

1 Running head: Anti-predator terrestrial diel migration

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3 Title: Zebra diel migrations reduce encounter risk with lions over selection for safe habitats.

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25 **Abstract**

26 Diel migrations (DMs) undertaken by prey to avoid visual predators during the day have been  
27 demonstrated in many taxa in aquatic ecosystems. We reveal that zebras in Hwange National  
28 Park (Zimbabwe) employ a similar anti-predator strategy. Zebras forage near waterholes  
29 during the day but move away from them at sunset. We demonstrate that this DM, occurring  
30 over a few km, dramatically reduces their night-time risk of encountering lions, which  
31 generally remain close to waterholes. By contrast, zebra changes in night-time selection for  
32 vegetation types marginally reduced their risk of encountering lions. This may arise from a  
33 trade-off between encounter risk and vulnerability across vegetation types, with zebras  
34 favouring low vulnerability once DM has reduced encounter risk. In summary, here we (1)  
35 quantify the effect of a predator-induced DM in a terrestrial system on the likelihood of  
36 encountering a predator, (2) distinguish the effects of the DM from those related to day/night  
37 changes in selection for vegetation types. We discuss how revealing how prey partition their  
38 risk between predator encounter risk and habitat-driven vulnerability is likely critical to  
39 understand the emergence of anti-predator behavioural strategies.

40

41 **Keywords:** anti-predator strategy, encounter risk, *Equus quagga*, lion, nyctohemeral  
42 adjustment, *Panthera leo*, plains zebra, predator-prey interaction, semi-arid wooded  
43 savannahs

## 44 INTRODUCTION

45 Prey species attempt to avoid predators that search for them, leading both predators and prey  
46 into a spatial game (Sih 1984, Lima 2002, Sih 2005, Laundré 2010), which has ecological and  
47 evolutionary implications for both players (Sih 1998, Flaxman et al. 2011) and sometimes  
48 other trophic levels (see Rosenheim 2004, Fortin et al. 2005 for spatial trophic cascade).  
49 Several simple one-predator-one-prey models have predicted that the race will revolve around  
50 the prey resource patches (Sih 2005). Experiments have confirmed in simple settings that  
51 predators often search for habitats rich in prey resources rather than for the prey themselves  
52 (Sih 1998, Williams and Flaxman 2012). Prey were found to use the richest but most risky  
53 resource patches less than expected under the assumption of an optimization of resource  
54 acquisition (Sih 2005, Hammond et al. 2007).

55         These predictions and experiments ignore, however, that the temporal variations in  
56 predation risk affect the spatial behaviour of prey. Variations in predation risk may occur at  
57 different temporal scales (e.g. day, seasons and year), but it is most obvious when looking at  
58 how most predator-prey interactions are affected by the day/night cycle. The hunting  
59 efficiency of many predators varies with light intensity, leading many predators to have well-  
60 defined and restricted windows of hunting activity over the 24h cycle (Clark and Levy 1988,  
61 Lima and Dill 1990, Kronfeld-Schor and Dayan 2003). Prey may thus optimize how they  
62 balance forage and predation risk by making strategic use of rich resource areas when the  
63 predator is inefficient and/or inactive. Thus, during the low-risk period, prey could tolerate  
64 predator presence. During the high-risk period, prey could reduce their overall predation risk  
65 by decreasing the probability of encountering the predator by moving away from the rich  
66 resource areas.

67         Such spatio-temporal strategy of prey is observed in diel migrations conducted by a  
68 wide range of taxa in aquatic ecosystems (Alonzo et al. 2003, Hays 2003, Benoit-Bird and Au

69 2006). For example, in marine systems, zooplankton forage on phytoplankton at the sea  
70 surface at night when their predators have a reduced visual acuity, and move towards deeper  
71 water during the day to reduce the risk of being detected, leading to the emergence of diel  
72 vertical migrations (Iwasa 1982, Hays 2003). Similarly, diel horizontal migrations have also  
73 been reported. For instance, in shallow lakes, zooplankton migrates to the safer vegetated  
74 littoral zone during daytime to avoid visual predators (Burks et al. 2002). Thus, diel  
75 migrations (DMs) are a common proactive strategy employed by aquatic organisms to exploit  
76 their environments in the context of food-safety trade-offs (Hays 2003), while DMs have been  
77 largely overlooked for terrestrial prey.

78 Predation risk arises not only from the risk of encountering the predator but also from  
79 the vulnerability of the prey (i.e. the likelihood of dying if attacked) (Prins and Iason 1989,  
80 Lima and Dill 1990, Hebblewhite et al. 2005). Therefore, during the high-risk diel period,  
81 prey could also remain near the resource rich areas and the predator, but shift to neighbouring  
82 safer habitats (Schmidt and Kuijper 2015). In many systems, the vegetation cover, which may  
83 change abruptly over short distances, is a strong determinant of predator hunting efficiency  
84 (Mysterud and Østbye 1999, Hopcraft et al. 2005) and hence of prey vulnerability. This may  
85 for instance be linked to the higher visibility, or the ambush opportunities, that some habitats  
86 provide (Lima and Dill 1990, Caro 2005). During diel periods of predator activity, prey can  
87 thus decrease predation risk without much travel by shifting their habitat selection towards  
88 neighbouring habitat where they are less vulnerable. This is commonly observed in many  
89 ungulate species facing natural predators such as wolves (Creel et al. 2005, Middleton et al.  
90 2013, Basille et al. 2015, Schmidt and Kuijper 2015) and puma (Laundré 2010), or hunters  
91 (Padié et al. 2015).

