

# Large carnivore dangerousness affects the reactive spatial response of prey

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## Highlights

- Zebras' reactive response is stronger after encountering a lion than a hyaena.
- Zebras were twice as likely to flee after an encounter with a lion than a hyaena.
- Zebras moved faster and further after an encounter with a lion than a hyaena.
- Large mammal predators' dangerousness may affect the reactive response of prey.

## Abstract

Predators differ in various attributes: body size, sociality, speed, preferred prey size, hunting mode, etc. Together, these characteristics contribute to the predator's overall dangerousness, which is likely to underlie variations in the nature and strength of a prey's antipredator responses. This link, although somehow intuitive, has rarely been quantified in natural ecosystems. The goal of this study was to compare the antipredator response of a prey to two predators with contrasting dangerousness in large terrestrial mammals, focusing on the less studied reactive spatial response. We assessed whether the reactive spatial response of plains zebras, *Equus quagga*, differed after an encounter with African lions, *Panthera leo*, or spotted hyaenas, *Crocuta crocuta*. We expected lions to be perceived as more dangerous and hence to induce a stronger reactive spatial response than hyaenas. Using data from GPS collars deployed simultaneously on the three species, we studied the reactive spatial responses of zebras after they came close to either predator. We found that zebras responded differently, and more strongly to lions than to hyaenas. Indeed, zebras were twice as likely to flee after encountering a lion than a hyaena and, immediately after an encounter with a lion, zebras moved on average faster and further than after an encounter with a hyaena. The results of this study are consistent with a correlation between predator dangerousness and the strength of the prey's antipredator response. Future studies covering other pairs of large carnivores are needed to rigorously assess the role of the different predator attributes (body size, speed, preferred prey and hunting mode).

**Keywords:** African lion; antipredator response; ecology of fear; plains zebra; predator–prey interaction; spotted hyaena

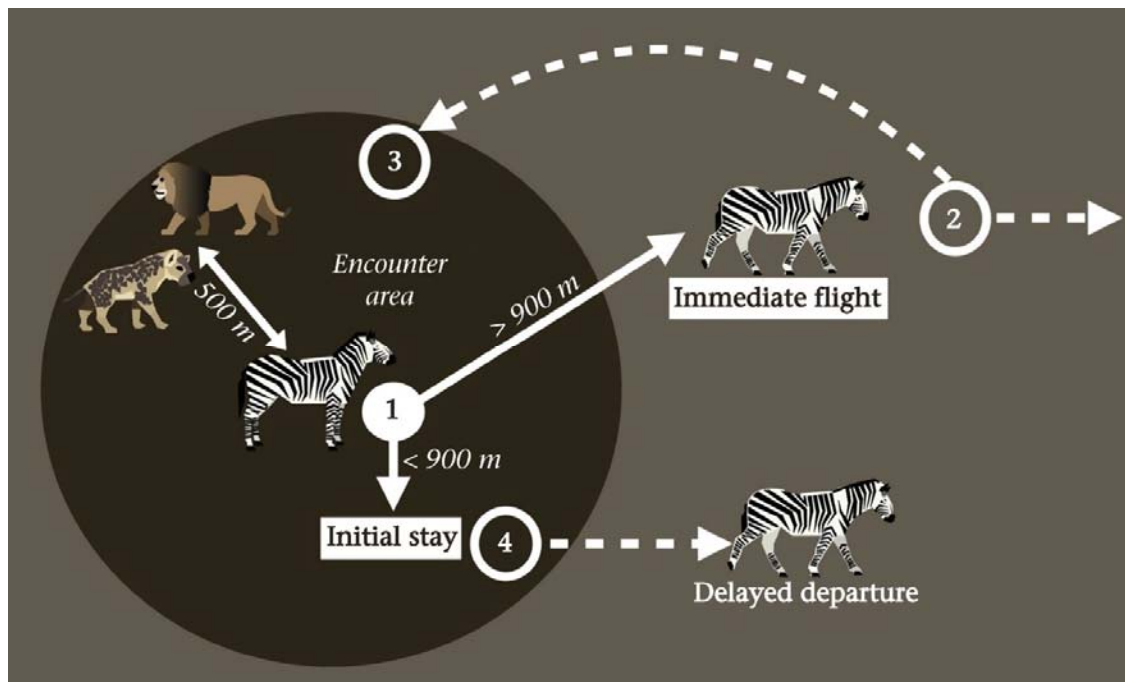
Most species alter their behaviour in response to changes in predation risk (Lima & Dill, 1990). For instance, in ungulates, these responses are as diverse as increased vigilance (Hunter & Skinner, 1998), altered grouping strategies (Creel & Winnie, 2005), relocation to safer areas (Fortin et al., 2005),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

