Zebra diel migrations reduce encounter risk with lions at night

Nicolas Courbin[1,2*], Andrew J. Loveridge[2], Hervé Fritz[3,4], David W. Macdonald[2], Rémi Patin[1], Marion Valeix[2,3,4], Simon Chamaillé-Jammes[1,4,5]

[1] CEFE, CNRS, Univ. Montpellier, Univ. Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

[2] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Oxford OX13 5QL, United Kingdom

[3] Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, Centre National de la Recherche Scientifique (CNRS), Université Claude Bernard Lyon 1, Bât Gregor Mendel, 43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France

[4] LTSER France, Zone Atelier "Hwange", Hwange National Park, Bag 62, Dete, Zimbabwe - CNRS HERD (Hwange Environmental Research Development) program

[5] Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa

*Corresponding author: ncourbin@gmail.com

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 nighttime risk of encountering lions, which generally remain close to waterholes. Zebra changes in nighttime 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 (1) quantify, in a terrestrial system, the effect of a predator-induced DM on the likelihood of encountering a predator, and (2) 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*.

INTRODUCTION

Predation is a pervasive evolutionary force that shape organisms behaviour (Lima & Dill, 1990; Caro, 2005). Most anti-predator behavioural responses are however balanced against other fitness-beneficial activities, in particular food resource acquisition (Lima & Dill, 1990; Brown & Kotler, 2004). 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 24h cycle (Clark & Levy, 1988; Lima & Dill, 1990; Kronfeld-Schor & Dayan, 2003; Kohl et al., 2018). 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 (Fischhoff, Sundaresan, Cordingley, & Rubenstein, 2007; Middleton et al., 2013; Basille et al., 2015; Padié et al., 2015; Kohl et al., 2018). 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 (Mysterud & Østbye, 1999; Hopcraft, Sinclair, & Packer, 2005; 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 (Creel, Winnie, Maxwell, Hamlin, & Creel, 2005; Middleton et al., 2013; Basille et al., 2015; Schmidt & Kuijper, 2015; Kittle et al., 2017).

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 (hereafter, 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 (Tolon et al. 2009; Fortin et al. 2015). Conversely, DMs have been commonly described in a wide range of taxa in aquatic ecosystems (Alonzo, Switzer, & Mangel, 2003; Hays, 2003; Benoit-Bird & Au, 2006). 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 (Iwasa, 1982; Hays, 2003). 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 (hereafter 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 (pers. obs.). 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 (Valeix et al., 2009; Courbin et al., 2016) 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 (Valeix et al., 2010; Davidson et al., 2013; Courbin et al., 2016). 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.

MATERIALS AND METHODS

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^2 (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/100km^2 (Chamaillé-Jammes, Valeix, Bourgarel, Murindagomo, & Fritz, 2009b; Grange et al., 2015; unpublished demographic data).

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), collared in different herds between August 2009 and November 2013, to assess if 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 Appendix S1: Fig. S1.1, for the sunrise/sunset-based definition of day/night periods.

We used least-squares spectral fitting to test that distance to waterhole displayed a 24h-periodicity. For each zebra in each season, we visually inspected Lomb-Scargle periodograms (Ruf, 1999) for peaks around 24h, and tested the significance of the largest peak within the 20 to 28h 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 24h-periodicity in distance to waterhole (i.e. those performing a diel migration), we investigated if displacement away from waterholes depended upon their proximity to waterholes during the previous daytime period. We did this by modelling the relationship between the nighttime 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).

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 daytime and nighttime because lions displayed day/night changes in habitat selection (see Fig. 1 and Appendix S2: Table S2.2). We validated the predictive performance of our daytime and nighttime risk maps using the k-fold cross validation method (Boyce et al., 2002).