92 The relative efficiency of the two strategies (DM vs. local habitat shift) will likely  
93 depend upon the correlation between encounter risk and vulnerability across habitat types and

94 the predator behaviour. If some nearby habitat simultaneously offers lower encounter risk and  
95 lower vulnerability, i.e. refuge habitat (Sih 1984, Hays 2003), these should be selected for by  
96 prey when the predator is active. If encounter risk and vulnerability are negatively correlated,  
97 then there is no refuge habitat and the cost of changing habitat will likely depend on the actual  
98 encounter risk and vulnerability within and across habitats and the predator behaviour. Some  
99 predators are spatio-temporally unpredictable, either because they roam over large areas in the  
100 quest of vulnerable prey (Latombe et al. 2014) or track prey resource patches in landscapes  
101 where these are common and scattered (Courbin et al. 2014). The use of habitat shift  
102 strategies could then be more efficient to decrease predation risk than a spatial redistribution  
103 towards areas for which information on the recent predator activity is not available or not  
104 reliable (Creel et al. 2005, Middleton et al. 2013, Basille et al. 2015, Schmidt and Kuijper  
105 2015). Conversely, some predators may be more predictable, anchored near scarce prey  
106 resource patches (Sih 2005), relying more on prey attraction to the patch than on selectively  
107 tracking individual prey to encounter them (Valeix et al. 2010). In such a context, a DM could  
108 be a more efficient strategy for prey to decrease predation risk than shifting to neighbouring  
109 safer habitats but where predators are still present. In known DM systems, however, the DM  
110 takes prey not only significantly away from visual predators but also to refuge habitats where  
111 these predators are less efficient (the predator evasion hypothesis, Hays 2003), so the effects  
112 of DM and habitat shift strategies are confounded by a positive correlation between encounter  
113 risk and vulnerability. Therefore, current studies on DM cannot fully shed light on the  
114 conditions under which DM may emerge, and cannot distinguish between the relative effects  
115 of encounter risk and vulnerability in shaping prey responses.

116 Here, we tested the hypothesis that predictable encounter risk with a primarily  
117 nocturnal predator (Schaller 1972) whose distribution is spatially anchored near prey resource  
118 patches, combined with the lack of refuge habitat for the prey, led the prey to develop a DM

119 strategy. We focused on the lion (*Panthera leo*) space use behaviour and on the spatial  
120 proactive response of plains zebras (*Equus quagga*) in Hwange National Park (hereafter  
121 Hwange NP; Zimbabwe). In this ecosystem, artificial waterholes are associated with large,  
122 well grazed, open areas (Chamaillé-Jammes 2009a, Courbin et al. 2016), which are rare (<2%  
123 of the study area) in this otherwise wooded savannah. Zebras favour these short-grasslands  
124 during daytime (Valeix et al. 2009, Courbin et al. 2016) as they provide profitable forage and  
125 high visibility. Lions hunt near waterholes at night (Valeix et al. 2010, Davidson et al. 2013,  
126 Courbin et al. 2016), and rest in their vicinity during the day (Valeix et al. 2010, Courbin et  
127 al. 2016). We therefore predicted that zebras should display DM, coming close to waterholes  
128 during the day to forage and drink when lions are inactive and moving away at night to  
129 decrease predation risk when lions become active. Our results supported this prediction, and  
130 so we then used lion GPS-tracking data to quantify to what extent these night-time  
131 displacements decreased the risk of encountering lions for zebras. Vegetation cover is a  
132 significant determinant of zebra vulnerability against lion attacks, as increased cover provides  
133 more and better ambush opportunities (Caro 2005, Davidson et al. 2012, Loarie et al. 2013).  
134 We therefore also evaluated to what extent day/night changes in the selection for vegetation  
135 cover types (e.g. grasslands vs. bushlands) modified the risk of encountering lions.  
136 Ultimately, our framework allowed us to compare the relative ability of DM and habitat shift  
137 strategies in reducing encounter risk with the predator. In summary, here we (1) quantified the  
138 effect of a predator-induced DM in a terrestrial system on the likelihood of encountering a  
139 predator, (2) distinguished its effects from those related to day/night changes in selection for  
140 vegetation types.

141

## 142 **METHODS**

### 143 *Study site*

144 The study was conducted in Hwange NP, Zimbabwe. The vegetation is typical of dystrophic  
145 semi-arid wooded savannahs (average annual rainfall is c. 600 mm), with woodlands and  
146 bushlands interspersed with small grassland patches (Chamaillé-Jammes 2006). We focused  
147 on two contrasting seasons: the wet season (November to April) and the late dry season  
148 (August to October). During the latter, zebras drink at artificial waterholes (hereafter referred  
149 to as 'waterholes') that are the only perennial sources of water. All statistical analyses were  
150 conducted for both seasons.

151 In the study area, zebra and lion densities were estimated at c. 100 zebra/100km<sup>2</sup>  
152 (Chamaillé-Jammes 2009b) and c. 3.5 lions/100 km<sup>2</sup> (Loveridge, unpublished data). Lions  
153 hunt for zebras (c. 10% of their diet) but also for other prey (Davidson et al. 2013). The zebra  
154 population in Hwange NP seems to be under top-down control by lions, their main predator,  
155 and is currently declining due to a high predation pressure (Grange et al. 2015).

156

#### 157 *Testing for the existence of zebra DM*

158 We used GPS locations collected hourly from 25 adult female zebras (18 zebras in dry season  
159 and 24 zebras in wet season), collared in different herds between August 2009 and November  
160 2013, to assess if zebras systematically moved further away from waterholes at night and if  
161 this depended on how close they were to waterholes during the day. For each day and night of  
162 each season, we estimated the distance to the closest waterhole (hereafter 'distance to  
163 waterhole') at which an individual was as the median distance to waterhole over its GPS  
164 locations for the given day or night. See Appendix S1: Fig. S1, for the sunrise/sunset-based  
165 definition of day/night periods.

