



## RESEARCH ARTICLE

# Zebra diel migrations reduce encounter risk with lions at night

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**Abstract**

1. Diel migrations (DM; back and forth diel movements along an ecological gradient) undertaken by prey to avoid predators during the day have been demonstrated in many taxa in aquatic ecosystems. In terrestrial ecosystems, prey often shift between various vegetation types whose cover determine their vulnerability (i.e., likelihood of being killed when attacked).
2. We conceptualized that in terrestrial ecosystems, DM could also occur and that the contribution of DM and shifts in vegetation cover use in reducing predation risk should depend upon the predator behaviour and the correlation between encounter risk and vulnerability across vegetation types. We further hypothesized that when the predator distribution is predictable, terrestrial prey could have evolved DM strategies taking them away from the predator when it is active or efficient.
3. We investigated whether plains zebras *Equus quagga* perform DM in Hwange National Park (Zimbabwe). There, zebras can forage in large patches of open grasslands located near waterholes where they can also easily detect predators. However, they are there at high risk of encountering their main predator, lions *Panthera leo*, especially at night.
4. We found out that zebras employ a DM anti-predator strategy. Zebras forage near waterholes during the day but move away from them at sunset, when lions become active. We demonstrated that this DM, occurring over a few kilometres, dramatically reduces their night-time risk of encountering lions, which generally remain close to waterholes. Zebra changes in night-time selection for vegetation cover types reduced their risk of encountering lions much less. This may arise from a trade-off between encounter risk and vulnerability across vegetation types, with zebras favouring low vulnerability once DM has reduced encounter risk.
5. In summary, here we (a) quantify, in a terrestrial system, the effect of a predator-induced DM on the likelihood of encountering a predator and (b) distinguish the effects of the DM on encounter risk from those related to day/night changes in selection for vegetation types. We discuss how prey partition their risk between encounter risk and habitat-driven vulnerability and why it is likely critical to understand the emergence of anti-predator behavioural strategies.

**KEYWORDS**

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

## 1 | INTRODUCTION

Predation is a pervasive evolutionary force that shapes organisms' behaviour (Caro, 2005; Lima & Dill, 1990). Most anti-predator behavioural responses are, however, balanced against other fitness-beneficial activities, in particular food resource acquisition (Brown & Kotler, 2004; Lima & Dill, 1990). Such food-safety trade-offs are central in predicting that prey, rather than minimizing predation risk, should have evolved finely tuned behavioural strategies to best use their environments, adjusting dynamically to spatio-temporal changes in resources and predation risk.

A clear example of such adjustments is the relocation undertaken by many prey species between day and night periods. The hunting efficiency of predators often varies with light intensity, leading them to have well-defined, restricted windows of hunting activity during the 24-hr cycle (Clark & Levy, 1988; Kohl et al., 2018; Kronfeld-Schor & Dayan, 2003; Lima & Dill, 1990). Prey thus experience alternating safer and riskier times and may optimize their daily balance between forage acquisition and predation risk avoidance by making strategic use of rich resource areas when predators are inefficient and less active, while retreating to safer places during risky times (Basille et al., 2015; Fischhoff, Sundaresan, Cordingley, & Rubenstein, 2007; Kohl et al., 2018; Middleton et al., 2013; Padié et al., 2015). Such dynamical adjustments in prey space use over the diel cycle could have implications for non-consumptive effects of predators and trophic cascades (Kohl et al., 2018).

In terrestrial ecosystems, prey often relocate themselves in different vegetation types between day and night. Vegetation cover is a strong determinant of predators hunting efficiency (Hopcraft, Sinclair, & Packer, 2005; Mysterud & Østbye, 1999; Wirsing, Cameron, & Heithaus, 2010), and prey may use these diel shifts in habitat selection to reach habitats where they are less vulnerable (i.e., have a lower likelihood of being killed if attacked). These diel habitat shifts are widely observed and could be particularly important when prey face predators such as wolves *Canis lupus*, whose space use at the landscape scale is poorly predictable (Basille et al., 2015; Creel, Winnie, Maxwell, Hamlin, & Creel, 2005; Kittle et al., 2017; Middleton et al., 2013; Schmidt & Kuijper, 2015).