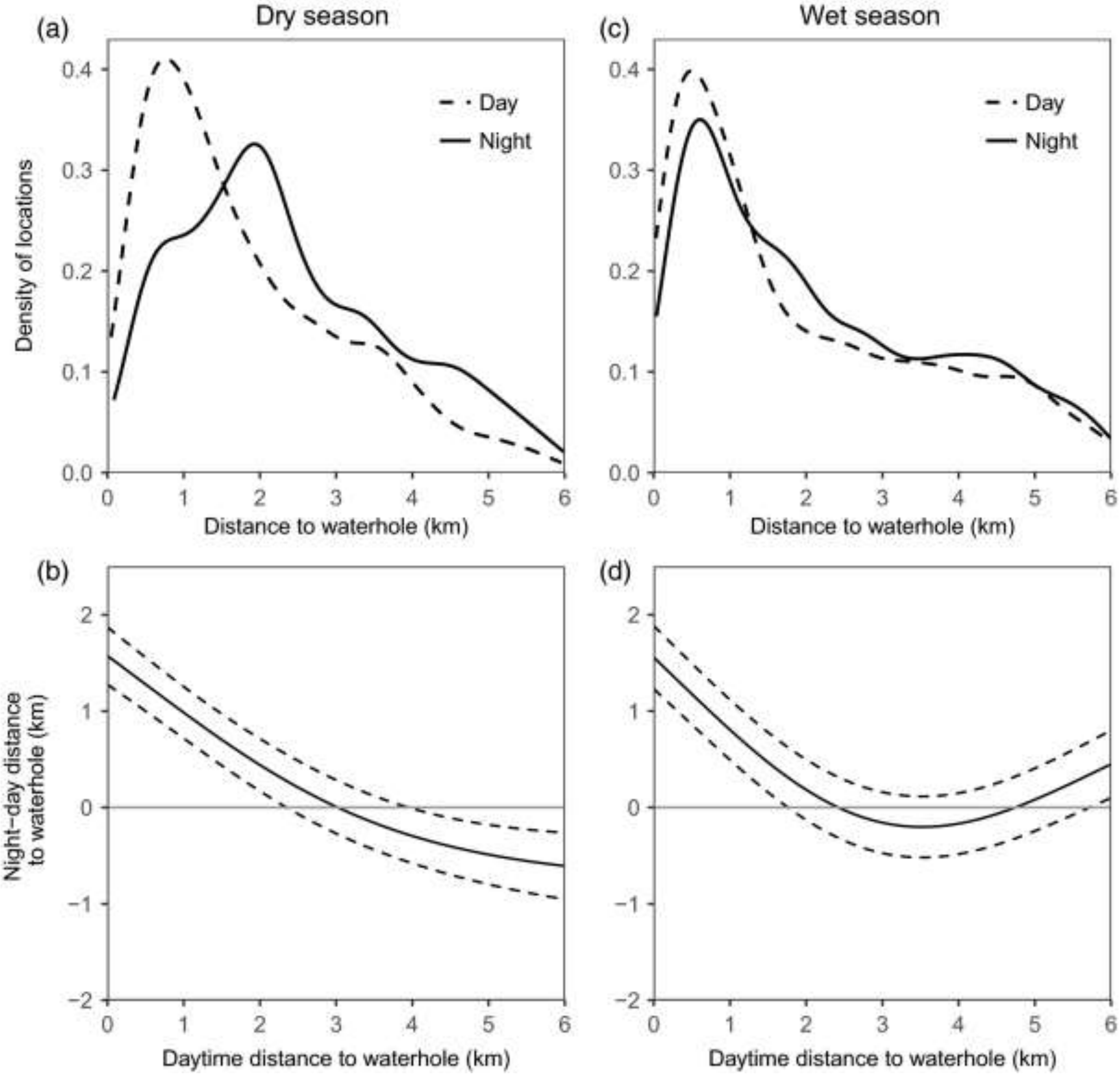

Figure 1. (A, C) Distribution of zebra locations as a function of distance to waterhole during daytime and nighttime. The distribution is truncated at 6km (dry season: for both day and night 90% of data are shown and the tail reaches c. 15km; wet season: 76% and 78% of daytime and nighttime data are shown, respectively, the tails of the distribution reach 38km [daytime] and 34km [nighttime]). (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.

