Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale

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The predator–prey space game and the costs associated with risk effects are affected by prey 1) proactive adjustments (when prey modify their behaviour in response to an a priori assessment of the risk level) and 2) reactive adjustments (when prey have detected an immediate threat). Proactive adjustments are generally well-studied, whereas the frequency, strength and duration of reactive adjustments remain largely unknown. We studied the space use and habitat selection of GPS-collared zebras *Equus quagga* from 2 to 48 h after an encounter with lions *Panthera leo*. Lion–zebra encounters generally occurred close to artificial waterholes (< 1 km). Two hours after an encounter, zebras were more likely to have fled than stay when the encounter occurred in more risky bushy areas. During their flight, zebras selected grasslands more than usual, getting great visibility. Regardless of their initial response, zebras finally fled at the end of the night and reached areas located far from waterholes where encounters with lions are less frequent. The large-scale flights (~4–5 km) of zebras led to a local zebra depression for lions. Zebras that had fled immediately after the encounter resumed their behaviour of coming close to waterholes on the following day. However, zebras that had initially stayed remained far from waterholes for an extra 24 h, remaining an elusive prey for longer. The delay in the flight decision had different short-term consequences on the lion–zebra game. We reveal that the spatial context of the encounter shapes the immediate response of prey, and that encountering predators induces strong behavioural responses: prey flee towards distant, safer, areas and have a constrained use of key resource areas which are at the heart of the predator–prey game at larger spatio-temporal scales. Nighttime encounters were infrequent (once every 35 days on average), zebra responses were short-lived (< 36 h) but occurred over a large spatial scale (several km).

Prey have evolved numerous anti-predator behaviours to reduce predation risk (Lima and Dill 1990, Caro 2005). These behaviours are costly, both in terms of energy and time, and can ultimately influence prey fitness and population dynamics (Preisser et al. 2005, Creel and Christianson 2008, Zanette et al. 2011). The effects of predation risk on prey (i.e. non-consumptive effects) had been largely overlooked in predator–prey studies until recently, although they may sometimes be stronger than lethal (i.e. consumptive) effects (Preisser et al. 2005, Creel and Christianson 2008). A common prey response at the heart of these risk effects is the change in space or habitat use in response to increasing risk thereby shaping the predator–prey space game (Lima 2002, Sih 2005) and preventing prey from consistently using the richest resource patches (Laundré 2010).

Prey behavioural adjustments to predation risk can be either proactive or reactive (sensu Creel et al. 2014). Proactive adjustments occur when prey modify their behaviour in response to an a priori assessment of the level of risk, in which the awareness of prey animals to spatial and temporal distribution of predators plays a key-role. This has been well studied for many taxa (invertebrates: Wojdak 2009; fish: Dupuch et al. 2009; birds: Heithaus et al. 2009; large mammals: Fortin et al. 2005, Latombe et al. 2014, Padié et al. 2015), and it has been shown that prey generally respond to an increase in perceived risk by selecting safer habitats. Reactive adjustments occur when prey have detected an immediate threat, i.e. encountered either the predator or cues of its presence (Creel et al. 2005, Wirsing et al. 2010). In particular, prey have to choose to either flee or stay within the area where they have detected a predator. It is accepted that the choice between these two immediate responses is based on a decision-making process involving a cost–benefit analysis weighting the estimation of the risk of being attacked and killed against the estimation of the future foraging gains (Stankowich and Blumstein 2005,

Cooper and Frederick 2007). The assessment of immediate predation risk integrates intrinsic characteristics of predator and prey biology (e.g. hunting and escape modes), environmental factors affecting prey vulnerability (e.g. presence of predator-concealing cover), and contextual information (e.g. distance to and behaviour of the predator, prey body condition) (Wirsing et al. 2010). The estimation of the foraging opportunities integrates the prey's expectation about food quality and quantity where foraging would take place, as well as its vigilance level which could ultimately reduce its foraging efficiency if increased while staying in the area with the predator (Fortin et al. 2004, Creel et al. 2014). Thus, a prey at a profitable patch with a high probability of escaping a predator if attacked might flee immediately to avoid bearing the costs of monitoring an approaching predator ("flush early and avoid the rush hypothesis", Blumstein 2010). Ultimately, the dynamics of the predator–prey space game is determined by the relative frequency at which the prey flee and by the spatial and temporal extents of their reactive responses to encounters.

In the short-run, spatially reactive adjustments are likely to be stronger than proactive ones, as prey must avoid being killed. The total cost of a spatially reactive response will not depend only on its intensity, however, but also on the time it takes for prey space use to return to its basal level (i.e. proactive behaviour). Yet, studies generally assess spatially reactive responses over very short time spans (seconds to minutes) and the full spatial and temporal dynamics of the prey responses remains poorly known. Studies from a wide range of taxa (but not large vertebrates) have focused on the time spent hiding in refuges after an attack (reviewed by Cooper 2009). Several studies of ungulates have investigated how the distance between the prey and the predator affect prey behaviour (e.g. vigilance: Liley and Creel 2008, Middleton et al. 2013, Creel et al. 2014), but very few have focused on its spatial behaviour and/or the temporal persistence of the predator-induced behavioural changes. A notable exception is Middleton et al. (2013), which revealed that elk *Cervus elaphus* net daily displacement was slightly elevated (by 450 m on average) after an encounter with wolves *Canis lupus*, and that elk movement rates returned to basal levels 24 h after the encounter. Therefore, further studies are required to understand the scale of the spatial response of prey to encounters with predators, and its temporal persistence. This is also a pre-requisite to assess to what extent the responses contribute to shaping the predator–prey space game and trophic cascades (Fortin et al. 2005).

