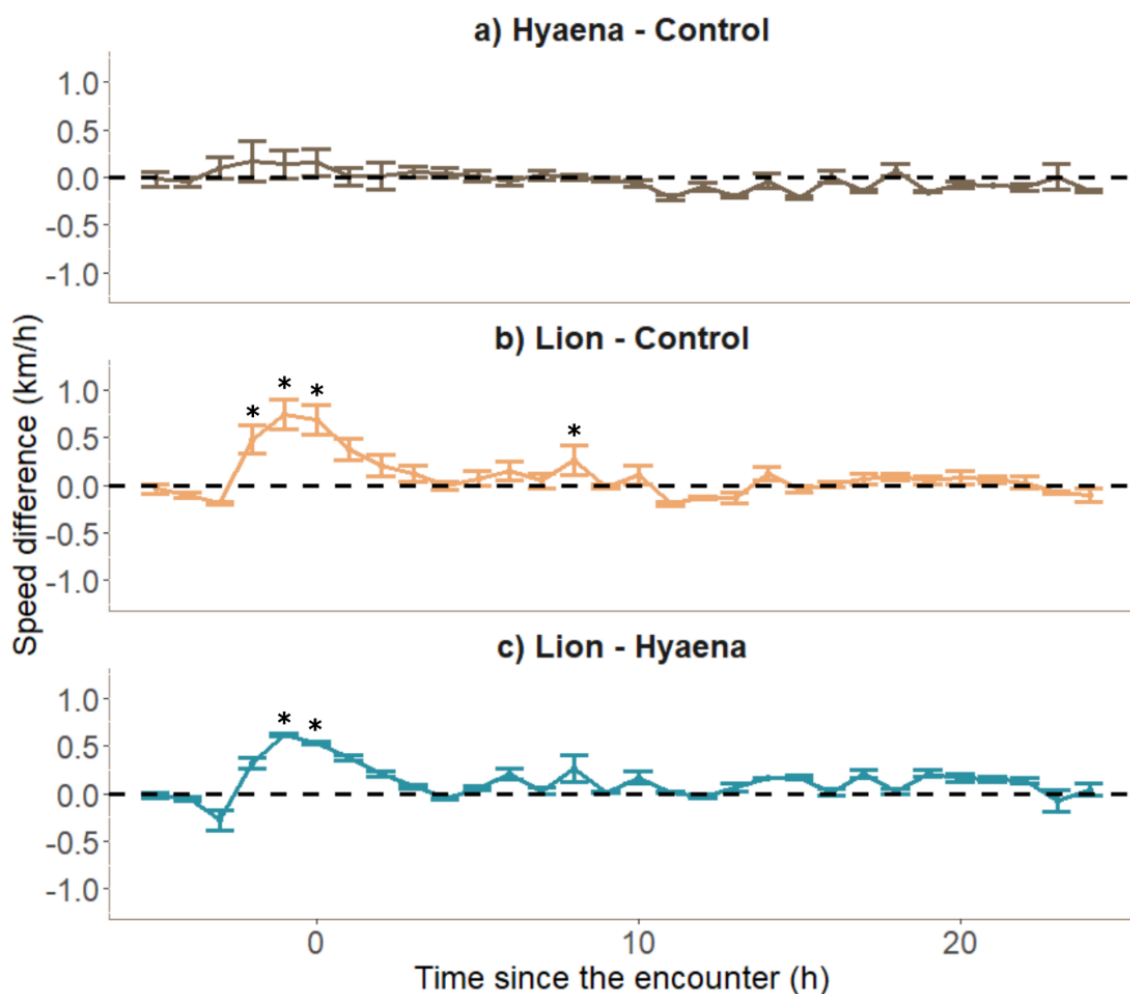
410 2. *Temporal dynamics of the spatial response for zebras that performed an 'immediate*
 411 *flight'*