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 nighttime 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 *Modelling the risk of encountering lions in the landscape*), 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 nighttime risk’: we estimated zebra risk of encountering lions during the night by extracting, for each zebra GPS location acquired during nighttime, the risk of encountering lions from the nighttime risk map, and calculated the median risk over each night.

- Situation 3, ‘hypothetical zebra nighttime 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 watehole were thus retained). We then extracted the risk of encountering lions from the nighttime risk map, and calculated the median risk over each night.

- Situation 4, ‘hypothetical zebra nighttime 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 diel migration between this night and the preceding daytime period (i.e., the difference between the median distance to waterhole over the actual nighttime 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 nighttime 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 nighttime 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 nighttime risk) and situation 3 (hypothetical nighttime 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 nighttime risk in absence of zebra behavioural adjustments) and situation 4 (hypothetical zebra nighttime risk with DM only) to estimate to what extent DM only decreased encounter risk at night. Finally, we compared situation 2 (actual nighttime risk) and situation 4 (hypothetical zebra nighttime 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).

RESULTS

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 (Figs 1A, 2). Periodogram analyses confirmed that distance to waterhole displayed a well-marked 24h cycle that was significant for 83% of the individuals, while DM frequency varied among individuals (note the variability in normalized power values, Fig. 3A). Zebras moved towards waterholes in the first hours of the morning and moved away at sunset (see Appendix S1: Fig. S1.1). 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 (Fig. 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 (Fig. 1B).

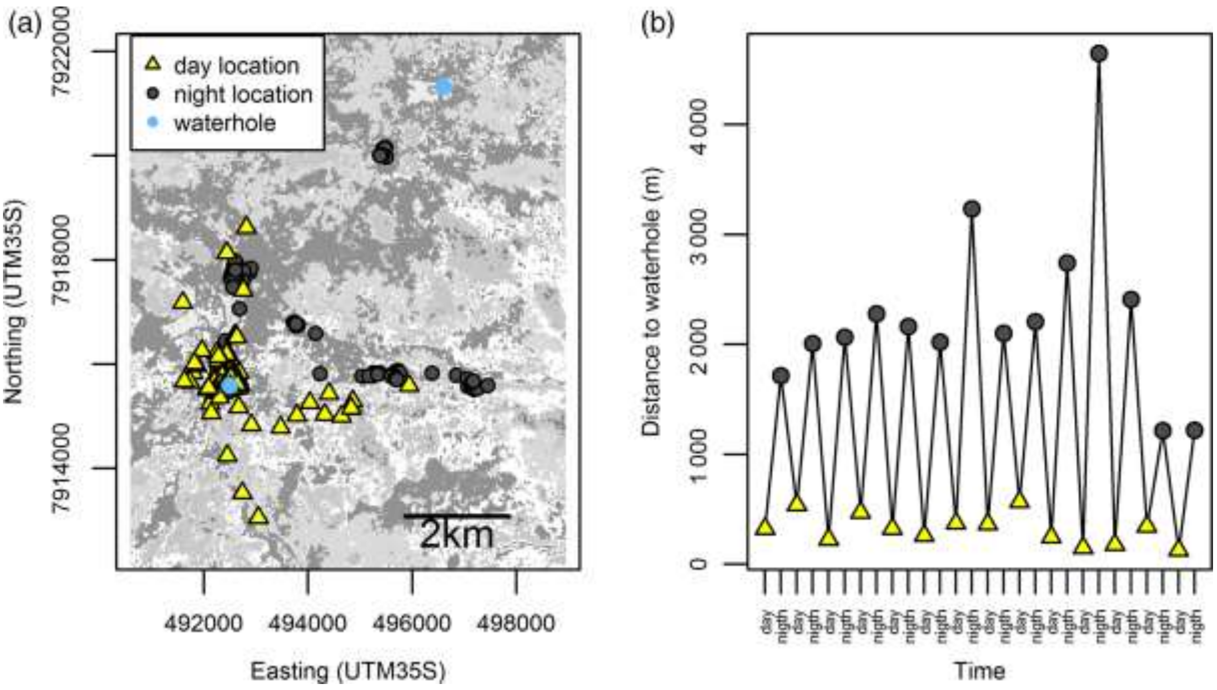

Figure 2. Example of diel migration behaviour. The panels display (A) GPS locations and (B) the median distance to the closest waterhole during day and night, using data obtained from zebra ID AU299 over a 14-day period during the 2009 dry season in the Hwange National Park, Zimbabwe.