166 We used least-squares spectral fitting to test that distance to waterhole displayed a  
167 24h-periodicity. For each zebra in each season, we visually inspected Lomb-Scargle  
168 periodograms (Ruf 1999) for peaks around 24h, and tested the significance of the largest peak

169 within the 20 to 28h window using the randomization procedure implemented in the *lomb*  
170 package (Ruf 1999) for the R software (R Development Core Team 2016).

171 For individuals displaying a significant 24h-periodicity in distance to waterhole (i.e.  
172 those performing a diel migration), we investigated if displacement away from waterholes  
173 depended upon their proximity to waterholes during the previous day. We did this by  
174 modelling the relationship between the night-time distance to waterhole and the distance to  
175 waterhole during the previous day using a generalized additive mixed model (GAMM) with  
176 thin plate regression splines (Wood 2003). Individuals were included as random factors to  
177 account for the unbalanced sampling among individuals (Gillies et al. 2006). The model was  
178 fitted using the *gamm4* package (Wood and Scheipl 2014) for the R software (R Development  
179 Core Team 2016).

180

#### 181 *Characterizing the spatial risk of lion encounter*

182 We first used GPS data from lions, collected over the same period as for zebras, and  
183 inhomogeneous point process models (Aarts et al. 2013, Johnson et al. 2013) to build  
184 predictive maps of the intensity of lion occurrence within the landscape (see Appendix S2).  
185 Separate maps were built for daytime and night-time because lions displayed day/night  
186 changes in habitat selection (see Appendix S2: Table S2 and Fig. S1).

187 We then used these maps to estimate how the risk of encountering lions decreased  
188 with the distance to waterhole at zebra locations during daytime (using daytime lion  
189 occurrence map and daytime zebra GPS locations; thereafter  $\text{LionRisk}_{\text{Day}}\text{ZebraUse}_{\text{Day}}$  model)  
190 and night-time (using night-time lion occurrence map and night-time zebra GPS locations;  
191 thereafter  $\text{LionRisk}_{\text{Night}}\text{ZebraUse}_{\text{Night}}$  model). We did so by fitting log-linear mixed-effects  
192 models (log-LMM) with the intensity of lion occurrence as the response variable and the log-  
193 transformed distance to waterhole as unique predictor, both measured at each zebra GPS  
194 location. We allowed for a random intercept for each zebra.



195

196 *Quantifying the impact of vegetation types on encounter risk*

197 At any distance to waterhole, the difference between the  $LionRisk_{Day}ZebraUse_{Day}$  and  
198  $LionRisk_{Night}ZebraUse_{Night}$  models measured how the combined effects of lion and zebra  
199 day/night changes in space use affected their likelihood of encounter. Previous studies  
200 conducted in the study area have shown that lions shift to selecting more open vegetation at  
201 night (Courbin et al. 2016, see also Appendix S2), and that zebras, although they still select  
202 open vegetation types at night, do so less than during the day (Courbin et al. 2016). We  
203 disentangled the relative contribution of lion and zebra selection for vegetation types on  
204 encounter probability by creating a  $LionRisk_{Night}ZebraUse_{Day}$  model, fitted on night-time lion  
205 occurrence map and daytime zebra GPS locations models. At any distance to waterhole, the  
206 difference between this  $LionRisk_{Night}ZebraUse_{Day}$  model and the  $LionRisk_{Day}ZebraUse_{Day}$   
207 model measured to what extent lion changes in selection for vegetation types at night would  
208 increase zebra risk of encountering lions if zebras behaved as they did during the day.  
209 Similarly, the difference between the  $LionRisk_{Night}ZebraUse_{Day}$  and the  
210  $LionRisk_{Night}ZebraUse_{Night}$  model measured to what extent zebra changes in selection for  
211 vegetation types at night reduced their risk of encountering lions, assuming night-time  
212 behaviour for lions. We additionally quantified the overall effect of zebra selection for  
213 specific vegetation type on the risk of encountering lions at night by comparing the  
214  $LionRisk_{Night}ZebraUse_{Night}$  model with one estimated using the night-time lion occurrence  
215 map but zebra locations randomly drawn in the landscape ( $LionRisk_{Night}ZebraUse_{Random}$   
216 model).

217

218 *Measuring the effect of DM on encounter risk*

219 Finally, using the above-described models relating the likelihood of encountering lions with  
220 the distance to waterhole, we quantified to what extent night-time behavioural adjustments

221 (including both DM and change in selection for vegetation types) allowed zebras to decrease  
222 their risk of encountering lions. We first used the GAMM model fitted in section *Testing for*  
223 *the existence of zebra DM* to predict zebra night-time displacement away from waterholes  
224 across the range of daytime distances to waterhole. We then used this distance and results  
225 from the  $LionRisk_{Night}ZebraUse_{Night}$  model to predict its night-time risk of encountering lions  
226 across a range of distance to waterhole. We then calculated the difference between this risk  
227 and the one expected if the zebra did not adjust its behaviour at night (estimating risk at the  
228 daytime distance to waterhole from the  $LionRisk_{Night}ZebraUse_{Day}$  model) across a range of  
229 distance to waterhole. To measure the effect of DM only, we compared the decrease in risk  
230 brought by all the night-time behavioural adjustments (calculated above from the  
231  $LionRisk_{Night}ZebraUse_{Night}$  model) with the decrease in risk induced by only the adjustment of  
232 the selection for vegetation types. We estimated this latter measure by calculating the  
233 difference between the  $LionRisk_{Night}ZebraUse_{Night}$  and the  $LionRisk_{Night}ZebraUse_{Day}$  models  
234 across a range of distances to waterhole.