412 Zebras that fled immediately after an encounter with a hyaena did not move on average faster
 413 than during control situations as no mean speed difference at any time period is significant
 414 (mean speed \pm SD = 1010 \pm 838 m/h and 854 \pm 741 m/h respectively; p-value=0.87; Fig. 3 a).
 415 After an encounter with a lion, zebras immediately moved on average faster (mean speed \pm
 416 SD =1544 \pm 1198 m/h) than after a control (mean speed \pm SD =854 \pm 741 m/h, Fig. 3 b, p-

417 value = $0.4e-05$), or than after an encounter with a hyaena (mean speed \pm SD = 1010 ± 838
418 m/h, Fig. 3 c, p-value=0.03). We also detected a significant mean speed difference for the
419 hour preceding the encounter (Fig. 3b, c). This is most probably because an encounter is
420 defined from simultaneous hourly GPS fixes and the actual encounter may have occurred
421 within the hour preceding the acquisition of these fixes. Afterwards, mean speed differences
422 between lion encounters and hyaena encounters or controls were not significant, indicating
423 that a higher mean speed characterized only the hour following the encounter (Fig. 3).

424 **Figure 3**

425



426

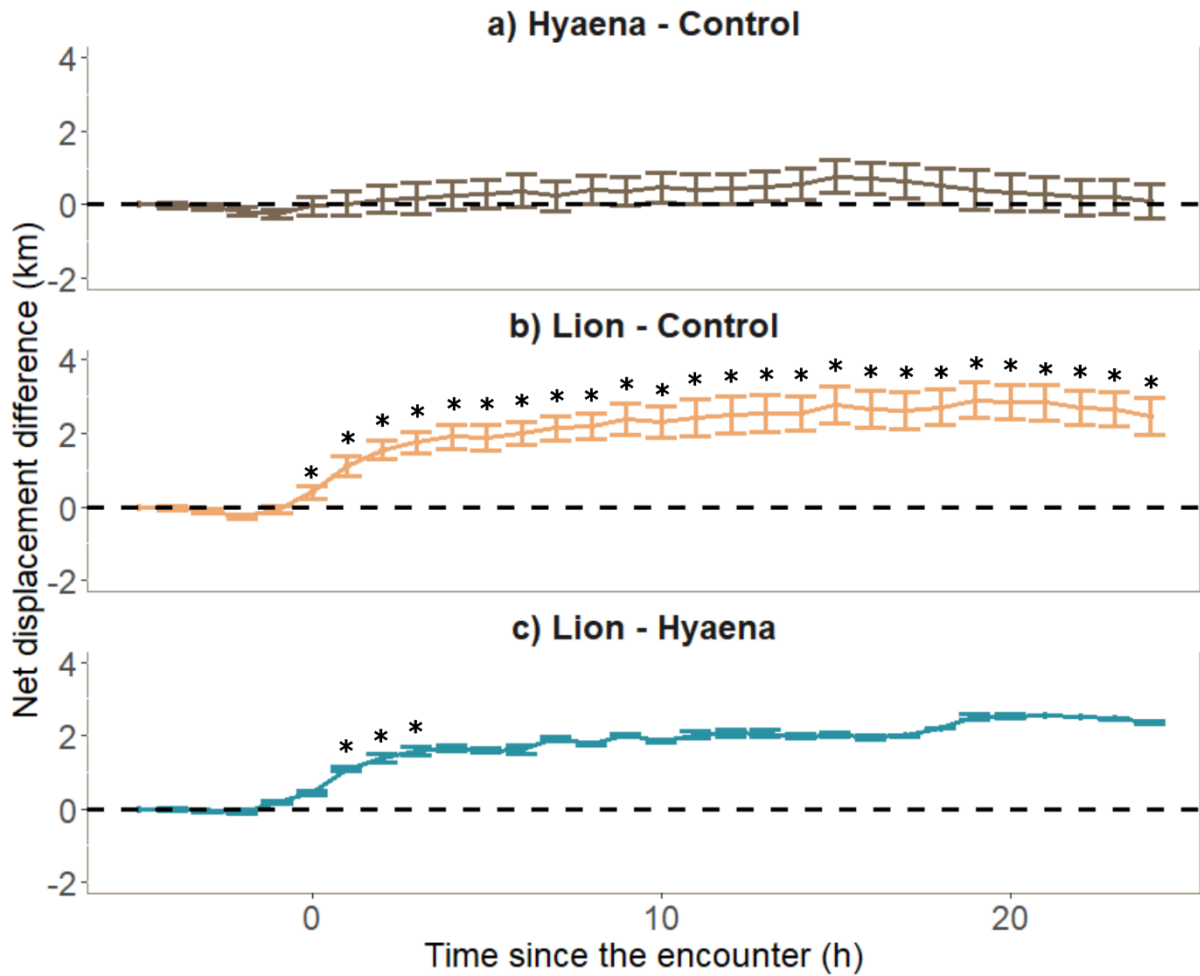
427 **Figure 3:** Difference of mean speed (between t and t+1) between pairs of situations a) hyaena
428 encounters vs. controls, b) lion encounters vs. controls, and c) lion encounters vs. hyaena