When prey face predators with a predictable space use (i.e., when predators focus on prey resource patches rather than on tracking prey themselves; Sih, 2005), prey may also reduce their encounter risk by moving away from risky areas during the active periods of the predator. Such strategy would lead to diel migrations (DM), defined as back and forth movements along a spatial, ecologically relevant, gradient. For instance, along a gradient of predation risk, prey would move away from spatially risky areas during the risky periods and move back to these risky areas when it becomes safer. There are surprisingly few examples of DM in terrestrial systems, except in the context of human hunting with hunted

species moving to protected areas during the day (Fortin et al., 2015; Tolon et al., 2009). Conversely, DMs have been commonly described in a wide range of taxa in aquatic ecosystems (Alonzo, Switzer, & Mangel, 2003; Benoit-Bird & Au, 2006; Hays, 2003). For example, in marine systems, zooplankton forage on phytoplankton at the sea surface at night when their predators have a reduced visual acuity and move towards deeper water during the day to reduce the risk of being detected, leading to the emergence of diel vertical migrations (Hays, 2003; Iwasa, 1982). In these systems, the DM takes prey not only significantly away from the predators during the risky periods but also to areas where these predators are less efficient (the predator evasion hypothesis; Hays, 2003). Thus, DM in aquatic ecosystems cannot shed light on whether prey would, in the presence of predictable predators, evolve DM strategies, irrespectively of their potential effect on vulnerability.

Here, we tested in a terrestrial ecosystem the hypothesis that prey develop a DM strategy when confronted with a primarily nocturnal predator whose distribution is predictable and spatially anchored near prey resource patches. We focused on the diel space use patterns of African lions *Panthera leo* and plains zebras *Equus quagga*, in Hwange National Park (Hwange NP), Zimbabwe. In HNP, zebra is one of the five main prey species of lions (Davidson et al., 2013), and lion is the main predator of zebras (S.C.-J.). In this mostly wooded savannah ecosystem, artificial waterholes are associated with large open areas (Chamaillé-Jammes, Fritz, & Madzikanda, 2009a; Courbin et al., 2016), which are rare (<2% of the study area), and the abundance of large herbivores is high in these areas, which can be considered prey hotspots. Zebras favour these short grasslands during daytime (Courbin et al., 2016; Valeix et al., 2009) as they provide profitable forage and high visibility. Lions are ambush predators that need vegetation cover to approach their prey undetected and launch a successful attack (Loarie, Tambling, & Asner, 2013). However, in HNP, lions search for prey in grasslands near waterholes at night (Courbin et al., 2016; Davidson et al., 2013; Valeix et al., 2010). We therefore predicted that zebras should display DM, coming close to waterholes during the day to forage when lions are less active and moving away at night to decrease the risk of encountering lions when they become active. Our results supported this prediction. We then quantified to what extent the DM of zebras decreased their risk of encountering lions. Given the lion distribution focused around waterholes, we predicted that the effect of DM on encounter risk should outweigh those of potential diel changes in the use of vegetation cover types.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study was conducted in Hwange NP, Zimbabwe. The vegetation is typical of dystrophic semi-arid wooded savannahs (average annual

rainfall is c. 600 mm), with woodlands and bushlands interspersed with small grassland patches (Chamaillé-Jammes, Fritz, & Murindagomo, 2006). We focused on two contrasting seasons: the wet season (November to April) and the late dry season (August to October). During the latter, zebras drink at artificial waterholes (hereafter referred to as “waterholes”) that are the only perennial sources of water. All statistical analyses were conducted for both seasons.

In the study area, zebras make up <10% of the lion diet (Davidson et al., 2013). Lion population density is however high at c. 3.5 lions/100 km<sup>2</sup> (Loveridge et al., 2016) and predation likely controls the zebra population (Grange et al., 2015), which is currently stable or slightly declining at c. 100 zebra/100 km<sup>2</sup> (Chamaillé-Jammes, Valeix, Bourgarel, Murindagomo, & Fritz, 2009b; Grange et al., 2015; unpublished demographic data).