In Hwange National Park (Zimbabwe), we studied the spatially reactive response of zebras *Equus quagga* from 2 to 48 h after encounters with lions *Panthera leo*, their main predator. This zebra population seems to be under top–down control by lions and currently declining due to a high predation pressure (Grange et al. 2015). Previous studies (using survey data rather than individual based data) in this system have revealed that during daytime zebras select areas located near artificial waterholes, which provide profitable open short-grass habitats with high visibility (Valeix et al. 2009) and lower mortality risk (Davidson et al. 2012). Lions select for these areas to benefit from high prey densities, but at night, they hunt more successfully in the dense vegetation at the edge of these areas (Davidson et al. 2012). Lions rest

in their vicinity during the day too (Davidson et al. 2013). However, it is not known how zebras respond to the presence of hunting lions at night, and specifically whether the immediate response of zebras is to flee to distant areas or is a more small-scale avoidance of lions. Equally, it is not known for how long zebras adjust their habitat and space use following an encounter with lions. Using simultaneously collected GPS locations for lions and zebras, we investigated the spatially reactive responses of a large herbivore in highly risky situations (i.e. < 500 m from lions) to understand how these responses can shape the predator–prey spatial game.

Accordingly, we addressed four questions:

Question 1: do zebras stay or flee immediately after encountering lions?
Question 2: is zebra response influenced by the resource/risk characteristics of the encounter area?
Question 3: do zebras that flee move away from the risky encounter site towards safer areas of the landscape (i.e. away from waterholes), and for how long do space use adjustments persist?
Question 4: while they are staying or moving away from lions, do zebras select grasslands (where they are less vulnerable because of greater visibility) more strongly than at other times, and for how long does increased selection for grasslands persist?

Methods

Study site

The study was conducted in the north-eastern region of Hwange National Park, Zimbabwe. The vegetation is typical of dystrophic semi-arid savannahs, dominated by bushlands (> 60% of the landscape; mostly *Combretum* spp., *Acacia* spp. and *Terminalia sericea*) but interspersed with small patches of grasslands and larger patches woodlands (mostly *Baikiaea plurijuga* woodlands) (Rogers 1993, Chamaillé-Jammes et al. 2006). Average annual rainfall is ca 600 mm, with most of the rains falling between November and April (wet season, Chamaillé-Jammes et al. 2006). There are no perennial rivers in the study area and natural pans progressively dry up. Water is only available during the late dry season (August to October) in waterholes artificially supplied with pumped groundwater. Artificial waterholes are largely situated in open areas characterized by greater availability of grasslands and open bushlands (bushland-1 in Supplementary material Appendix 1 Fig. A1; see also Chamaillé-Jammes et al. 2009a), which are habitats favoured by zebras (Fischhoff et al. 2007, Valeix et al. 2009). Artificial waterholes also drive the space use of lions all year round (Valeix et al. 2010, Davidson et al. 2012). In preliminary analyses, we found that the proportions of immediate responses – staying versus fleeing – were similar between wet and dry seasons, and we did not find qualitative changes in the space use of zebras after an encounter with lions between seasons. We therefore favoured greater statistical power and conducted all analyses without distinguishing between seasons.

Zebra density in the study area was estimated from road-transects driven at least twice a year between 1999 and 2010 and was ca 1 individual km^{-2} (Chamaillé-Jammes et al.

2009b, Grange et al. 2015). Lion density in the study area was estimated from an individual-based database where almost all lions were known and identified by whisker patterns and other natural physical characteristics, and was ca 3.5 lions 100 km^{-2} over the study period (Loveridge et al. unpubl.).

Environmental covariates

We used Landsat-7 ETM+ satellite images (30-m resolution) taken in August 2002, November 2002 and April 2003 to conduct an unsupervised classification of habitat types. We first performed a k-means analysis on these images. Then, for each cluster, we identified large homogeneous patches and within these patches conducted field vegetation surveys: during each survey, every 2 m along two 60-m transects, we recorded the presence and species identity of any woody species within the <1 m, 1 to 3 m, 3 to 8 m and >8 m height-class. We also recorded the presence or absence of grass. Overall, 168 transects were conducted. We used these field data to classify k-means clusters in six habitat types of increasing woody cover: grassland, three types of bushlands (bushland-1, bushland-2, bushland-3) representing a decreasing gradient of openness, wooded bushland, woodland. Wooded bushland was the baseline habitat type in the subsequent analyses. We found no strong correlations (–0.30 < r < 0.19) between all habitat types and distance to artificial waterholes in our study area.