235

## 236 **RESULTS**

### 237 *Zebras undertake DM*

238 During the dry season, zebras were generally within a few km of waterholes, but were closer  
239 to waterholes during the day than at night (Figs 1A, 2). Periodogram analyses confirmed that  
240 distance to waterhole displayed a well-marked 24h cycle that was significant for 83% of the  
241 individuals, while DM frequency varied among individuals (note the variability in normalized  
242 power values, Fig. 3A). Zebras moved towards waterholes in the first hours of the morning  
243 and moved away at sunset with an average DM of 0.5 +/- 0.4 km (mean +/- SD) (see  
244 Appendix S1: Fig. S1). However, for zebras with a significant DM pattern, night-time  
245 displacement away from waterholes declined as daytime distance from a waterhole increased

246 (Fig. 1B). No night-time displacement away from water occurred beyond a daytime distance  
247 of 2.4 km.

248 During the wet season, zebras remained close to waterholes at night more often than  
249 during the dry season (Fig. 1E). Zebras also used DM but, compared to the dry season the  
250 24h-periodicity in back-and-forth movement to waterholes was significant for a lower  
251 proportion of zebras (54%) and DMs were less frequent (i.e., lower normalized power values,  
252 Fig. 3B). Also, for zebras with a significant DM pattern, the night-time displacements away  
253 from waterholes vanished at shorter daytime distance from a waterhole (1.8 km, Fig. 1F).

254

### 255 *Zebra mechanisms of reducing lion encounter risk*

256 During the dry season, zebras' risk of encountering lions, as indexed by our model, always  
257 decreased rapidly with the distance from waterholes (Fig. 1C). At any distance to waterhole,  
258 this risk would increase at night if zebras did not adjust their night-time behaviour (Table 1,  
259 compare  $LionRisk_{Night}ZebraUse_{Day}$  and  $LionRisk_{Day}ZebraUse_{Day}$  models in Fig. 1C). Zebras  
260 would be at a higher risk at night because lions always selected for areas close to waterholes,  
261 and increased their selection for grasslands and the most open bushlands at night (see  
262 Appendix S2: Table S2 and Fig. S1). In response, zebras however only slightly reduced their  
263 use of risky vegetation types at night (Table 1, see that  $LionRisk_{Night}ZebraUse_{Night} <$   
264  $LionRisk_{Night}ZebraUse_{Day}$  in Fig. 1C), and these remained highly selected for (Table 1, see  
265 that  $LionRisk_{Night}ZebraUse_{Night} > LionRisk_{Night}ZebraUse_{Random}$  in Fig. 1C). Zebras reduced  
266 their night-time risk of encountering lions only marginally by decreasing their selection for  
267 risky vegetation types (see 'Night-time risk with changes in vegetation type use only' in Fig.  
268 1D).

269 By contrast, the DM that zebras undertook allowed them to dramatically reduce their  
270 risk of encountering lions at night (compare curves in Fig. 1D). This reduction was  
271 particularly strong when they had spent the daytime near water, where risk would have been

272 high at night (Fig. 1D). Although zebras sometimes stayed at c. 0.6 km away from waterholes  
273 at night (Fig. 1A, see Appendix S1: Fig. S2), greater displacements were actually more  
274 common (Fig. 1A). Within a few km from waterholes, even moderate displacements had a  
275 dramatic influence on the risk of encountering lions: for instance in the dry season, zebras  
276 moving from 0.4km to 1.74km away from water between day and night (diel migration =  
277 1.34km, Fig. 1B) decreased by 72% the night-time risk of encountering lions (Fig. 1D).  
278 Beyond 2 km, displacement away from water brought little reduction in risk as it was already  
279 very low (Fig. 1D).

280           During the wet season, similar patterns were apparent (Figs 1F-G-H), but because  
281 DM where of shorter distances when they occurred (Figs 1E-F), the reduction in encounter  
282 risk was lower. Zebras moving from 0.4km to 1.65km away from water between day and  
283 night (diel migration = 1.25km, Fig. 1F) decreased by 64% the night-time risk of  
284 encountering lions (Fig. 1H).

285

## 286 **DISCUSSION**

287 Our study shows that, in Hwange NP, zebras use areas located near artificial waterholes  
288 during daytime, benefiting from the large open grasslands (Chamaillé-Jammes 2009a,  
289 Courbin et al. 2016), but routinely moved away from them at risky night period, thus reducing  
290 their risk of encountering lions. The diel cycle of predator-avoidance revealed here relies on  
291 diel migration and is independent of vegetation cover types, conveying an alternative strategy  
292 to the well-known day/night habitat selection shift reported so far in terrestrial systems  
293 (Mysterud and Østbye 1999, Kronfeld-Schor and Dayan 2003, Laundré 2010). Indeed, at  
294 night zebras still use open grasslands. We did not have data to test whether grass quality is  
295 higher closer or further away from waterholes. However, if forage was of better quality away  
296 from waterholes, we would expect zebras to forage away from waterholes during the day, as

297 they would find the best resources and be the least likely to be predated upon. This is not what  
298 we observed, even less so in the wet season when zebras don't need to drink and would have  
299 foraged away from waterholes during the day if resources were of better quality there.  
300 Moreover, the comparison of previous studies suggests that vigilance levels is likely higher  
301 when zebras are very near waterholes (Périquet et al. 2010, 2012). Therefore, we assume that  
302 predator avoidance, rather than attraction towards better resources, is driving the observed  
303 diel migration. Interestingly, the diel migration occurring here or in aquatic systems (Iwasa  
304 1982, Burks et al. 2002, Hays 2003, Benoit-Bird and Au 2006) where no absolute refuge  
305 areas occurred differs from the diel response showed by hunted ungulates that take refuge  
306 during the day in protected areas completely free of risk (no hunting) (e.g. wild boars [*Sus*  
307 *scrofa* L.] [Tolon et al. 2009] and bison [*Bison bison*] [Fortin et al. 2015]).