429 encounters for zebras that performed an ‘immediate flight’ response. The bars represent
430 standards errors. The stars indicate significant ($p < 0.05$) differences from the multiple mean
431 comparisons’ tests.

432 We detected no significant difference between mean net displacements after an encounter
433 with a hyaena and after a control (Fig. 4 a, p -value=0.89). Zebras moved further away after an
434 encounter with a lion (mean net displacement \pm SD = 6.2 ± 4.4 km 24 hours after; Fig. 4 b)
435 than after a control (mean net displacement \pm SD = 4.1 ± 3.8 kilometres 24 hours after; p -
436 value=0.004; Fig. 4 b). However, in the 3 hours following an encounter, zebras moved further
437 away after a lion encounter (mean net displacement \pm SD = 4.8 ± 2.5 km 3 hours after; Fig. 4
438 c) than after a hyaena encounter (mean net displacement \pm SD = 3.2 ± 2.4 km 3 hours after p -
439 value=0.004; Fig. 4c).

440 **Figure 4**

441



442

443 **Figure 4:** Difference of mean net displacement between pairs of situations a) hyaena
444 encounters vs. controls, b) lion encounters vs. controls, and c) lion encounters vs. hyaena
445 encounters, for zebras that performed an ‘immediate flight’ response. The bars indicate the
446 standard errors. The stars indicate significant ($p < 0.05$) differences from the multiple mean
447 comparison tests.

448

449 3. *Avoidance of the encounter area by zebras that performed an ‘immediate flight’*

450 Zebras returned sooner to an encounter area after an encounter with a hyaena (mean =7.17h;
 451 CI=3.74-13.74) or after a control (mean=10.81; CI=3.10-37.71) than after a lion encounter
 452 (mean = 14.90h; CI=4.22-52.46, Table 2 Appendix F, gof p-value=0.99).

453 Table 2: Estimates of the variables explaining the time spent by a zebra that performed an
 454 ‘immediate flight’ response before returning to the encounter area (hyaena being the reference
 455 level for the predator variable) within 72 hours. Significant values are in bold.

| | Estimates | Std. Error | z | pr(> z) | Confidence Interval | |
|-----------------------------|-------------|-------------|-------------|-----------------|---------------------|-------------|
| | | | | | 2.5% | 97.5% |
| Intercept | 1.97 | 0.33 | 6.00 | 2.00e-09 | 1.32 | 2.62 |
| Control (predator) | 0.41 | 0.30 | 1.35 | 0.18 | -0.19 | 1.01 |
| Lion (predator) | 0.73 | 0.31 | 2.39 | 0.02 | 0.12 | 1.34 |
| End (night period) | 0.21 | 0.17 | 1.23 | 0.22 | -0.13 | 0.54 |
| Open (vegetation type) | 0.14 | 0.24 | 0.57 | 0.57 | -0.34 | 0.61 |
| Distant (distance to water) | 0.27 | 0.23 | 1.19 | 0.24 | -0.18 | 0.73 |