During the wet season, zebras remained close to waterholes at night more often than during the dry season (Fig. 1C). Zebras also used DM but, compared to the dry season the 24h-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, Fig. 3B). Also, for zebras with a significant DM pattern, the DM vanished at shorter daytime distance to waterhole (1.8 km, Fig. 1D).

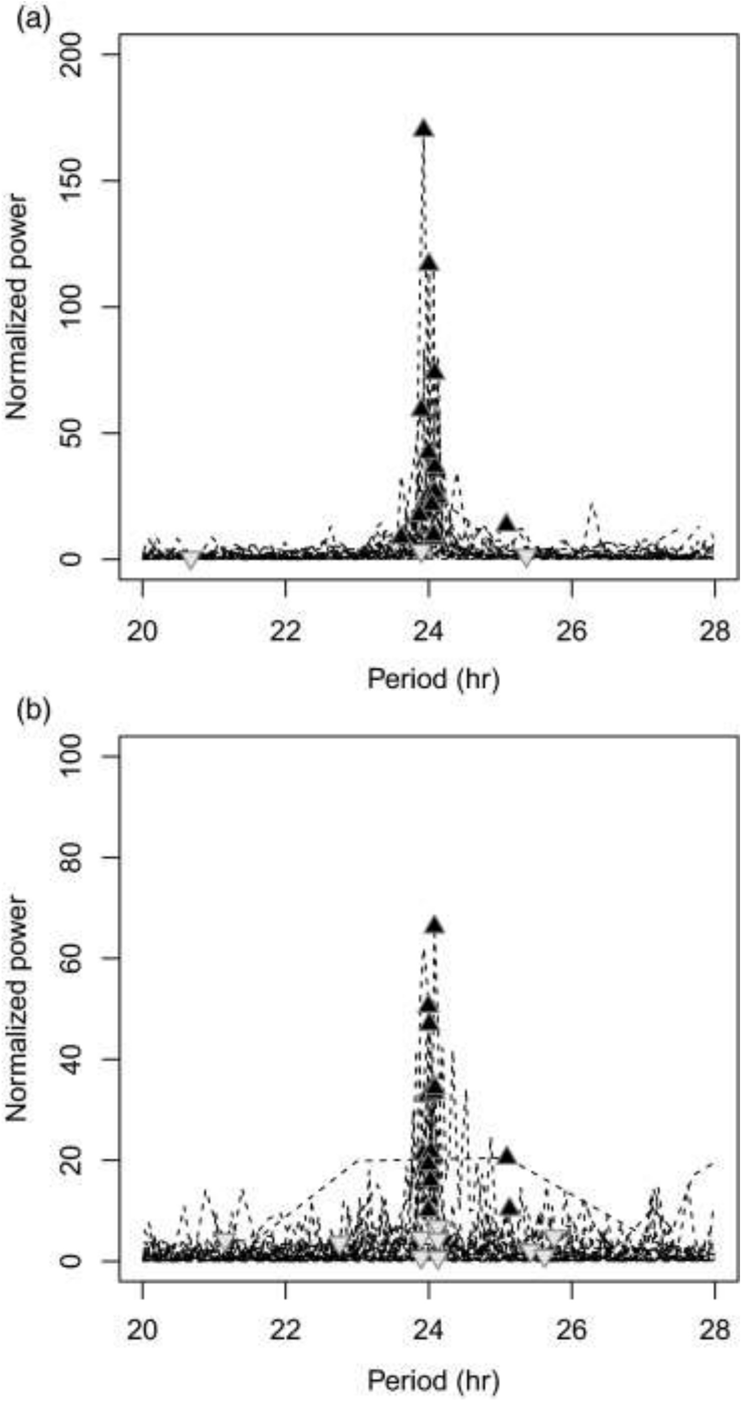

Figure 3. Periodograms of the distance to waterhole time-series for (A) the dry season and (B) the wet season. Each line represents the periodogram for one individual zebra, and the maximum value of each periodogram spectrum within the 20 to 28h-period window is indicated by a triangle. Black triangles pointing up and grey triangles pointing down indicate significant (*P*<0.05) and non-significant (*P*≥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.

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

During the wet season, patterns were broadly similar (Figs 1D, 4), but zebras generally stayed closer to waterholes and DM were shorter when they occurred (Figs 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 nighttime encounter risk was of 58% $(\frac{risk_{situation\ 3}-risk_{situation\ 4}}{risk_{situation\ 3}-risk_{situation\ 2}} \times 100)$ while changes in vegetation types use at night contributed for 42% $(1 - \left[\frac{risk_{situation\ 3}-risk_{situation\ 4}}{risk_{situation\ 3}-risk_{situation\ 2}} \times 100\right])$ in decreasing encounter risk (Fig. 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 (Appendix 2, Fig. S2.1).