## 2.2 | Testing for the existence of zebra DM

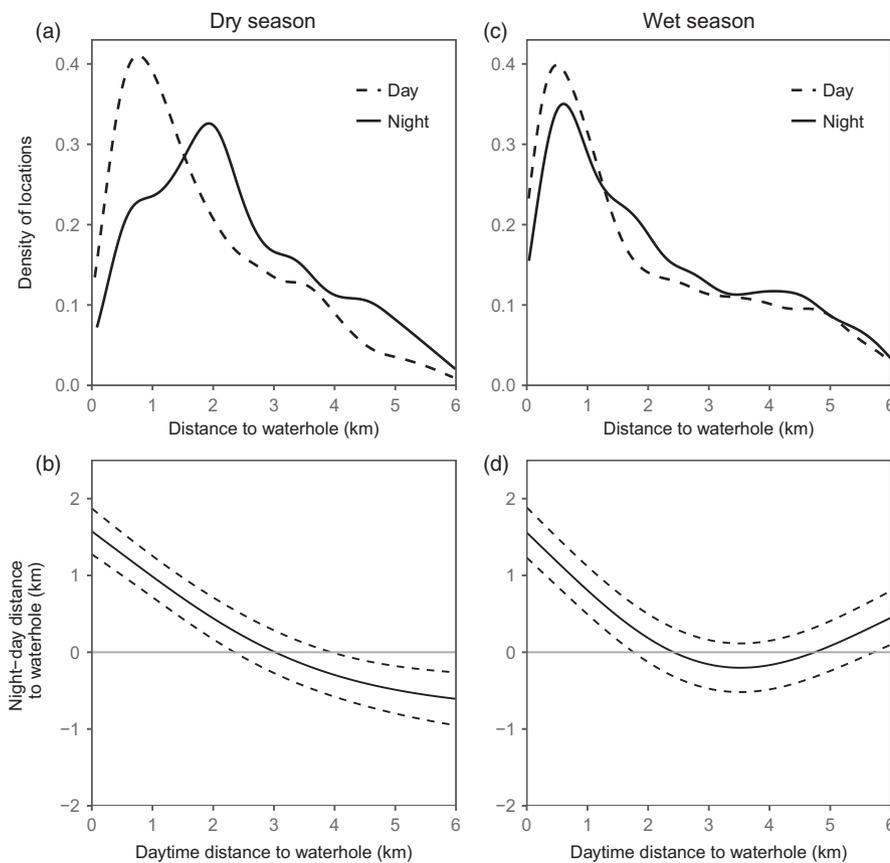
We used GPS locations collected hourly from 25 adult female zebras (18 zebras in dry season and 24 zebras in wet season), colored in different herds between August 2009 and November 2013, to assess whether zebras moved away from waterholes at night. For each day and night of each season, we estimated the distance to the closest waterhole (hereafter “distance to waterhole”) as the median of the distances to a waterhole an individual was over its GPS locations for the given day or night. See Supporting Information Figure S1.1 in Appendix S1, for the sunrise-/sunset-based definition of day/night periods.

We used least-squares spectral fitting to test that distance to waterhole displayed a 24-hr periodicity. For each zebra in each season, we visually inspected Lomb–Scargle periodograms (Ruf, 1999) for peaks around 24 hr and tested the significance of the largest peak within the 20- to 28-hr window using the randomization procedure implemented in the *lomb* package (Ruf, 1999) for the R software (R Development Core Team, 2016).

For individuals displaying a significant 24-hr periodicity in distance to waterhole (i.e., those performing a DM), we investigated whether displacement away from waterholes depended upon their proximity to waterholes during the previous daytime period. We did this by modelling the relationship between the night-time movement away from waterholes and the distance to waterhole during the preceding day using a generalized additive mixed model (GAMM) with thin plate regression splines (Wood, 2003). Individuals were included as random factors to account for non-independence of GPS locations within an individual. The model was fitted using the *gamm4* package (Wood & Scheipl, 2014) for the R software (R Development Core Team, 2016).

## 2.3 | Modelling the risk of encountering lions in the landscape

We first used GPS data from lions, collected over the same period as for zebras, and inhomogeneous Poisson point process models (Aarts, Fieberg, Brasseur, & Matthiopoulos, 2013; Johnson, Hooten, & Kuhn, 2013) to build predictive maps of the risk of encountering lions across the landscape (see Appendix S2). Separate risk maps were built for



**FIGURE 1** (a, c) Distribution of zebra locations as a function of distance to waterhole during daytime and night-time. The distribution is truncated at 6 km (dry season: for both day and night, 90% of data are shown and the tail reaches c. 15 km; wet season: 76% and 78% of daytime and night-time data are shown, respectively, the tails of the distribution reach 38 km [daytime] and 34 km [night-time]). (b, d) Difference between zebra distance to waterhole at night and their distance to waterhole during the previous day, as predicted by a generalized additive mixed model (dry season:  $df = 2.827$ ,  $F = 119.8$ ,  $p < 0.001$ ; wet season:  $df = 2.986$ ,  $F = 134$ ,  $p < 0.001$ ). Positive (negative) values indicate that zebras moved away from (closer to) waterhole at night. Dotted lines represent the 95% confidence interval

daytime and night-time because lions displayed day/night changes in habitat selection (see Figure 1 and Supporting Information Table S2.2 in Appendix S2). We validated the predictive performance of our daytime and night-time risk maps using the k-fold cross-validation method (Boyce, Vernier, Nielsen, & Schmiegelow, 2002).