GPS data and identification of lion–zebra encounters

GPS collars were fitted to zebras by qualified personnel using standard protocols for the species. Collars were deployed for an average of 357 ± 43 (mean ± SE) days per zebra and in analyses we used location data collected hourly between August 2009 and November 2013 from 22 female zebras belonging to different herds. Zebras move more during the day than at night (382 ± 2 m h^{-1} versus 224 ± 2 m h^{-1} respectively). Over the same period, 21 lions (15 males and 6 females) equipped with GPS collars (fitted by qualified personnel using standard protocols for the species, Fahlman et al. 2005) also used the area exploited by the monitored zebras. Not all lions in the study area were collared (this would be logistically impossible and ethically questionable). As all females of a pride are sighted together ca 90% of the time (revealing very little fusion/fission dynamics, Valeix et al. 2009), efforts were made to have at least one female with a collar in each pride, and the intensive field monitoring suggests that this was virtually achieved in the study area. Males are only infrequently seen with females (ca 7% of the sightings, Davidson et al. 2013), suggesting that they do hunt themselves and explaining why monitoring this sex required more collars to track territorial males, coalitions and dispersers. Overall, only 1% of zebra locations felt outside of the GPS-tracked lion home ranges. Lion GPS collars acquired locations at 1 h or 2 h intervals during the night and every 2 h or 2 or 3 times during the day. Lions were monitored for an average of 630 ± 62 days per individual. Lions move 596 ± 3 m h^{-1} at night and much less during the day (181 ± 5 m h^{-1}).

We assumed that a zebra encountered a lion when their simultaneous locations were less than 500 m apart at night. Although it is likely that zebras can detect and respond to lion presence when these are further away (Valeix et al. 2009), this short distance threshold was chosen to ensure that we studied zebra response in a highly risky situation, during which it was unlikely that risk was not perceived. We focused on nighttime locations only as lions mainly hunt during this period and we therefore anticipated that their presence would induce spatially reactive responses from their prey. For a given zebra, if several encounters occurred during the same night, we considered that the encounter had taken place when the distance between the zebra and a lion was smallest. We kept 192 encounters, being 8.2 ± 1.3 (mean ± SE) encounters per zebra, interspaced by at least 48 h for a given zebra, allowing assessing the dynamics of space use and habitat selection of zebras during the next 48 h after an encounter. To evaluate whether the spatially reactive responses of zebras after encountering lions departed from zebra behaviours in the absence of lion (i.e. proactive response), we used a set of 'no-encounter' locations: for each encounter we randomly selected 10 (when possible) 'no-encounter' locations among all locations (for the same zebra and the same hour of the night) when no lions where within 500 m. As for the encounter case, the 'no encounter' locations retained were spaced by at least 48 h for a given zebra. Choosing a small distance threshold (< 500 m) to define encounter cases is a conservative approach as possibly excluding encounter events occurring over larger distance decreases our ability to detect differences between the 'encounter' and 'no encounter' cases.

Habitat selection of lions and zebras and habitat characteristics of encounter areas

We used resource selection functions (RSF, Manly et al. 2002) to estimate habitat selection of lions and zebras within their home range during both day and night periods. For each species and period, the RSF models compared the different habitat types and the distance to the closest artificial waterhole (referred to as distance to waterhole thereafter) at the GPS locations of a given individual with those at an equal number of locations drawn randomly within its home range (Courbin et al. 2014). We estimated RSF coefficients using a generalized linear mixed model (GLMM) with a logit link and a binomial distribution for errors. We added a random intercept to account for the unbalanced sampling design among individuals of a given species (Gillies et al. 2006). To account for non-independence among observations of different lions, we kept only one location (randomly chosen) at each time step when distance between individuals was < 300 m (as lions travelling together are most often located less than 300 m apart, Supplementary material Appendix 1 Fig. A2). Following recommendations of Koper and Manseau (2009), we used GLMM with robust empirical standard errors that are robust to both among- and within-individual correlations and that provide robust estimates of significance. RSFs were fitted with the GLIMMIX procedure of SAS 9.2 software (SAS Inst.) and took the following form:

$$w\left(\mathbf{x}_{ij}\right) = exp\left(\beta_0 + \beta_h \, habitat_{hij} + \beta_{waterhole} \, waterhole_{ij} + \gamma_{0j}\right)$$

(1)

where $w(\mathbf{x}_{ij})$ is the relative probability of selection for lion or zebra during the day or the night, $\mathbf{x}$ is a vector, β_0 is the mean intercept, β_h is the estimated fixed regression coefficient for habitat type h and $\beta_{waterhole}$ is the coefficient for distance to waterhole, i represents the ith observation, j represents the jth individual, and γ_{0j} is the random effect on the intercept β_0 for animal j. We used a cuberoot transformed variable for distance to waterhole as 1) untransformed variable was highly right-skewed distributed implying high leverage effects, and 2) model fit was largely improved based on the Akaike information criterion ($\Delta AIC > 592$ for day and night periods). No multicollinearity issue was detected (variance inflation factors [VIFs] < 1.3) in all models (Dormann et al. 2013). We evaluated model robustness using k-fold cross-validation as suggested by Boyce et al. (2002).