456

457

458 4. *Time spent in the encounter area for zebras that initially stayed*

459 The duration of zebra stay in the encounter area did not differ between encounters with lions
 460 or hyaenas (Table 3, Fig. 5, gof p-value=1.00) and was ~10 hours on average
 461 (CI=8.25:12.31), but was a couple of hours shorter than under control situations (mean = 12h;
 462 CI=8.01-17.29, Table 3, Fig. 5). Zebras stayed longer (2 hours more on average) in the
 463 encounter area when it was close to a waterhole (Table 3, Fig. 5).

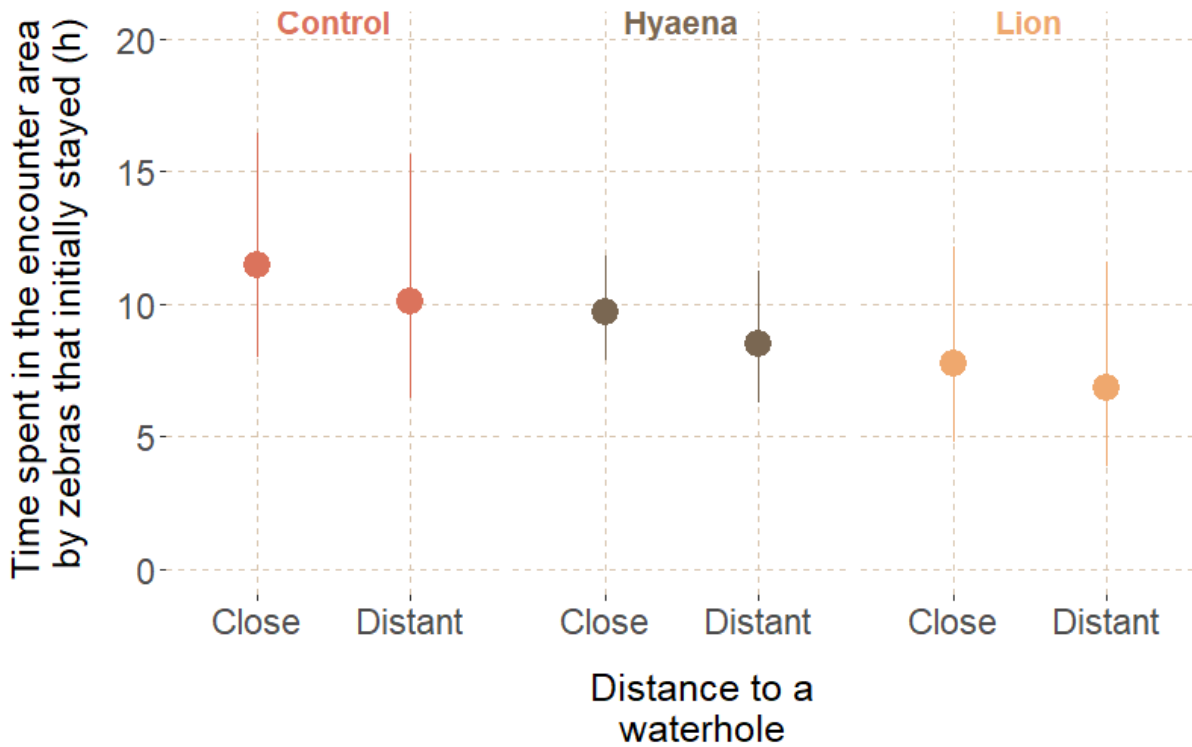
464 Table 3: Estimates of the variables explaining the time spent by a zebra in the encounter area
 465 before leaving the encounter area for zebras that performed an ‘initial stay’ response (hyaena
 466 being the reference level for the predator variable).