## 2.4 | Quantifying the relative effects of DM and changes in use of vegetation cover on the risk of encountering lions

To disentangle the relative effects of DM and changes in selection for cover at night in decreasing the risk of encounter between zebras and lions, we estimated and compared the actual risk experienced by zebras during the daytime and night-time situations (situations 1 and 2 respectively) and two hypothetical situations reflecting either a lack of behavioural adjustments of zebras at night (situation 3 whereby zebras do not move away from waterholes and do not alter their selection for vegetation cover type) or the use of DM only, without changes in the use of vegetation cover at night (situation 4). We combined zebra GPS locations and encounter risk maps (Section 2.3), and for each situation, we estimated risk experienced by zebras as follow:

Situation 1, "actual zebra daytime risk": We estimated zebra risk of encountering lions during the day by extracting, for each zebra GPS location acquired during daytime, the risk of encountering lions from the daytime risk map, and calculated the median risk over each day.

Situation 2, "actual zebra night-time risk": We estimated zebra risk of encountering lions during the night by extracting, for each zebra GPS location acquired during night-time, the risk of encountering lions from the night-time risk map, and calculated the median risk over each night.

Situation 3, "hypothetical zebra night-time risk in absence of behavioural adjustments": for this hypothetical situation, we assumed that zebras neither moved away from waterholes nor altered their selection for vegetation cover type at night. To calculate risk, we considered that, for each night, zebra GPS locations were those of the preceding daytime period (i.e., the use of vegetation types and distance to waterhole were thus retained). We then extracted the risk of encountering lions from the night-time risk map and calculated the median risk over each night.

Situation 4, "hypothetical zebra night-time risk with DM only": for this hypothetical situation, we assumed that at night, zebras used the various vegetation types exactly as during the preceding daytime period, but adjusted their distance to waterhole. To calculate risk, we considered that, for each night, zebra GPS locations were those of the preceding daytime period (i.e., the use of vegetation types was thus retained), but that their distance to waterhole was shifted by a distance equal to the particular observed DM between this night and the preceding daytime period (i.e., the difference between the median distance to waterhole over the actual night-time GPS locations and the median distance to waterhole over the GPS locations of the preceding daytime period). Then,

for each zebra GPS location, we extracted the risk of encountering lions from the night-time risk map and calculated the median risk over each night.

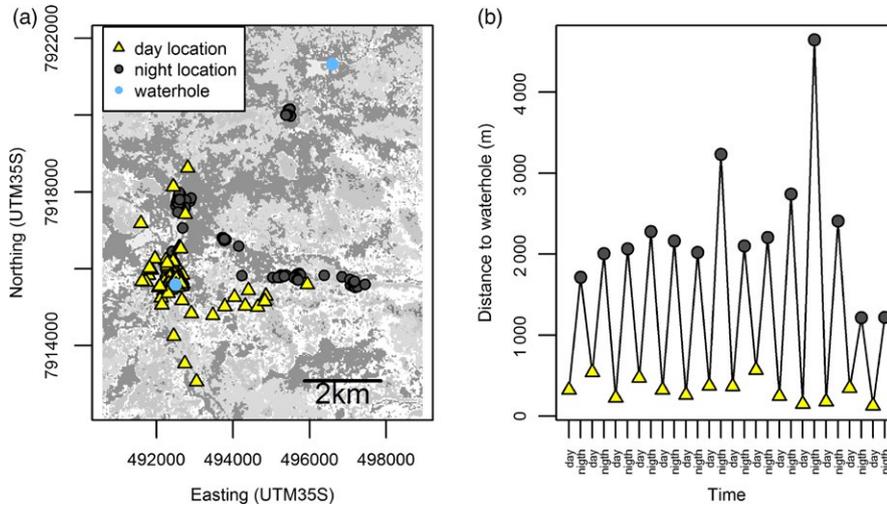
We compared these situations to estimate the changes in risk levels experienced by zebras and quantify the contribution of the various behavioural adjustments underlying these changes. We compared situation 1 (actual daytime risk) and situation 3 (hypothetical night-time risk in absence of zebra behavioural adjustments) to estimate to what extent lion behavioural changes at night would increase zebra risk of encountering lions if zebras behaved as they did during the day. We compared situation 2 (actual night-time risk) and situation 3 (hypothetical night-time risk in absence of zebra behavioural adjustments) to estimate to what extent zebra behavioural changes at night (i.e., changes in selection for vegetation types and DM) reduced their risk of encountering lions. We compared situation 3 (hypothetical night-time risk in absence of zebra behavioural adjustments) and situation 4 (hypothetical zebra night-time risk with DM only) to estimate to what extent DM only decreased encounter risk at night. Finally, we compared situation 2 (actual night-time risk) and situation 4 (hypothetical zebra night-time risk with DM only) to estimate the extent to which changes in vegetation cover types used reduced encounter risk.