308

### 309 *Diel migration is advantageous when space use of the predator is predictable*

310 Diel migration may emerge as an efficient strategy to deal with food-safety trade-offs when  
311 prey can reliably identify and travel to places where the absence of a predator is likely (Iwasa  
312 1982, Sainmont et al. 2013). In Hwange NP, lions remain near waterholes most of the time,  
313 despite being free to move anywhere (Valeix et al. 2010, Courbin et al. 2016, this study).  
314 Areas away from waterholes are therefore predictably safer, and our results show that zebras  
315 benefit from this predictability. Zebras have developed a DM strategy allowing them to more  
316 than halve their risk of encountering lions during their hunting period, compared to staying to  
317 near waterholes. Thus, daily zebra movements to and from waterholes may provide a  
318 mechanistic explanation for the low night-time lion-zebra encounter rate observed in Hwange  
319 NP (one encounter every 35 days on average, Courbin et al. 2016).

320 The predictability of the predator distribution however depends on both the  
321 landscape configuration and the predators hunting strategies. Ambush sites for sit-and-wait

322 predators are usually predictable (Schmidt and Kuijper 2015), and the actual presence of the  
323 predator will be even more predictable if ambush predators focus around prey hotspots. In  
324 Hwange NP, the large patches of grasslands located near these waterholes attract grazers and  
325 mixed-feeders all year round, and the many water-dependent species naturally use these  
326 waterholes during the dry season. Waterholes can thus be considered as prey hotspots in this  
327 ecosystem. Lions, being generalist predators (Davidson et al. 2013), may not need to track  
328 zebras moving away from waterhole areas if some other prey species do not perform DM.  
329 This is yet unknown, but field observations suggest that certain species (e.g. impala, kudu)  
330 indeed do not perform DM (unpublished data). This is to be expected as DM should emerge  
331 only when predation risk is predictable in space and time, and negatively correlated to  
332 resource abundance/quality. This will not be the case for many prey species, especially those  
333 that are significantly preyed upon by cursorial predators that roam over vast areas and  
334 whose distribution is unpredictable (Latombe et al. 2014) Prey of cursorial predators should  
335 therefore shift towards safer neighbouring habitats when the predator is detected or is likely to  
336 revisit the area rather than moving towards areas where predation risk is uncertain (see  
337 examples with wolves, [Creel et al. 2005, Middleton et al. 2013, Latombe et al. 2014, Basille  
338 et al. 2015, Schmidt and Kuijper 2015]).

339 Overall, a better understanding of the landscape and behavioural constraints driving  
340 the spatial behaviour of the species making the food web would shed light on the interaction  
341 driving the emergence, or not, of diel migration. In this context, it would prove valuable to  
342 test the existence of DM in other prey and other ecosystems, contrasting situations with  
343 varying levels of prey and predator predictability.

344

345 *Does the absence of safe vegetation types facilitate the emergence of DM?*

346 We found that zebras did not alter their selection for vegetation types at night to an extent that  
347 would reduce encounter risk with lions significantly. We suspect that this is due to a trade-off

348 between encounter risk and vulnerability across vegetation types. At night, lions strongly  
349 select for more open vegetation, possibly to benefit from increased visibility and to maximize  
350 encounter rates with prey (Courbin et al. 2016, see Appendix S2: Fig. S1). Zebras could  
351 reduce the risk of encountering lions by selecting for more bushy vegetation (see Appendix  
352 S2: Fig. S1), but they would then become highly vulnerable in case of an encounter with lions  
353 which are primarily ambush/stalking predators (Caro 2005, Davidson et al. 2012, Loarie et al.  
354 2013). Therefore, zebras may decrease encounter risk while maintaining a low vulnerability  
355 by conducting DM towards open vegetation types localized in relatively safe areas (i.e. far  
356 from waterholes).

357

358 *Do DMs have population-level consequences?*

359 Our results could suggest that DM, which strongly decreases zebra likelihood of encountering  
360 lions, is a prime determinant of zebra survival rate. However, data from both lion kill surveys  
361 (Davidson et al. 2013) and zebra demographic monitoring (Grange et al. 2015) show that  
362 adult zebras are less likely to be predated upon by lions during the wet season, when we found  
363 that DMs were much less prevalent than in the dry season. It is yet unknown if this seasonal  
364 difference in DM patterns is driven by resources or predation sensitivity. They could be  
365 linked to the higher cost of leaving the best foraging patches at a time when grass quality is  
366 high. Also, it could be that lion favour other prey during the wet season. This itself could be  
367 because prey abundance and vulnerability vary seasonally. Adult zebras may be a challenging  
368 prey when body condition is good during the wet season (pers. obs.), and this itself could lead  
369 them to accept higher chances of meeting lions, especially to forage on good quality grass. All  
370 these explanations could explain the lack of relationship between predation rate on adults and  
371 prevalence of the diel migration across seasons. Also, this may be because in the wet season  
372 lions favour hunting juvenile zebras. Almost half of the juvenile zebras are killed during their  
373 first 6 months, mostly by lions (Grange et al. 2015). Therefore, the link between DM and

374 adult predation rate may be distorted by the seasonal presence of juveniles, which may itself  
375 constrain the DM as young ones will be less mobile. It remains to be investigated if individual  
376 variability in juvenile survival rate could be linked to the ability of some herds to perform  
377 longer DM earlier after the birth season. This would allow assessing the population-level  
378 consequences of DM, which may occur via consumptive or non-consumptive (e.g. increased  
379 energetic expenditure) effects.