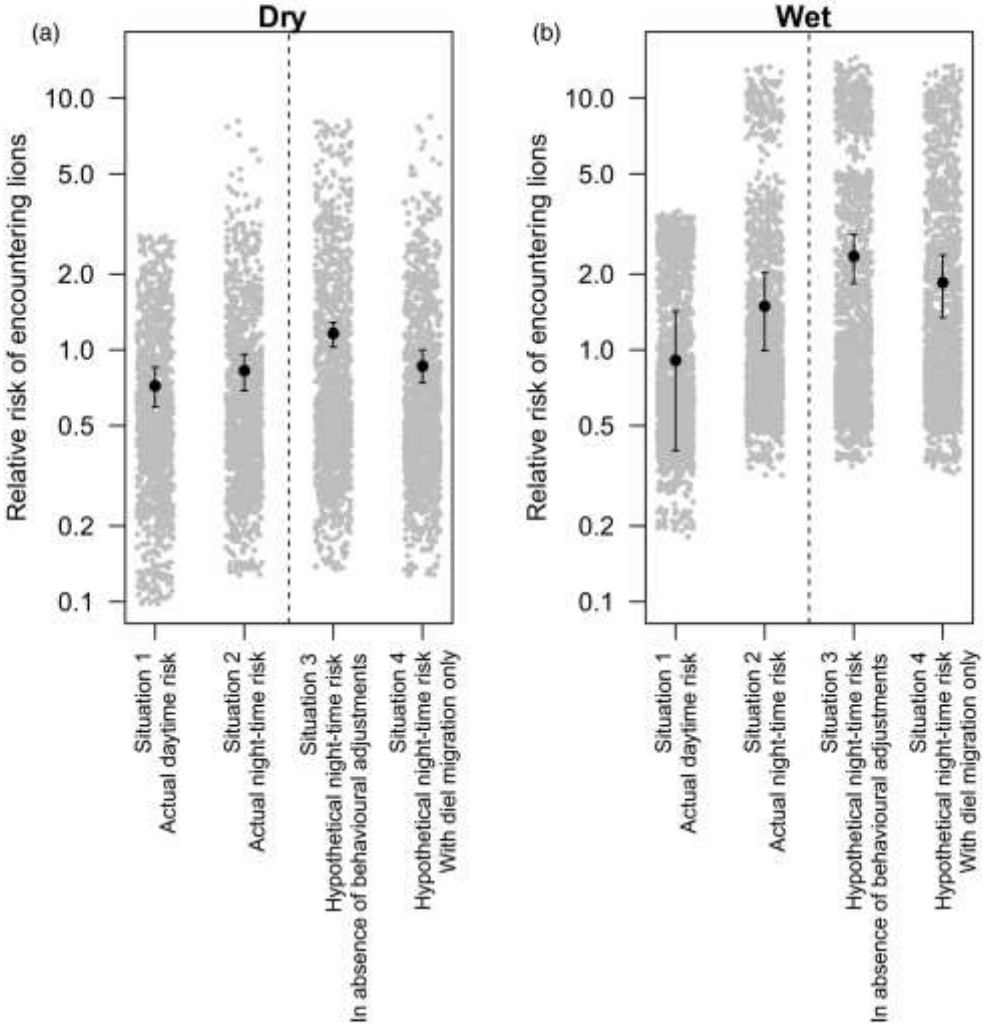

Figure 4. Expected risk of encountering lions for zebras during the dry (A) and wet (B) seasons, in four situations: actual daytime risk (situation 1), actual nighttime risk (situation 2), hypothetical nighttime risk in absence of behavioural adjustments of zebras (no DM and no change in selection for vegetation types) (situation 3), hypothetical nighttime 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 the *Results* section for details.

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 diel migration 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 (Mysterud & Østbye, 1999; Kronfeld-Schor & Dayan, 2003; Laundré, 2010). Also, the anti-predator diel migration occurring here or in aquatic systems (Iwasa, 1982; Burks, Lodge, Jeppesen, & Lauridsen, 2002; Hays, 2003; Benoit-Bird & Au, 2006), 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), e.g. wild boars *Sus scrofa* L. (Tolon et al., 2009) and bison *Bison bison* (Fortin et al., 2015).

An alternative hypothesis unrelated to predation risk

Although our results are highly consistent with zebra diel migration being an anti-predator behaviour, we considered the alternative hypothesis that the zebra diel migration 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 (Chamaillé-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 nighttime avoidance of lions explains the diel migration of zebras away from their preferred foraging areas located near waterholes.

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 that 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, Chamaillé-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 nighttime 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 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, Creel et al., 2005; Middleton et al., 2013; Latombe, Fortin, & Parrott, 2014; Basille et al., 2015; Schmidt & Kuijper 2015; Kittle et al., 2017; Kohl et al., 2018).

Overall, the emergence of diel migration 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.