Statistical analyses were conducted by fitting a linear mixed model, with the response variable containing the risk values for each day (situation 1) or night (situations 2, 3, 4) and the predictor coding the situation. We used random intercepts for individual IDs to consider the non-independence among multiple periods for each individual. From this model, we obtained both estimates of the mean risk value and the associated 95% confidence intervals for each situation (no intercept model) and estimates of differences in risk between situations (model with intercept). Models were fitted using the *lme4* package (Bates, Maechler, Bolker, & Walker, 2015) for the R software (R Development Core Team, 2016).

## 3 | RESULTS

### 3.1 | Zebras undertake DM

During the dry season, zebras were generally within a few kilometres of a waterhole, but were closer to waterholes during the day than at night (Figures 1a and 2). Periodogram analyses confirmed that distance to waterhole displayed a well-marked 24-hr cycle that was significant for 83% of the individuals, while DM frequency varied among individuals (note the variability in normalized power values; Figure 3a). Zebras moved towards waterholes in the first hours of the morning and moved away at sunset (see Supporting Information Figure S1.1 in Appendix S1). For zebras with a significant DM pattern, the magnitude of DM declined as daytime distance to waterhole increased, the estimated DM being up to 1.7 km when zebras were in the close proximity of a waterhole during the day (Figure 1b). No DM occurred beyond a daytime distance of 2.4 km. Zebras possibly even moved towards waterholes at night when >4 km from them during the day, although the magnitude of DM was small and kept zebras at intermediate distance to waterholes at night (Figure 1b).



**FIGURE 2** Example of diel migration behaviour. The panels display (a) GPS locations and (b) the median distance to the closest waterhole during day and night, using data obtained from zebra ID AU299 over a 14-day period during the 2009 dry season in the Hwange National Park, Zimbabwe

During the wet season, zebras remained close to waterholes at night more often than during the dry season (Figure 1c). Zebras also used DM but, compared to the dry season, the 24-hr periodicity in back-and-forth movement to waterholes was significant for a lower proportion of zebras (54%) and DMs were less frequent (i.e., lower normalized power values; Figure 3b). Also, for zebras with a significant DM pattern, the DM vanished at shorter daytime distance to waterhole (1.8 km, Figure 1d).

### 3.2 | Relative importance of zebra behaviours in reducing encounter risk with lions

During the dry season, the risk of encountering lions, as indexed by our models of lion habitat selection, always decreased rapidly with the distance to waterhole and increased with vegetation openness, especially at night (Supporting Information Figure S2.1 and Table S2.2 in Appendix S2). This would lead zebras to experience a 160% increase in risk at night if they did not adjust their behaviour ( $\text{risk}_{\text{situation 3}}$  (hypothetical night-time risk in absence of behavioural adjustments) [mean (95% CI): 1.16 (0.96;1.37)] >  $\text{risk}_{\text{situation 1}}$  (actual daytime risk) [0.72 (0.47;0.92)],  $p < 0.001$ ; Figure 4). The DM undertaken by zebras allowed them to largely reduce their risk of encountering lions at night ( $\text{risk}_{\text{situation 4}}$  (hypothetical night-time risk with DM only) [0.86 (0.64;1.05)] <  $\text{risk}_{\text{situation 3}}$  (hypothetical night-time risk in absence of behavioural adjustments),  $p < 0.001$ , Figure 4). Quantitatively, the relative contribution of DM in decreasing zebra night-time encounter risk with lions was of 90% ( $\frac{\text{risk}_{\text{situation 3}} - \text{risk}_{\text{situation 4}}}{\text{risk}_{\text{situation 3}} - \text{risk}_{\text{situation 2}}} \times 100$ ), while changes in vegetation types used by zebras at night contributed for 10% only ( $1 - \frac{\text{risk}_{\text{situation 3}} - \text{risk}_{\text{situation 4}}}{\text{risk}_{\text{situation 3}} - \text{risk}_{\text{situation 2}}}$ ) of the total decrease in observed encounter risk (Figure 4). Consistently, we did not find empirical support that changes in vegetation types used by zebras at night decreased their night-time encounter risk with lions ( $\text{risk}_{\text{situation 2}}$  (actual night-time risk) [0.83 (0.69;0.96)] did not differ significantly from  $\text{risk}_{\text{situation 4}}$  (hypothetical night-time risk with DM only):  $p > 0.10$ , Figure 4).