380

## 381 **CONCLUSIONS**

382 The study of DM may thus help to clarify the respective roles of encounter risk and  
383 vulnerability in driving anti-predation behaviour. Our study emphasizes that DM could  
384 possibly be a more general anti-predator strategy than previously thought, and opens new  
385 research avenues to better understand the conditions under which it may evolve. In particular,  
386 it offers opportunities to study how the behaviour of the predator (i.e. mobility and hunting  
387 mode), the constraints for the prey (i.e. resource needs, presence of young) and the spatial  
388 context of their interactions (i.e. availability and spatial arrangement of the resource patches)  
389 determine the efficiency of DM compared to other anti-predator strategies. Generally, our  
390 study answers previous calls to consider the temporal patterns in the predator-prey space race  
391 (Hammond et al. 2007). Prey may use high risk, rich food patches during periods of predator  
392 inactivity or inefficiency, and move away from these patches when an encounter with the  
393 predator becomes more likely or dangerous.

394

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405 23(1)(c)(ii): 03/2009, 01/2010, 25/2010, 05/2011, 06/2011, 12/2012, 15/2012, 08/2013).

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550 Table 1. Log-linear mixed-effect models of the expected risk of encountering lions for zebras  
 551 as a function of distance to waterhole and four situations: (1) lion daytime space use and zebra  
 552 daytime locations ( $LionRisk_{Day}ZebraUse_{Day}$ ); (2) lion night-time space use and zebra night-  
 553 time locations ( $LionRisk_{Night}ZebraUse_{Night}$ , serving as baseline), (3) lion night-time space use  
 554 risk and zebra daytime locations ( $LionRisk_{Night}ZebraUse_{Day}$ ), and (4) lion night-time space use  
 555 risk and random locations ( $LionRisk_{Day}ZebraUse_{Random}$ ). Models were fitted for the dry (n=15  
 556 individuals) and wet (n=13 individuals) seasons. Coefficients ( $\beta$ ) and their 95% confidence  
 557 intervals (95% CI) are shown. The distance to waterhole was log-transformed.  
 558

Season	Variable	$\beta$	95% CI
Dry	$LionRisk_{Night}ZebraUse_{Night}$ (baseline)	-5.86*	-5.97;-5.76
	Distance to waterhole	-0.85*	-0.85;-0.84
	$LionRisk_{Day}ZebraUse_{Day}$	-0.37*	-0.38;-0.36
	$LionRisk_{Night}ZebraUse_{Day}$	0.01*	0.002;0.02
	$LionRisk_{Night}ZebraUse_{Random}$	-0.06*	-0.07;-0.05
Wet	$LionRisk_{Night}ZebraUse_{Night}$ (baseline)	-6.00*	-6.07;-5.93
	Distance to waterhole	-0.68*	-0.69;-0.68
	$LionRisk_{Day}ZebraUse_{Day}$	-0.25*	-0.26;-0.24
	$LionRisk_{Night}ZebraUse_{Day}$	0.09*	0.08;0.10
	$LionRisk_{Night}ZebraUse_{Random}$	-0.16*	-0.17;-0.15

559 \* 95% confidence intervals exclude zero.

560

561 Figure legends.

562

563 Figure 1. (A,E) Distribution of zebra locations as a function of distance to waterhole during  
564 daytime and night-time. The distribution is truncated at 6km (dry season: for both day and  
565 night 90% of data are shown and the tail reaches c. 15km; wet season: 76% and 78% of  
566 daytime and night-time data are shown, respectively, the tails of the distribution reach 38km  
567 [daytime] and 34km [night-time]). (B,F) Difference between zebra distance to waterhole at  
568 night and their distance to waterhole during the previous day, as predicted by a generalized  
569 additive mixed model (dry season:  $df=2.827$ ,  $F=119.8$ ,  $P<0.001$ ; wet season:  $df=2.986$ ,  
570  $F=134$ ,  $P<0.001$ ). Positive (negative) values indicate that zebras moved away from (closer to)  
571 waterhole at night. Dotted lines represent the 95% confidence interval. (C,G) Expected risk of  
572 encountering lions as a function of distance to waterhole and four situations: (1) lion daytime  
573 space use and zebra daytime locations ( $LionRisk_{Day}ZebraUse_{Day}$ ); (2) lion night-time space  
574 use and zebra night-time locations ( $LionRisk_{Night}ZebraUse_{Night}$ ), (3) lion night-time space use  
575 risk and zebra daytime locations ( $LionRisk_{Night}ZebraUse_{Day}$ ), and (4) lion night-time space use  
576 risk and random locations ( $LionRisk_{Day}ZebraUse_{Random}$ ). (D,H) Differences between the night-  
577 time encounter risk expected for zebras displaying full night-time behavioural adjustments  
578 (diel migration and change in selection for vegetation types; solid line), or displaying only a  
579 change in selection for vegetation types (dotted line), and the night-time risk expected under  
580 the assumption of no behavioural adjustment (represented by the horizontal line at 0). More  
581 negative values indicated greater reduction in risk.