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 Appendix S2: Fig. S2.1). Zebras could reduce the risk of encountering lions by selecting for more bushy vegetation (see Appendix S2: Fig. S2.1), 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).

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 if 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 diel migration 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 new-borns 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 if 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.

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.

ACKNOWLEDGMENTS

This research was partly funded by the grants ANR-08-BLAN-0022, ANR-11-CEPS-003, ANR-16-CE02-0001-01, Darwin Initiative for Biodiversity Grants 162-09-015 and EIDPO002, and International Program for Scientific Cooperation (PICS) from the CNRS. Beyond academic grants, this study was partly funded by Mitsubishi Fund for Europe and Africa, R.G. Frankenberg Foundation, Boesak and Kruger Foundation, Rufford Maurice Laing Foundation, SATIB Trust, Eppley Foundation, Riv and Joan Winant and Recanati-Kaplan Foundation. We thank M. Muzamba, J. Hunt, B. Stapelkamp, N. Elliot and H. Valls Fox contributed to fieldwork. The late N. Ganzin obtained and did some initial work on the Landsat images used for the vegetation map. This research was authorized by the Zimbabwe Parks and Wildlife Management Authority under permits (permit numbers: REF:DM/Gen/(T) 23(1)(c)(ii): 03/2009, 01/2010, 25/2010, 05/2011, 06/2011, 12/2012, 15/2012, 08/2013).

AUTHOR’S CONTRIBUTIONS

NC and SCJ conceived the ideas and designed methodology; AJL, DWM, HF, MV and SCJ organized data collection; NC conducted the statistical analyses; NC and SCJ led the writing of the manuscript; AJL, DWM, HF, RP and MV 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)

REFERENCES

Aarts, G., Fieberg, J., Brasseur, S., & Matthiopoulos, J. (2013). Quantifying the effect of habitat availability on species distributions. *Journal of Animal Ecology*, *82*, 1135-1145.