During the wet season, patterns were broadly similar (Figures 1d and 4), but zebras generally stayed closer to waterholes and DM

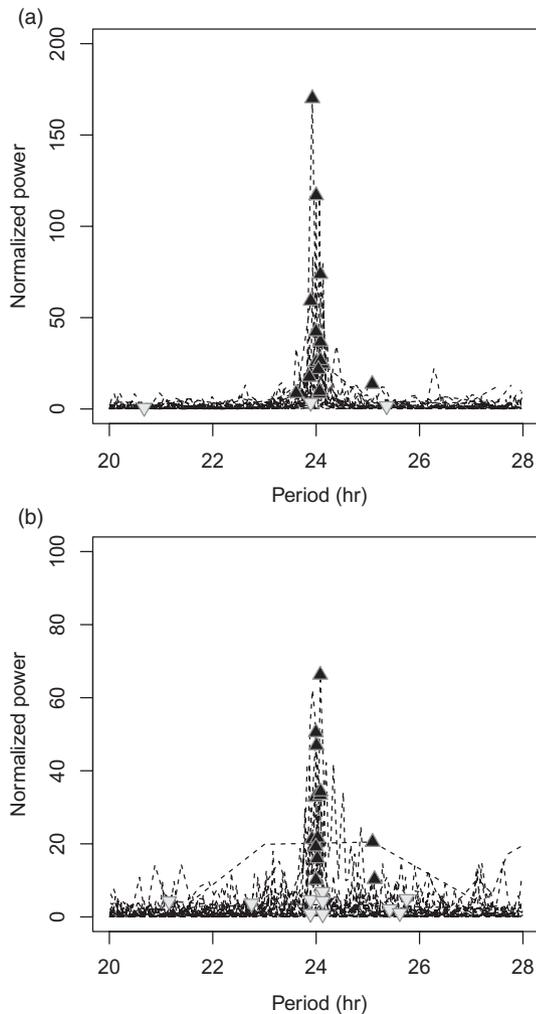
were shorter when they occurred (Figure 1c,d). Consequently, zebra risk of encountering lions was generally larger for all situations, and the reductions in encounter risk were smaller. The relative contribution of DM in decreasing night-time encounter risk was of 58% ( $\frac{\text{risk}_{\text{situation 3}} - \text{risk}_{\text{situation 4}}}{\text{risk}_{\text{situation 3}} - \text{risk}_{\text{situation 2}}} \times 100$ ), while changes in vegetation types use at night contributed for 42% ( $1 - \frac{\text{risk}_{\text{situation 3}} - \text{risk}_{\text{situation 4}}}{\text{risk}_{\text{situation 3}} - \text{risk}_{\text{situation 2}}}$ ) in decreasing encounter risk (Figure 4). The lower contribution of DM to the reduction in risk, compared to the one observed in the dry season, was likely due to the fact that lions are more spread away from waterholes in the wet season (Supporting Information Figure S2.1 in Appendix S2).

## 4 | DISCUSSION

Our study shows that, in Hwange NP, zebras use areas located near artificial waterholes during daytime, benefiting from the large open grasslands (Chamaillé-Jammes et al., 2009a; Courbin et al., 2016), but routinely move away from them at risky night period, thereby reducing their risk of encountering lions. The diel cycle of predator avoidance revealed here relies on DM and is independent of vegetation cover types, as at night, zebras still use open grasslands (Courbin et al., 2016), conveying an alternative strategy to the well-known day/night habitat selection shift reported so far in terrestrial systems (Kronfeld-Schor & Dayan, 2003; Laundré, 2010; Mysterud & Østbye, 1999). Also, the anti-predator DM occurring here or in aquatic systems (Benoit-Bird & Au, 2006; Burks, Lodge, Jeppesen, & Lauridsen, 2002; Hays, 2003; Iwasa, 1982), where prey can never be free of predation risk, differs from the diel response showed by hunted ungulates that take refuge during the day in protected areas completely free of risk (no hunting), for example, wild boars *Sus scrofa* L. (Tolon et al., 2009) and bison *Bison bison* (Fortin et al., 2015).

### 4.1 | An alternative hypothesis unrelated to predation risk

Although our results are highly consistent with zebra DM being an anti-predator behaviour, we considered the alternative hypothesis