582

583 Figure 2. Example of diel migration behaviour. The panels display (A) GPS locations and (B)  
584 the median distance to the closest waterhole during day and night, using data obtained from

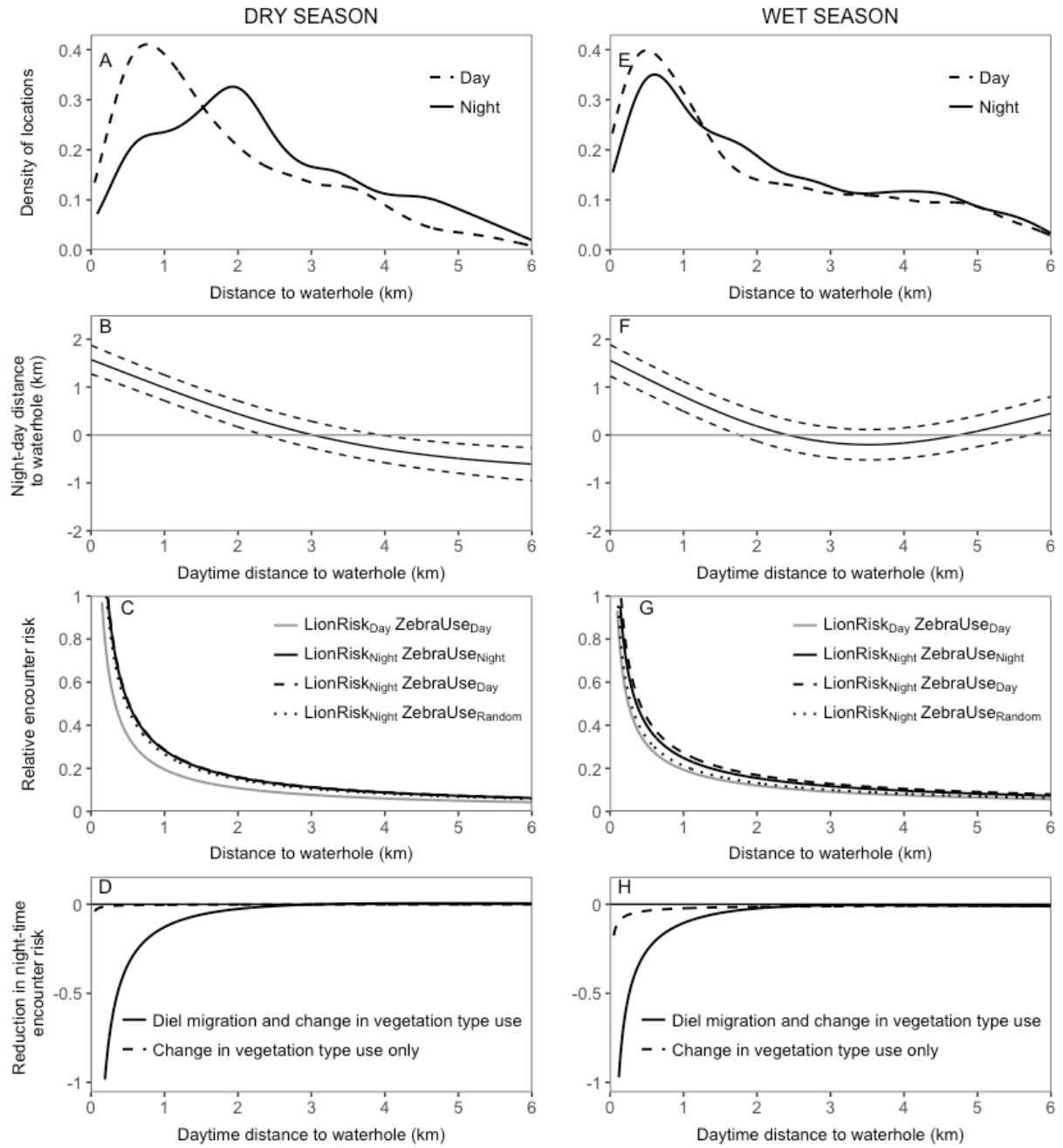


585 zebra ID AU299 over a 14-day period during the 2009 dry season in the Hwange National  
586 Park, Zimbabwe.

587

588 Figure 3. Periodograms of the distance to waterhole time-series for (A) the dry season and (B)  
589 the wet season. Each line represents the periodogram for one individual zebra, and the  
590 maximum value of each periodogram spectrum within the 20 to 28h-period window is  
591 indicated by a triangle. Black triangles pointing up and grey triangles pointing down indicate  
592 significant ( $P < 0.05$ ) and non-significant ( $P \geq 0.05$ ) peak values, respectively. Peak values were  
593 significant for 83% (15 out of 18) of the individuals in the dry season, and for 54% (13 out of  
594 24) of the individuals in the wet season.