| | Estimates | Std. Error | z | pr(> z) | Confidence Interval | |
|---------------------------|-------------|-------------|--------------|------------------|---------------------|-------------|
| | | | | | 2.5% | 97.5% |
| Intercept | 2.27 | 0.10 | 22.58 | <2e-16 | 2.06 | 2.47 |
| Control (predator) | 0.17 | 0.08 | 2.12 | 0.03 | 0.02 | 0.33 |

| | | | | | | |
|------------------------------------|--------------|-------------|--------------|-------------|--------------|--------------|
| Lion (predator) | -0.22 | 0.13 | -1.68 | 0.09 | -0.49 | 0.03 |
| End (night period) | 0.06 | 0.04 | 1.73 | 0.08 | -0.01 | 0.12 |
| Open (vegetation type) | 0.001 | 0.05 | 0.02 | 0.99 | -0.10 | 0.10 |
| Distant (distance to water) | -0.13 | 0.05 | -2.73 | 0.01 | -0.22 | -0.05 |

467

468 **Figure 5**



469

470 **Figure 5:** For zebras that initially stayed, time spent in the encounter area (calculated from the
471 model estimates, with error bars for the 95% confidence interval) according to the distance to
472 water ('Close' or 'Distant'). Times were calculated for the default values of the other
473 variables (at the beginning of the night and in a dense vegetation).

474

475 **Discussion**

476 *Zebras' immediate spatial response to predation risk differs according to the dangerousness*
477 *of the predator species encountered* – Overall, our study shows that zebras were more likely
478 to leave an area after an encounter with a lion than after an encounter with a hyaena, and fled

479 faster when it happened. The spatial response of zebras to predation risk by lions depicted in
480 Hwange (this study; Courbin et al., 2016) was also demonstrated in Kruger National Park,
481 South Africa, where GPS data from simultaneously collared zebras, wildebeests
482 *Connochaetes taurinus* and lions showed that zebras leave an encounter area more often than
483 wildebeests (Martin & Owen-Smith, 2016). However, both herbivores were more active near
484 lions, particularly during new moon (Traill et al., 2016). No study, to our knowledge, has been
485 conducted on the spatial response of zebras to predation risk by hyaenas.

486 Overall, our results are consistent with prey anti-predator responses strengthening as the
487 dangerousness of the predator increases. The differences observed in the zebra reactive spatial
488 response between encounters with both predators can be intuitively explained by the
489 difference in body size between lions and hyaenas, as the larger body size of lions gives this
490 predator an obvious advantage over hyaenas to capture zebras. More originally, our results are
491 also consistent with the hypothesis originating from the invertebrate literature that prey
492 exposed to cues from sit-and-pursue predators (equivalent to ambush predators) should
493 display stronger anti-predator responses than prey exposed to cues from actively hunting
494 predators (Preisser et al., 2007; Miller et al., 2014). The underlying mechanism would be that
495 sit-and-pursue predators tend to spend longer periods in the same area, and hence cues of their
496 presence should be more indicative of imminent predation risk, and therefore evoke stronger
497 prey responses. The idea that predator hunting mode can affect prey antipredator responses
498 this way has started to become present in the literature on large mammals, with support for the
499 above hypothesis at the scale of the proactive responses of prey (Thaker et al., 2011; Moll et
500 al., 2016; Makin et al., 2017). Furthermore, the hunting success of ambush predators, such as
501 lions, benefits from a surprise effect, as they can run at a very high speed but over short
502 distances. Hence, once a prey has detected an ambush predator and leaves the encounter area,
503 the probability that it will be pursued is low. This is different for cursorial predators, such as

504 hyaenas, which can chase down prey over long distances and thus remain dangerous once
505 detected. Hence, upon an encounter with a cursorial predator, leaving the area might not
506 decrease the probability that the predator will pursue the prey. It has been shown that cursorial
507 predators, such as hyaenas or wild dogs, are often more successful hunters when prey flee
508 right after the encounter (Mills, 1990; Creel & Creel, 2002). It is therefore possible that zebras
509 do not leave the area immediately after encountering a hyaena, as this may be the most
510 effective antipredator response, in particular if they increase their vigilance level. Our
511 findings thus complement the other studies that found that lions elicited stronger proactive
512 antipredator responses in African herbivores than hyaenas (Thaker et al., 2011; Moll et al.,
513 2016; Makin et al., 2017), and suggest that this may hold for reactive antipredator spatial
514 responses too. However, more studies covering other pairs of large carnivores are clearly
515 needed to rigorously assess the role of the predator hunting mode.