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

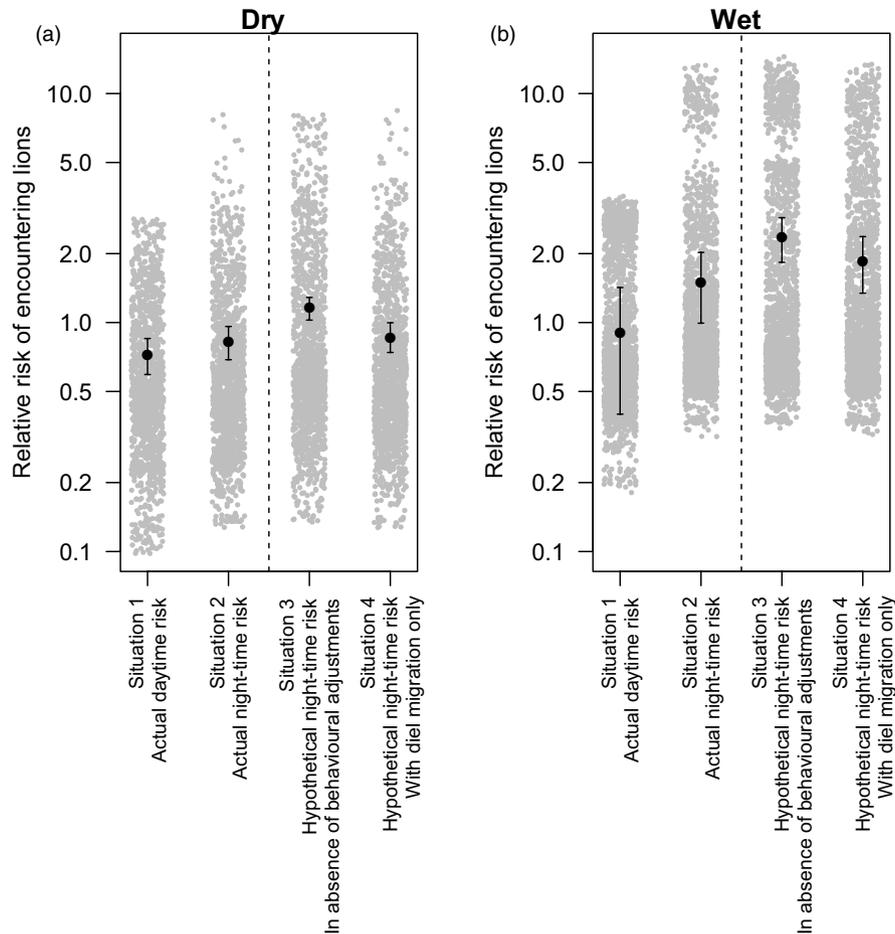
that the zebra DM could be driven by a daily need to drink but also to forage in better places located far away from water, which could potentially be less depleted. Although we did not have data to test whether forage is more available or of higher quality further away from waterholes, we argue this hypothesis very unlikely. If it was beneficial to forage away from waterholes, we would expect zebras to minimize their time near waterholes, as found in other ecosystems where the best foraging places are located far from water (Cain, Owen-Smith, & Macandza, 2012). This is not what we observed, as during the day, zebras stayed close to waterholes for much longer than what would be required to simply come and drink (which they would do in an hour or so, Périquet et al., 2010). When in open grasslands near waterholes, zebras are not only seen travelling, but

mostly commonly are observed foraging or resting (S. Chamailé-Jammes, pers. obs.). Daytime preference of zebras for areas located near waterholes was also observed in Valeix et al. (2009), a study conducted in the same area but with different data. In addition, zebras would have no reasons to be near waterholes in the wet season when they do not need to drink. However, their attraction to areas near waterholes is more marked in the wet season than in the dry season. Generally, our results are not consistent with the hypothesis that zebras would prefer foraging away from waterholes. Results are more consistent with the hypothesis that night-time avoidance of lions explains the DM of zebras away from their preferred foraging areas located near waterholes.

#### 4.2 | Diel migration is advantageous when space use of the predator is predictable

Diel migration may emerge as an efficient strategy to deal with food-safety trade-offs when prey can reliably identify and travel to places where the absence of a predator is likely (Iwasa, 1982; Sainmont, Thygesen, & Visser, 2013). This could in particular occur with ambush predators that focus around prey hotspots, and have multiple prey species to hunt, some being more spatially constrained than others. This creates an asymmetry by which the most mobile prey greatly benefit from moving away from these hotspot during the risky times, while the predator has little incentive to do so and engage in a costly search. In Hwange NP, lions remain near waterholes most of the time, despite being free to move anywhere (Valeix et al., 2010; Courbin et al., 2016; this study). The large patches of grasslands located near these waterholes attract grazers and mixed feeders all year round, and the many water-dependent species naturally use these waterholes during the dry season. Lions, which can feed on a large number of species, do not need to track zebras moving away from waterhole areas if some other prey species remain near waterholes at night. This is the case of several large species (e.g., buffalo *Syncerus caffer*, giraffe *Giraffa camelopardalis*, elephant *Loxodonta africana*) whose individuals are regularly seen drinking at night (Valeix, Chamailé-Jammes, & Fritz, 2007), are killed close to water (Davidson et al., 2013) and make a dominant share of the lions' diet in Hwange NP (Davidson et al., 2013). Irrespective of why lions remain near waterhole areas, their behaviour makes areas away from waterholes predictably safer, and our results show that zebras benefit from this predictability. Zebras have developed a DM strategy allowing them to more than halve their risk of encountering lions at night, when lions hunt, compared to staying near waterholes. Thus, daily zebra movements to and from waterholes may provide a mechanistic explanation for the low night-time lion-zebra encounter rate observed in Hwange NP (one encounter every 35 days on average; Courbin et al., 2016).