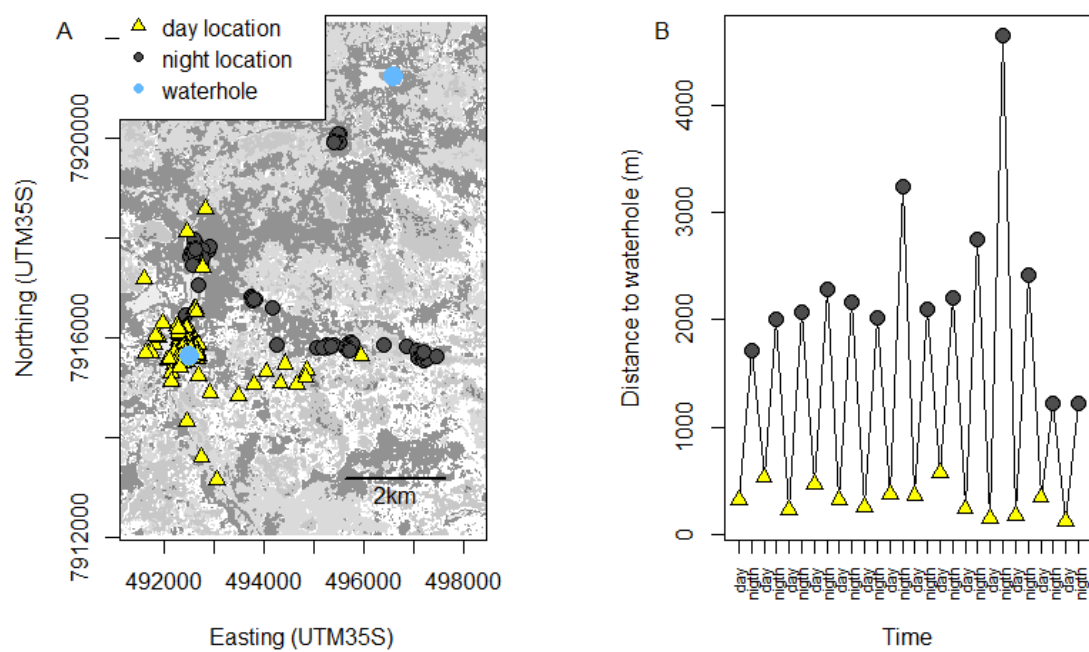
595



596

597 Figure 1

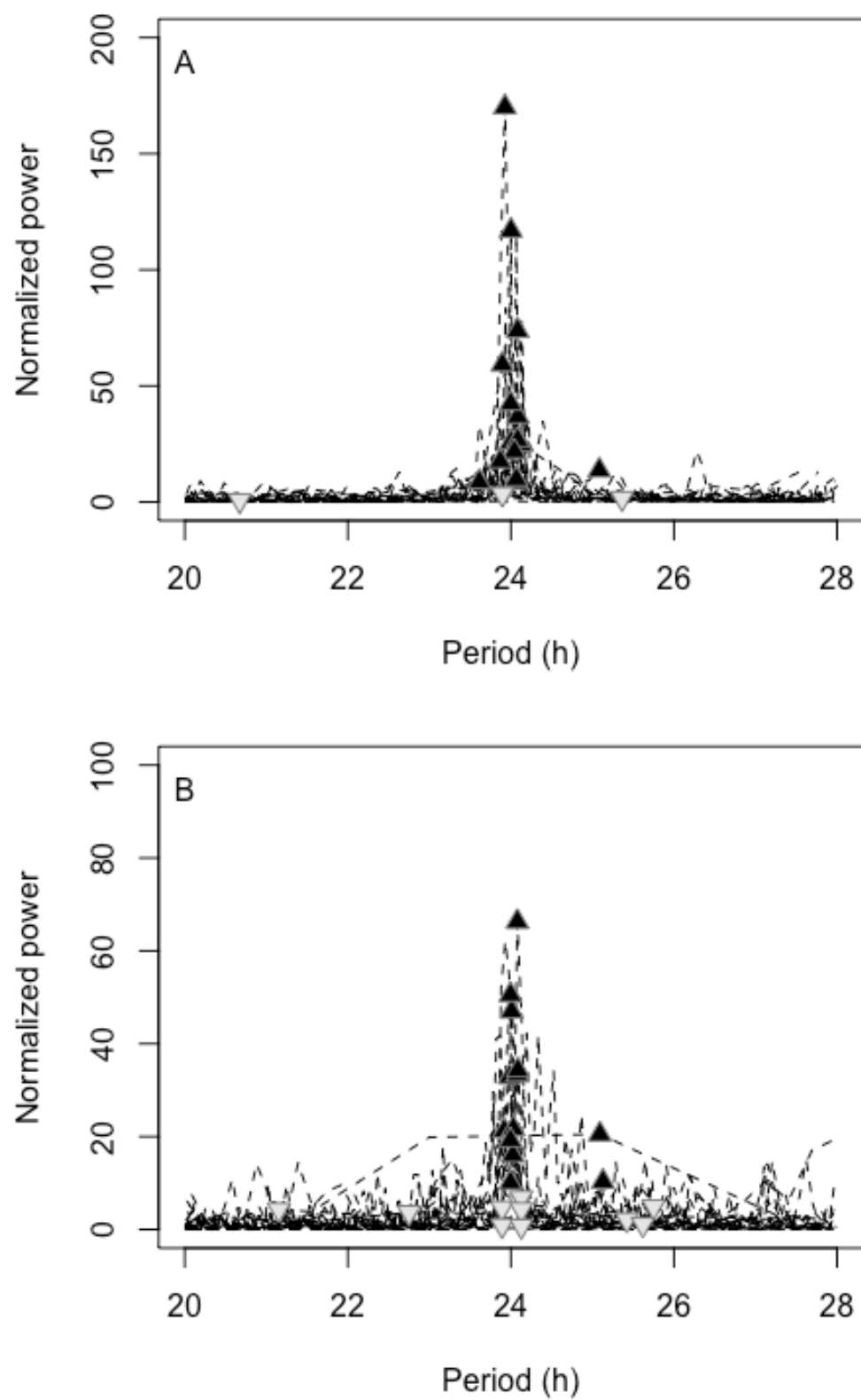
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599

600 Figure 2

601



602

603 Figure 3