We then tested if encounters between zebras and lions occurred randomly along the zebra movement paths or if they occurred within areas with specific habitat composition and at a specific distance to water. Because GPS-sampling of zebra and lion locations was discrete, we had only an approximate idea of where the encounter occurred. We therefore calculated the proportion of each habitat type within a 500-m radius buffer of the location defined as encounter location as defined above (see details in Supplementary material Appendix 2 Fig. A1 for explanations about the choice of this radius). We compared the characteristics of areas occupied by zebra when an encounter occurred with those occupied at times when lions were absent (i.e. 'no-encounter' set) using a GLMM with a logit link and a binomial distribution for errors and a random intercept for each zebra. We assessed the relative probability that an encounter occurred along the movement paths of zebras, $w(\mathbf{x}_{ij})_{encounter}$, using Eq. 1, where β_h is the estimated fixed regression coefficient for proportion of habitat type h and $\beta_{waterhole}$ is the coefficient for distance to waterhole. No multicollinearity issue was detected (VIFs < 1.6). The models were fitted using the R software (< www.r-project.org >).

Typology of immediate spatial responses of zebras after an encounter with lions (question 1)

We ascertained that zebras could display two contrasted responses (stay or flight) immediately (i.e. within 2 h) after encountering lions. We hypothesized that the actual proximity of lions during encounters could influence zebra decision on whether to stay or flee. We therefore used an unsupervised model-based clustering analysis with two axes: distance between zebra and lion at the time of the encounter, and net displacement of zebra 2 h after the encounter. We evaluated whether the data were best described by one or two clusters, and if the best two-cluster model separated the data along the axis of net displacement after the encounter, thereby indicating the existence of two contrasted spatial responses (see details in Supplementary material Appendix 3 Fig. A1).

Habitat determinants of immediate response choice (question 2)

We tested whether the likelihood that zebras displayed a given immediate response (stay or flight) depended on the habitat composition of the encounter area and its proximity to a waterhole. We compared characteristics of encounter areas were zebras had fled with those of encounter areas where zebras had stayed, using a GLMM with a logit link and a binomial distribution for errors, while accounting for the unbalanced number of observations among individuals with a random intercept. The model took the form:

$$P(\mathbf{x}_{ij})_{\text{response choice}} = \frac{exp\left(\beta_0 + \beta_h \, habitat_{hij} + \beta_{waterhole} \, waterhole_{ij} + \gamma_{0j}\right)}{1 + exp\left(\beta_0 + \beta_h \, habitat_{hij} + \beta_{waterhole} \, waterhole_{ij} + \gamma_{0j}\right)}$$

(2)

where $P(\mathbf{x}_{ij})_{\text{response choice}}$ is the probability to flee immediately rather than stay, $\mathbf{x}$ is a vector, β_h is the estimated fixed regression coefficient for proportion of habitat type h and $\beta_{waterhole}$ is the coefficient for distance to waterhole, i represents the ith observation, j represents the jth individual, and γ_{0j} is the random effect on the intercept β_0 for animal j. No multicollinearity issue was detected (VIFs < 1.6). The models were fitted using the R software.

Temporal dynamics of zebra space use after an encounter (question 3)

We studied the dynamics of zebra space use after encounters for each type of response (stay and flight). For each encounter we computed the zebra's net displacement from the encounter site and the distance to waterhole on several occasions (encounter, 2 h, …, 3rd sunrise after the encounter; Fig. 1). We also calculated the differences in the net displacement from the encounter site between these consecutive occasions. For each interval between occasions we assessed whether changes in the net displacement were different from those expected if zebras had not encountered a lion, and if they differed between the different immediate responses. We did so by fitting linear mixed-effects models (LMM) with random intercepts for each zebra and a dummy binary variable as predictor, allowing to compare stay versus proactive, flight versus proactive or flight versus stay. We used a similar approach to assess if the dynamics of the distance to waterhole between occasions varied between proactive behaviour and the two types immediate response, and between these responses. Distance to waterhole was cube root transformed. LMMs were fitted using the R software.

Temporal dynamics of fine-scale habitat selection of zebras after an encounter (question 4)

We used step selection functions (SSF, Fortin et al. 2005) to study the habitat selection of zebras after encounters with lions, at three consecutive occasions: immediately (2 h-later), the day after the encounter and the night after the encounter. At each occasion, we compared habitat selection between proactive behaviour and each type of immediate response by fitting one SSF per response. For each SSF, we extracted the movement path collected during the occasion
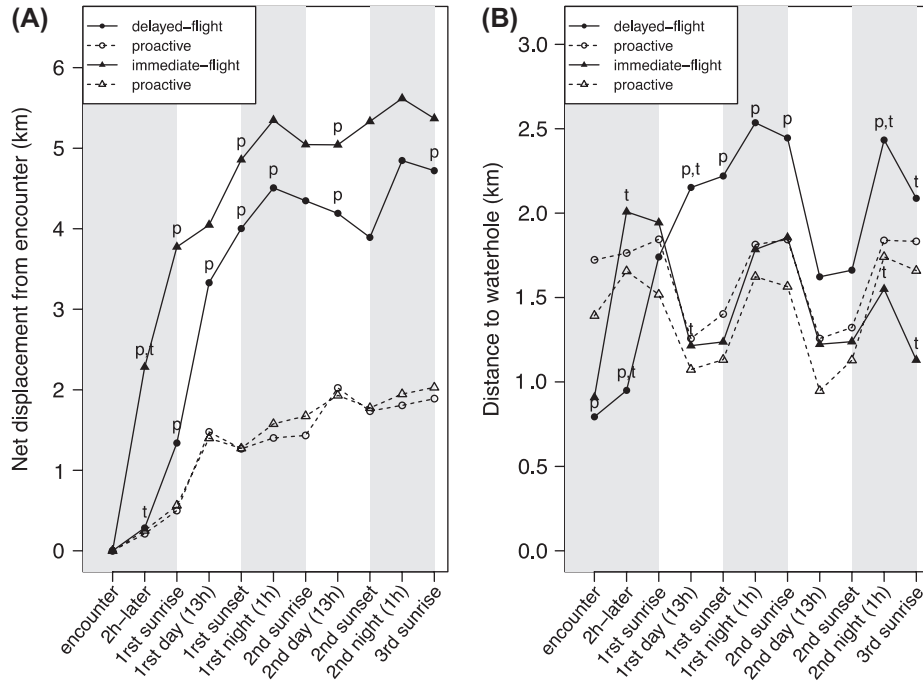
Figure 1. Temporal dynamics of spatial large-scale movement patterns of zebras for each reactive tactic with the median net displacement from the encounter site (A) and the median distance to the closest waterhole (B) calculated at different occasions. Proactive behaviour of zebras in the absence of lion is shown. The letter 'p' means that the changes in net displacement between consecutive occasions or the distance to waterhole were different between a given tactic and the proactive behaviour, while 't' indicates differences between tactics.