516 Our study focused on the reactive spatial response, but prey can invest in other types
517 of reactive responses, such as exclusive vigilance (Creel et al., 2017), resistance display such
518 as bunching (Dannock et al., 2019) or fighting behaviours (Lingle & Pellis, 2002). This
519 illustrates the limits of studies based on GPS data only, for which detailed information on
520 prey non-spatial behaviour is missing. Furthermore, GPS data that records hourly locations
521 miss spatial response at a finer time scale, as zebras might also move away for a few minutes
522 only. Tackling the full complexity of the role of behaviour in predator-prey interactions will
523 likely require a suite of data that new technologies can now provide (Suraci et al., 2022).

524 *The behavioural ecology of predator-prey interactions is context-dependent* – One important
525 finding from our work is the high variability in the zebra spatial responses, as zebras did not
526 always leave an encounter area after a predator encounter and there was a high variability in
527 the speed of the movement following the encounter. In some cases, it is possible that
528 predation risk was wrongly assessed, or assessed as not warranting a response, or that another

529 antipredator response was more appropriate. The ecology of predator-prey interactions is
530 context-dependent and influenced by attributes of the predator, the prey and the environment
531 (Wirsing et al., 2021). First, the behaviour of the predator, its group size and its hunger state
532 can influence prey antipredator behaviour. For instance, an ‘immediate flight’ response might
533 be the most appropriate to a hunting predator with a thin belly, likely hungry, while an ‘initial
534 stay’ response might be the most appropriate to a walking predator with a fully distended
535 belly that suggests that the predator is satiated. For instance, gerbils adjust their foraging
536 behaviour to the hunger state of owls (Berger-Tal et al., 2010). Prey attributes may affect the
537 perception of predation risk and the associated antipredator responses such as group size
538 (Childress & Lung, 2003), presence of young (Gochfeld & Burger, 1994), hunger state
539 (Berger-Tal et al., 2010), and personality (Belgrad & Blaine, 2016). Another prey attribute is
540 diet and more precisely the importance of their diet in their habitat selection. For instance, by
541 having a selective diet for patches of short grass, blue wildebeests are less likely to leave a
542 short grass patch after an encounter with a lion, while zebras, which are generalists, are less
543 constrained and thus more likely to leave (Martin & Owen-Smith, 2016). Finally, the
544 assessment of predation risk and the associated antipredator response may be influenced by
545 the habitat configuration at the landscape level with an important role of the relative
546 abundance and distribution of safe and risky areas (Laundré et al., 2014; Smith et al., 2019).
547 In our study, habitat (vegetation structure and distance to water) at the encounter location did
548 not play an important role in zebra immediate spatial response. The probability of a zebra
549 initiating an ‘immediate flight’ response increased at the beginning of the night, suggesting
550 that encounters occurring at that time are riskier or that the costs associated to staying in the
551 same area as their predator is too high when they need to monitor the predator for the whole
552 night (‘risky times’ and ‘risky place’ hypotheses – Dröge et al., 2017).