Contrary to ambush predators such as lions, coursing predators such as wild dogs *Lycaon pictus* in African savannahs or wolves in temperate systems roam over vast areas to locate suitable prey, and presence/absence of such predators could be less predictable. Prey of cursorial predators should therefore shift towards safer



**FIGURE 4** Expected risk of encountering lions for zebras during the dry (a) and wet (b) seasons, in four situations: actual daytime risk (situation 1), actual night-time risk (situation 2), hypothetical night-time risk in absence of behavioural adjustments of zebras (no DM and no change in selection for vegetation types) (situation 3), hypothetical night-time risk with zebra diel migration but unchanged zebra use of the different vegetation cover types (situation 4). The actual risk situations were separated from the hypothetical risk situations with a dotted line. Risk is shown on a log scale. All possible comparisons are significant at  $\alpha = 0.05$  for each season, except between situations 2 and 4 in the dry season. See Section 3 for details

neighbouring habitats when the predator is detected or is likely to revisit the area rather than moving towards areas where predation risk is uncertain (see examples with wolves; Basille et al., 2015; Creel et al., 2005; Kittle et al., 2017; Kohl et al., 2018; Latombe, Fortin, & Parrott, 2014; Middleton et al., 2013; Schmidt & Kuijper, 2015).

Overall, the emergence of DM is closely linked to the landscape context constraining the spatial behaviour of predators (i.e., presence of a spatial anchor) and to the food web complexity (i.e., predator–multi-prey system) potentially relaxing the need for a predator to search for one prey species in particular. In this context, it would prove valuable to test the existence of DM in other prey and other ecosystems, contrasting situations with varying levels of prey and predator predictability.

#### 4.3 | Does the absence of safe vegetation types facilitate the emergence of DM?

We found that zebras did not alter their selection for vegetation types at night to an extent that would significantly reduce encounter

risk with lions. We suspect that this is due to a trade-off between encounter risk and vulnerability across vegetation types. At night, lions strongly select for more open vegetation, possibly to benefit from increased visibility and to maximize encounter rates with prey (Courbin et al., 2016; see Supporting Information Figure S2.1 in Appendix S2). Zebras could reduce the risk of encountering lions by selecting for more bushy vegetation (see Supporting Information Figure S2.1 in Appendix S2), but they would then become highly vulnerable in case of an encounter with lions which are primarily ambush/stalking predators (Caro, 2005; Davidson et al., 2012; Loarie et al., 2013). **Therefore, zebras may decrease encounter risk while maintaining a low vulnerability by conducting DM towards open vegetation types localized in relatively safe areas (i.e., far from waterholes).**

#### 4.4 | Do DMs have population-level consequences?

Our results could suggest that DM, which strongly decreases zebra likelihood of encountering lions, is a prime determinant of zebra

survival rate. However, data from both lion kill surveys (Davidson et al., 2013) and zebra demographic monitoring (Grange et al., 2015) show that adult zebras are less likely to be predated upon by lions during the wet season, when we found that DMs were much less prevalent than in the dry season. It is yet unknown whether this seasonal difference in DM patterns is driven by resources or predation sensitivity. It could be linked to the higher cost of leaving the best foraging patches at a time when grass quality is high. Also, it could be that lion favour other prey during the wet season, although previous work does not suggest so (Davidson et al., 2013). All these explanations could explain the lack of relationship between predation rate on adults and prevalence of the DM across seasons, but all remain speculative. Also, it is possible that in the wet season, during which most zebra foals are born, lions favour hunting juvenile zebras. Almost half of the juvenile zebras are killed during their first 6 months, mostly by lions (Grange et al., 2015). Therefore, the link between DM and adult predation rate may be distorted by the seasonal presence of juveniles. Groups with newborns may be less mobile. However, the presence of juveniles, which are more vulnerable than adults, could actually increase the impetus for DM to reduce encounter rate. Overall, it remains to be investigated whether individual variability in juvenile survival rate could be linked to the ability of some herds to perform longer DM earlier after the birth season. This would allow assessing the population-level consequences of DM, which may occur via consumptive or non-consumptive (e.g., increased energetic expenditure) effects.

## 5 | CONCLUSIONS

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

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## AUTHORS' CONTRIBUTIONS

N.C. and S.C.-J. conceived the ideas and designed methodology; A.J.L., D.W.M., H.F., M.V. and S.C.-J. organized data collection; N.C. conducted the statistical analyses; N.C. and S.C.-J. led the writing of the manuscript; A.J.L., D.W.M., H.F., R.P. and M.V. revised the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5d48n33> (Courbin et al., 2018).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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