of interest, after encounters and in the 'no-encounter' data set. Movement paths were decomposed into a series of steps (i.e. straight-line segments linking successive 1 h locations), and each step was paired with 10 random steps to create a stratum. Random steps had the same starting location as observed steps, but differed in that length and turning angle were randomly drawn from the empirical distribution of step lengths and turning angles obtained by pooling steps data from all other individuals, as recommended by Fortin et al. (2005) and Forester et al. (2009). We estimated SSF parameters using conditional logistic regression within a generalized estimating equation (GEE) framework. Temporal autocorrelation between the steps occurring the same day or night can bias the standard errors of parameter estimates, and we therefore calculated robust standard errors after having grouped all steps occurring the same day or the same night in independent clusters (Fortin et al. 2005, Craiu et al. 2008). The SSF models took the form:

$$w(\mathbf{x}_{ij})_{zebra, step} = exp \begin{pmatrix} \beta_h \, habitat_{hij} + \beta_{steplength} \, steplength_{ij} \\ + \beta_{h, encounter} \, habitat_{hij} \times encounter_{ij} \\ + \beta_{steplength, encounter} \, steplength_{ij} \times encounter_{ij} \end{pmatrix}$$

(3)

where $w(\mathbf{x}_{ij})_{zebra, step}$ is the relative probability of selecting a step for zebra, $\mathbf{x}$ is a vector, β_h is the selection coefficient for the habitat type h at the step's ending point, $\beta_{h, encounter}$ is the selection coefficient for the interaction between habitat type h and a dummy variable allowing to distinguish if the steps occurred after an encounter or a no-encounter location, i

represents the ith observation and j represents the th individual. The interactions allowed us to test whether habitat selection after an encounter differed from the one observed during proactive behaviour. We added a spline function of step length, with knots at the first, second, and third quartiles of observed step lengths, which have been shown to remove bias in other model parameters (Forester et al. 2009). No multicollinearity issue was detected (VIFs < 2.6) in all these SSFs. We tested the robustness of the models using k-fold cross-validation adapted for paired designs (Fortin et al. 2009, Courbin et al. 2014).

Data deposition

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.tn20t > (Courbin et al. 2015).

Results

Habitat selection of lions and zebras and habitat characteristics of encounter areas

RSFs models had high to very high predictive power ($\bar{r}_s > 0.55$; Supplementary material Appendix 1 Table A1). As expected, zebras strongly selected the most open habitats (grasslands, and to a lesser extent, the two most open bush-lands; Supplementary material Appendix 1 Table A1) during both day and night within their home range. Zebras selected woodlands during the day. Lions selected grasslands, and the most open bushlands, during day and night, and they

tended to avoid woodlands at night (Supplementary material Appendix 1 Table A1). Both species strongly selected areas located near waterholes within their home range (Supplementary material Appendix 1 Table A1), but zebras stayed further away from waterholes at night (Fig. 1B). Relatively to areas visited along their paths, at night when lions hunt, zebras were more likely to encounter lions in areas with a higher proportion of grasslands and a lower proportion of bushlands (bushland-3; Table 1; mean proportion of grasslands around locations was 0.18 (95% CI: 0.16–0.20) and 0.09 (95% CI: 0.08–0.10) during encounter and proactive behaviour, respectively; mean proportion of bushland-3 around locations was 0.045 (95% CI: 0.04–0.05) and 0.085 (95% CI: 0.08–0.09) during encounter and proactive behaviour, respectively).

Typology of immediate spatial responses of zebras after an encounter with lions (question 1)

The best two-cluster model classifying zebra immediate responses after encounters was superior to the model assuming only one cluster (ΔICL = 78), suggesting that two immediate responses were indeed present. One two-cluster model was much better than other two-cluster models (ΔICL > 3.9; Supplementary material Appendix 3 Table A1), and it discriminated encounters based on the zebra net displacement only: one cluster identified a 'stay' immediate response (net displacement 2 h after the encounter < 900 m, n = 108), and the other cluster identified a 'flight' immediate response (net displacement 2 h after the encounter > 900 m, 2567 ± 165 [mean ± SE], ranging 910 to 6540 m, n = 84). The mean proportion of stay responses per zebra weighted for the number of observations for each zebra had a very low standard error (0.56 ± 0.05, mean ± SE), revealing that responses were not individual-specific.