Alonzo, S. H., Switzer, P. V., & Mangel, M. (2003). Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. *Ecology*, *84*, 1598-1607.

Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J.-P., & Courtois, R. (2015). Plastic response of fearful prey to the spatio-temporal dynamics of predator distribution. *Ecology*, *96*, 2622-2631.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1-48.

Benoit-Bird, K. J., & Au, W. W. L. (2006). Extreme diel horizontal migrations by a tropical nearshore resident micronekton community. *Marine Ecology Progress Series, 319*, 1-14.

Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology letters*, *7*, 999-1014.

Burks, R. L., Lodge, D. M., Jeppesen, E., & Lauridsen, T. L. (2002). Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshwater Biology, 47*, 343-365.

Cain, J. W., Owen-Smith, N., & Macandza, V. A. (2012). The costs of drinking: comparative water dependency of sable antelope and zebra. *Journal of Zoology*, *286*, 58-67. doi:10.1111/j.1469-7998.2011.00848.x

Caro, T. M. (2005). *Antipredator defenses in birds and mammals*. Chicago, IL: University of Chicago Press.

Chamaillé-Jammes, S., Fritz, H., & Murindagomo, F. (2006). Spatial patterns of the NDVI-rainfall relationship at the seasonal and interannual time scales in an African savanna. *International Journal of Remote Sensing*, *27*, 5185-5200.

Chamaillé-Jammes, S., Fritz, H., & Madzikanda, H. (2009a). Piosphere contribution to landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant density landscape. *Ecography*, *32*, 871-880.

Chamaillé-Jammes, S., Valeix, M., Bourgarel, M., Murindagomo, F., & Fritz, H. (2009b). Seasonal density estimates of common large herbivores in Hwange National Park, Zimbabwe. *African Journal of Ecology*, *47*, 804-808.

Clark, C. W., & Levy, D. A. (1988). Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *The American Naturalist*, *131*, 271-290.

Courbin, N., Loveridge, A. J., Macdonald, D. W., Fritz, H., Valeix, M., Makuwe, E. T., & Chamaillé-Jammes, S. (2016). Reactive responses of zebras to lion encounters shape their predator-prey space game at large scale. *Oikos*, *125*, 829-838.

Courbin, N., Loveridge, A. J., Fritz, H., Macdonald, D. W., Patin, R., Valeix, M., & Chamaillé-Jammes, S. (2018). Data from: Zebra diel migrations reduce encounter risk with lions at night. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.5d48n33.

Creel, S., Winnie, J. Jr, Maxwell, B., Hamlin, K., & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology, 86*, 3387-3397.

Davidson, Z., Valeix, M., Loveridge, A. J., Hunt, J. E., Johnson, P. J., Madzikanda, H., & Macdonald, D. W. (2012). Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy, 93*, 677-685.

Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A. J., Hunt, J. E., Murindagomo, F., & Macdonald, D. W. (2013). Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. *PLoS ONE*, *8*, e55182.

Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., & Rubenstein, D. I. (2007). Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions. *Behavioral Ecology*, *18*, 725-729.

Fortin, D., Merkle, J. A., Sigaud, M., Cherry, S. G., Plante, S., Drolet, A., & Labrecque, M. (2015). Temporal dynamics in the foraging decisions of large herbivores. *Animal Production Science*, *55*, 376-383.

Grange, S., Barnier, F., Duncan, P., Gaillard, J.-M., Valeix, M., Ncube, H., … Fritz, H. (2015). Demography of plains zebras (Equus quagga) under heavy predation. *Population Ecology*, *57*, 201-214.

Hammond, J. I., Luttbeg, B., & Sih, A. (2007). Predator and prey space use: dragonflies and tadpoles in an interactive game. *Ecology*, *88,* 1525-1535.

Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, *503*, 163-170.

Hopcraft, G. J. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, *75*, 559-566.

Iwasa, Y. 1982. Vertical migration of zooplankton: a game between predator and prey. *The American Naturalist*, *120,* 171-180.

Johnson, D. S., Hooten, M. B., & Kuhn, C. E. (2013). Estimating animal resource selection from telemetry data using point process models. *Journal of Animal Ecology, 82*, 1155-1164.

Kittle, A. M., Anderson, M., Avgar, T., Baker, J. A., Brown, G. S., Hagens, J., … Fryxell, J. M. (2017). Landscape-level wolf space use is correlated with prey abundance, ease of mobility, and the distribution of prey habitat. Ecosphere, 8(4), e01783.

Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., … MacNulty, D. R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs*, *0,* 1-15.

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution and Systematics, 34*, 153-181.

Latombe, G., Fortin, D., & Parrott, L. (2014). Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology, 83,* 185-198.

Laundré, J. W. (2010). Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology*, *91*, 2995-3007.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology, 68*, 619-640.

Loarie, S. R., Tambling, C. J., & Asner, G. P. (2013). Lion hunting behaviour and vegetation structure in an African savanna. *Animal Behaviour, 85,* 899-906.

Loveridge, A. J., Valeix, M., Chapron, G., Davidson, Z., Mtare, G., & Macdonald, D. W. (2016). Conservation of large predator populations: Demographic and spatial responses of African lions to the intensity of trophy hunting. *Biological Conservation, 204*, 247-254.

Middleton, A. D., Kauffman, M. J., McWhirter, D. E., Jimenez, M. D., Cook, R. C., Cook, J. G., … White, P. J. (2013). Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters*, *16,* 1023-1030.

Mysterud, A., & Østbye, E. (1999). Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildlife Society Bulletin*, *27,* 385-394.

Padié, S., Morellet, N., Hewison, J. M., Martin, J.-L., Bonnot, N., Cargnelutti, B., & Chamaillé-Jammes, S. (2015). Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. *Oikos*, *124*, 1536-1546.

Périquet, S., Valeix, M., Loveridge, A. J., Madzikanda, H., Macdonald, D. W., & Fritz, H. (2010). Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Animal Behaviour*, *79*, 665-671.

R Development Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/.

Ruf, T. (1999). The Lomb-Scargle periodogram in biological rhythm research: analysis of incomplete and unequally spaced time-series. *Biological Rhythm Res*earch, *30*,178-201.

Sainmont, J., Thygesen, U. H., & Visser, A. W. (2013). Diel vertical migration arising in a habitat selection game. *Theoretical Ecology*, *6*, 241-251.

Schmidt, K., & Kuijper, D. P. J. (2015). A “death trap” in the landscape of fear. *Mammal Research, 60*, 275-284.

Sih, A. (2005). Predator–prey space use as an emergent outcome of a behavioral response race. In P. Barbosa & I. Castellanos (Eds.), *Ecology of predator–prey interactions* (pp. 240-255). New York, NY: Oxford University Press.

Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C., & Baubet, E. (2009). Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Canadian Journal of Zoology*, *87*, 1129-1137.

Valeix, M., Chamaillé-Jammes, S., & Fritz, H. (2007). Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia*, *153*, 739-748.

Valeix, M., Loveridge, A. J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, *90*, 23-30.

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D. W. (2010). How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of northwestern Zimbabwe. *Landscape Ecology, 25*, 337-351.

Wirsing, A. J., Cameron, K. E., & Heithaus, M. R. (2010). Spatial responses to predators vary with prey escape mode. *Animal Behaviour, 79*, 531-537.

Wood, S. N. (2003). Thin plate regression splines. *Journal of the Royal Statistical Society B, 65*, 95-114.

Wood, S. N., & Scheipl, F. (2014). gamm4: Generalized additive mixed models using mgcv and lme4. R package version 0.2-3. http://CRAN.R-project.org/package=gamm4.