553 *Predator influence on prey space use at the landscape level and on a longer temporal scale –*

554 In our study, we further explored how far a zebra went after an encounter with a predator and
555 how long it avoided an encounter area (already studied for encounters with lions in Courbin et
556 al., 2016). We believe such results provide useful insights into the predator-prey space game
557 at the landscape scale (Sih, 2005). Our results show that lions influenced zebra space use over
558 larger spatial scales than hyaenas. Indeed, zebras performed an “immediate flight” more often
559 after an encounter with a lion, they also moved further away when they encountered a lion (>
560 6 km away on average 24h after the encounter) than a hyaena (~ 4 km on average). The
561 immediate flight response is therefore associated to a missed opportunity cost in terms of
562 foraging, as zebras forage a lot at night (unpublished data), and prematurely leave their
563 foraging patch for ‘immediate flight’ responses; but also to travelling costs (higher when
564 zebras encounter lions because of higher speed immediately after the encounter and longer
565 distances covered). Additionally, our results mirror previous findings on lions leaving a kill
566 area, probably because of prey behavioural depression after prey have located the lions and
567 moving to a different area (> 5km away – Valeix et al., 2011). This illustrates the predator-
568 prey space game at the landscape scale. However, it is noteworthy that zebras that performed
569 an “immediate flight”, often came back in the encounter area by the next night, which may
570 indicate a strong but non-lasting avoidance.

571 Zebras that initially stayed in the encounter area stayed longer in control situation than
572 when they encounter a predator, especially when close to water. Waterholes are important
573 drivers of zebra habitat selection, as zebras are water dependant and need to drink daily
574 (Redfern et al., 2003). Furthermore, open grassland areas where zebras mainly forage are
575 scarce and often associated with waterhole areas in the study ecosystem (Arraut et al., 2018).
576 This result is consistent with a scenario whereby zebras in control conditions left the area
577 because they had finished exploiting the resource patch (Searle et al., 2005), whereas zebras
578 disturbed by a predator likely had to leave prematurely their resource patch. Zebras that had

579 left immediately returned sooner to an encounter area after a hyaena encounter than after a
580 lion encounter. This result suggests that zebras may perceive the environment risky for a
581 longer period after a lion encounter and is again consistent with the hypothesis that ambush
582 predators induce stronger antipredator response.

583 *Emergent multiple predator effects?* – Different predators may affect prey’s landscape of fear
584 in complex ways (Sih et al, 1998). They can interfere directly by chasing each other (Périquet
585 et al., 2021). They can interfere indirectly by reducing their hunting efficiency leading to risk
586 reduction for the prey (Hoset et al., 2009). They can also facilitate each other if the prey
587 response to one predator makes the prey more vulnerable to the other (Leblond et al., 2016).
588 At a small spatial scale (the encounter area), our results suggest that lion presence may lead to
589 a prey depression for hyaenas, while at a larger spatial scale, hyaenas may benefit from lions
590 that force zebras to move across the landscape at night. Indeed, in Hwange National Park,
591 hyaena density is high, hyaenas show no strong habitat selection pattern (Périquet, 2014), and
592 hyaena distribution is rather homogeneous across the landscape (unpublished camera-trap
593 data). Therefore, hyaenas are likely to represent a uniform risk of predation over the
594 landscape and lions may increase the probability that a zebra will encounter a hyaena by
595 increasing zebra movements at night.

596 Our study builds upon and completes the study on the reactive spatial response of
597 zebras to encounters with lions by Courbin et al. (2016). The controlled comparison with the
598 reactive spatial response to encounters with hyaenas is a first step towards a better
599 understanding of the role of the predator identity and overall dangerousness on the nature and
600 strength of this antipredator response. Our work further emphasizes that the immediate flight
601 response is not that frequent, even after an encounter with a lion. It also highlights the limits
602 of knowledge exclusively based on GPS information regarding the biological context of the
603 encounter (predator behaviour, predator group size, prey context). Our study calls for further

604 studies on other pairs of large mammalian predator species to be able to draw general
605 conclusions on the impact of different predator attributes (e.g., body size, hunting mode) on
606 prey antipredator response.

607

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794 **Highlights**

- 795 • Zebras reactive response is stronger after encountering a lion than a hyaena.
- 796 • Zebras were twice more likely to flee after an encounter with a lion than a hyaena.
- 797 • Zebras moved on average faster and further than after an encounter with a hyaena.
- 798 • Large mammal predators hunting mode may affect the reactive response of prey.

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