Habitat determinants of immediate response choice (question 2)

We found that habitat characteristics influenced the choice of immediate response of zebras. Zebras were more likely to flee than stay when the encounter occurred in an area where bushlands (bushland-3) were more common (Table 1; mean proportion of bushland-3 was 0.07 and 0.03 for flight and stay, respectively).

Temporal dynamics of zebra space use after an encounter (question 3)

At longer time scales, all zebras left the area where the encounter with lions occurred and reached areas 4 km away in less than 24 h, while they usually moved away less than 1.5 km from where they were when lions were absent (Fig. 1A). However, the two contrasting immediate responses of zebras, flight or stay, were associated with widely different space use that we termed immediate-flight and delayed-flight tactics, respectively. In the immediate-flight tactic, zebras moved very rapidly away from both the encounter site and waterholes before the first sunrise after the encounter occurred (Fig. 1A–B; Supplementary material Appendix 1 Table A2). By the day following an encounter,

Table 1. Coefficients (β) with 95% confidence intervals (CI) for mixed resource selection functions contrasting 1) features of areas occupied by zebra at the time of encounter (n = 192) and during proactive behaviour (n = 1809, baseline), and 2) features of areas occupied by zebra at the encounter time for immediate-flight (n = 84) and for delayed-flight tactics (n = 108, delayed-flight was the baseline).

Variable	Encounter vs proactive		Immediate-flight vs delayed-flight	
	β	95% CI	β	95% CI
Intercept	–2.26*	–2.79;–1.74	0.14	–0.91;1.18
Grassland	1.30*	0.50;2.11	–0.27	–1.88;1.33
Bushland-1	0.41	–0.33;1.16	–1.31[†]	–2.83;0.22
Bushland-2	–0.08	–0.99;0.84	–0.32	–2.35;1.70
Bushland-3	–1.78*	–3.50;–0.06	4.48*	0.19;8.77
Woodland	–1.08	–5.35;3.18	–2.27	–9.75;5.21
Distance to waterhole (km)	–0.04	–0.11;0.02	–0.05	–0.20;0.10

*95% confidence intervals exclude zero.
[†]90% confidence intervals exclude zero.
Notes: variance and covariance of random intercept were < 0.001 for the first model, and equal to 0.04 and 0.19, respectively.

zebras resumed their daily patterns of visits to areas close to water during the day and moving away at night, as done during their proactive behaviour (Fig. 1B). Zebras did not come back to where the encounter occurred however (compare net displacement and distance to water in Fig. 1A–B). In the delayed-flight tactic, the movement of zebras towards safer areas (i.e. away from waterholes) that started later during the night went on during the day following the encounter (Fig. 1A–B; Supplementary material Appendix 1 Table A2). Zebras resumed visiting areas near waterholes only the second day after the encounter.

Temporal dynamics of fine-scale habitat selection of zebras after an encounter (question 4)

All SSFs had very high predictive power ($\bar{r}_s$ > 0.79; Supplementary material Appendix 1 Table A3, A4). The habitat selection of zebras immediately after an encounter depended on whether they stayed or fled immediately. The next 2 hours after the encounter zebras using a delayed-flight tactic had similar selection coefficients than during proactive behaviour, selecting the most open habitat types (Fig. 2A; Supplementary material Appendix 1 Table A3). However, because grassland availability increased in encounter areas (Fig. 2A), zebras used grasslands more. Zebras using the immediate-flight tactic altered their habitat selection after an encounter. They selected grasslands (and possibly woodlands) even more strongly during their flight than during proactive behaviour (Fig. 2D; Supplementary material Appendix 1 Table A4). The day and the night following an encounter, habitat selection of zebras did not differ from the one observed during proactive behaviour (Fig. 2B–C, E–F; Supplementary material Appendix 1 Table A3, A4).

Discussion

Our study is one of the first to provide a comprehensive analysis of the spatially reactive response of a prey species to
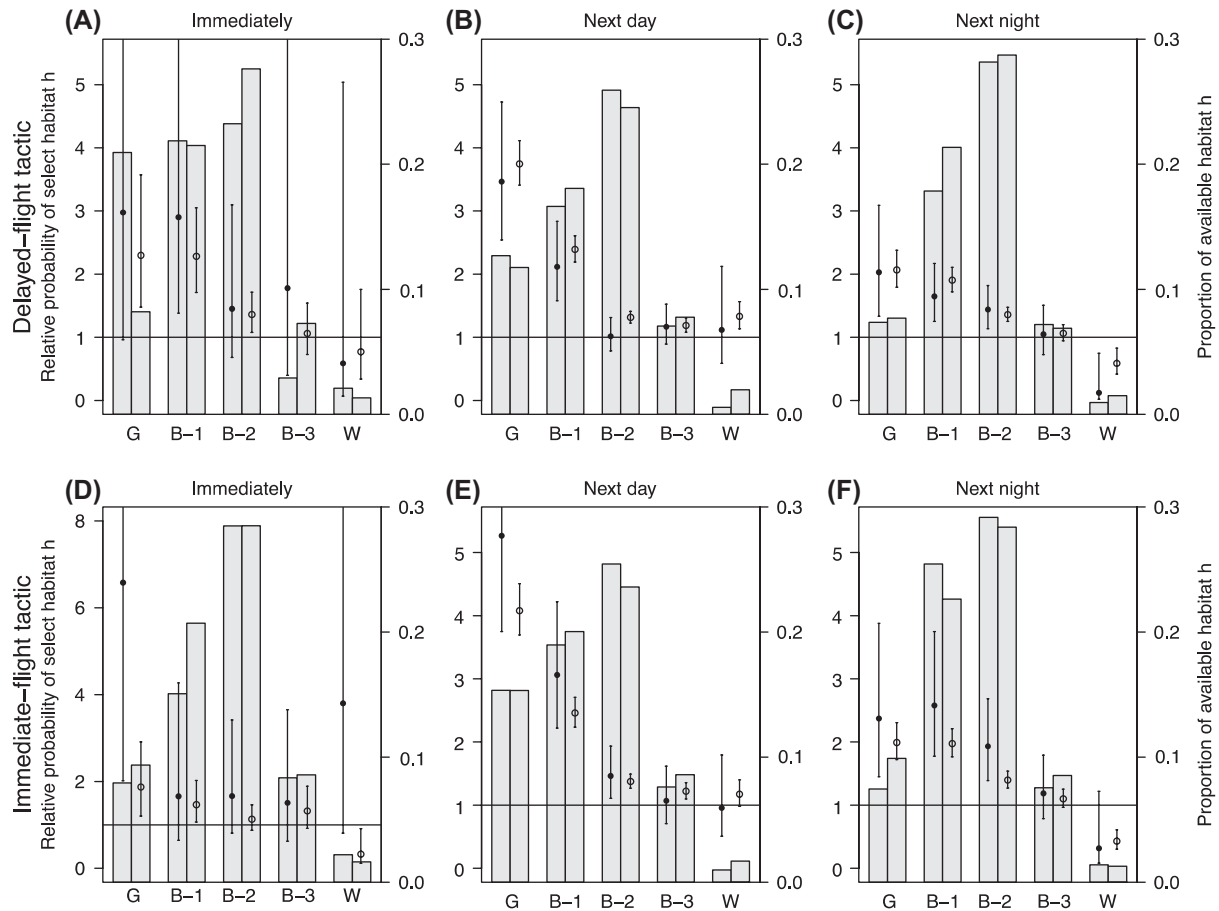
Figure 2. Relative probability that zebras selected a given habitat type at the end of their step after an encounter with lions (solid circle) at three occasions: immediately after an encounter (A and D), during the next day (B and E), and during the next night (C and F), depending on whether zebras used delayed-flight (A–C) or immediate-flight tactic (D–F). Proactive behaviour of zebras in the absence of lion is shown (open circle). The 95% confidence intervals are presented. Grey areas represent availability of respective habitats.

encounters with its primary predator over large spatial and temporal scales. In particular, we reveal how short-term reactive decisions (immediate or delayed-flight) were associated with different space use patterns during subsequent days that likely affected the predator–prey space game at the landscape scale.

Zebras encounter lions within waterhole areas

In our system, the predator–prey space race revolves around artificial waterholes that are at the heart of a spatial tradeoff between food and safety. Grasslands surrounding waterholes provide suitable foraging habitats with good visibility and were particularly selected by zebras during the day (this study, Valeix et al. 2009), but also sometimes at night (this study, Fischhoff et al. 2007), although we found that zebras were commonly away from waterholes at night. Lions always selected these areas (this study, Valeix et al. 2010, Davidson et al. 2012, 2013). Zebras were thus more likely to encounter lions at night whether they reached the most open areas close to waterhole (< 1 km, Fig. 2B). Our study reveals that lions may favour areas of the landscape where encounter rate is the greatest: areas close to artificial waterholes attract many species and open habitats provide high detectability of the prey.

Zebras flee after encountering lions

Lions are ambush predators that use cover to approach prey and hunt successfully (Hopcraft et al. 2005, Davidson et al. 2012). This likely explains why zebras were far more likely to flee immediately than stay once they had encountered lions in more bushy areas. When zebras decided to leave the encounter area immediately, they did so by shifting their selection towards habitat types with high visibility (mostly open areas and high canopy woodlands with little understory) and habitat types where the likelihood of meeting lions was reduced (woodlands), probably to maximize their safety. Zebras staying in the vicinity of lions did not alter their habitat selection pattern. Note that individual zebras used a mix of both types of immediate response, pointing out that the response choice seemed to rely more on the context of the encounter (habitat type, but also possibly lion pride size, which we did not have sufficient data to study) than on fixed innate (personality-driven) or acquired (previous experience) response by individuals. The potential costs associated with the close presence of lions (e.g. potential costs of monitoring, risk of injury or death) might possibly explain why, irrespectively of their immediate response, zebras fled (with a delay or not) and they generally left the encountered area by the end of the night towards safer areas located far from

waterholes. Our results support previous studies suggesting that ambush predators induce strong anti-predator behavioural responses because risk is spatially predictable, particularly once the presence of the predator is actually established (Preisser et al. 2007, Thaker et al. 2011, but see discussion in Creel et al. 2014).

Consequences of the flight decision on the lion–zebra space game

Zebras rapidly moved ca 4–5 km away from lions after an encounter, and thus became unavailable prey for these lions during the subsequent days. Our results thus support Valeix et al's (2011) hypothesis that changes in prey behaviour, possibly leading to changes in prey abundance (if most of individuals flee, if this is true for most prey and if lions presence elsewhere does not increase the number of incoming individuals), could explain why in Hwange NP lions move to another waterhole after having made a kill. This may be a general phenomenon underlying the lion–zebra space game: a reduction of local zebra abundance when lions are present has also been observed in the Laikipia ecosystem (Fischhoff et al. 2007). Fortin et al. (2013) have demonstrated theoretically and empirically for caribou *Rangifer tarandus* that avoidance behaviour might indeed lead to prey aggregation at intermediate distance from their disturbance or threat source, here logging areas. A depression in the local abundance of zebra at disturbed waterholes is likely to induce a temporary peak of zebra abundance at the surrounding waterholes (i.e. ~4–5 km away from the disturbed waterhole), which could affect future prey search patterns of lions involved in the encounter, but could also benefit other lions and other carnivores occupying neighbouring waterholes. Our results emphasize that prey avoidance behaviour is critical to the understanding of the predator–prey space game. They further highlight how it likely also creates indirect relationships between predators that use different areas of the landscape. In Hwange NP, zebras make a significant contribution to the lion diet (~10%) but are not, however, a species highly selected by lions (Davidson et al. 2013). It is therefore unclear how changes in zebra distribution within the landscape might actually affect lion hunting strategies and their shifts towards other prey species. Further studies should also investigate whether the large-scale movements after an encounter with lions is a common response of prey, and more generally whether local prey depression may drive the predator–prey space game in landscapes with strong spatial anchors of the prey (Sih 2005). Ultimately, what needs to be clarified is under what conditions will prey display large-scale reactive avoidance of predators to complement, or replace, other anti-predator strategies (e.g. increasing vigilance, changing grouping patterns), and how the costs of staying may vary with the environmental context or prey and predator ecology (Wirsing et al. 2010).

The fact that zebras either immediately fled or delayed their decision to flee by a few hours had different consequences for the predator–prey space game. The day following the night of the encounter, zebras using immediate-flight tactic resumed the proactive behaviour of

coming closer to waterholes during the day and moving away at night. Their behaviour thus caused an immediate movement of prey towards areas of the landscape where other lions could be present. Conversely, zebras using delayed-flight tactic mainly moved across the landscape, away from waterholes, the day after the encounter. They were also further away from water than usual on the two consecutive nights. This behaviour therefore led to a wider – but still short – temporal window during which these zebras were unavailable to lions.

On the importance of the spatially reactive responses of zebras

For zebras, the overall fitness consequences of their reactive responses depend on the frequency of the encounters, on the duration of the response and on the strength of the response (i.e. on cost of a time unit spent in reactive response). Very few studies have estimated these three properties of reactive responses *in natura*. In a rare example, Middleton et al. (2013) showed that in the Great Yellowstone Ecosystem, elk have infrequent (every 9 and 50 days on average for migratory and resident elk, respectively), short-lived (< 24 h) and probably weakly costly reactive responses (no reduction in feeding rate and no shift in habitat use) after encounters with wolves. Ultimately, the frequency of encounters with wolves was not associated with reduced body fat or pregnancy. In Hwange NP, nighttime encounters between zebras and lions are probably also infrequent: zebras encountered lions at night every 35 days on average in the dataset used here. The actual encounter rate (that cannot be calculated using the available data) is probably higher. First, zebras are more likely to encounter lions during the day as they use waterhole areas more often. Daytime encounters are likely to be far less risky and may not lead to a large-scale spatial response however. Second, the GPS-based measures of encounter rates could be underestimated (e.g. lions were not all monitored, an encounter could occur between GPS fixes, see details in Creel et al. 2013), although these effects are likely to be low here given the coverage and frequency of the lion tracking. The frequency of risky encounter is therefore low, and we have also showed that the reactive response of zebras to these encounters is short-lived (< 36 h). Thus, each response would have to be particularly costly for these responses to significantly reduce zebra fitness in this system. The actual cost of a single response is complex to estimate. The large-scale displacement induced by lions probably bears some energetic costs, as zebras travelled three times more kilometers than usual in a few hours to leave the encounter area. Walking is, however, not so energetically costly and the significance of this increase should be low. A few recent studies points towards foraging costs for zebras having been in the vicinity of lions (Barnier et al. 2014, Creel et al. 2014), but again, the significance of a small reduction in intake (Creel. et al. 2014) or forage quality (Barnier et al. 2014) is unknown. Altogether, this suggests that currently no obvious link could be made between the strong large-scale behavioural response observed here and zebra fitness in this population. This would only be formally demonstrated by monitoring the lion-encounter

history and demography of zebra herds over time. This will be logistically challenging, but will be required to deepen our understanding of risk effects, disentangling the relative contribution of proactive and reactive responses on prey fitness.

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