Not all predatory species are the same and understanding how their characteristics may influence antipredator responses of prey may shed light on some of these variations. Indeed, predators differ in body size, sociality, speed, preferred prey size and hunting mode, which all have the potential to play a role in predator–prey interactions, with larger, quicker, social forager and ambush predators perceived as the most dangerous (Thaker et al., 2011; Chamaillé-Jammes et al., 2014; Makin et al., 2017; Cuthbert et al., 2020; Hirt et al., 2020). In addition, a response that is efficient towards one predator may not be an efficient defence against another (Leblond et al., 2016). For all these reasons, prey are unlikely to respond the same way to different predators (Relyea, 2001). Studies assessing the effect of several sympatric predators are lacking (Montgomery et al., 2019; Say-Sallaz et al., 2019) and needed if we want to understand the role of predator dangerousness in general, and of predator attributes (e.g. body size, speed, hunting mode) in particular, in the antipredator behaviour of prey.

Our work contributes to filling this gap. Using GPS data acquired simultaneously on plains zebras, *Equus quagga*, and their two main predators, lions, *Panthera leo*, and spotted hyaenas, *Crocuta crocuta*, we explored whether the reactive spatial response of zebras is influenced by the predator species encountered. Most studies investigating the role of the predator species in prey responses in large mammals have considered proactive responses, that is, when prey modify their behaviour in response to an a priori assessment of the level of risk based on the cumulative knowledge a prey has of its environment (independently from the actual presence of the predator; e.g. Thaker et al., 2011; Makin et al., 2017). In this study, we assessed the much less studied reactive response, that is, when prey detect the presence of a predator that presents an immediate threat (either an attack, an impending attack or the mere presence of a predator that may launch an attack any time). Lions are more than twice the body size of hyaenas, and in general can intuitively be considered to pose a higher level of threat to zebras. Further, lions are ambush predators, whereas hyaenas are cursorial predators. Following the same logic as that developed in the literature for the role of predator cues in proactive responses (Preisser et al., 2007; Thaker et al., 2011; Miller et al., 2014), we assumed that lions are more likely to stay in a given area than hyaenas, which can chase down their prey over long distances. Hence, the detected presence of a lion should be more strongly associated with the probability of presence of this predator in the near future. Consequently, we hypothesized that zebras should display stronger reactive spatial responses to encounters with lions (larger and ambush predators, which are expected to be perceived as more dangerous) than to encounters with hyaenas.

To test this hypothesis, we specifically addressed four questions corresponding to different steps in the reactive spatial response of zebras (Fig. 1; see Methods for details). (1) Does a zebra leave an area more often after an encounter with a lion than with a hyaena? (2) When a zebra leaves an encounter area, does it do so more quickly and does it go further away after an encounter with a lion than with a hyaena? (3) For a zebra leaving an encounter area, does it

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



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

## Methods

### Study Area

The study area was Hwange National Park, a large unfenced protected area (ca. 15 000 km<sup>2</sup>) in western Zimbabwe (19°00'S, 26°30'E). This ecosystem is characterized by a dystrophic (low nutrient soil) semiarid savannah where the vegetation is dominated by bushlands and woodlands with small patches of grasslands (Arraut et al., 2018). The main woody plant species are *Baikiaea plurijuga*, *Colophospermum mopane*, *Terminalia sericea*, *Acacia* spp. and *Combretum* spp. (Arraut et al., 2018). The long-term mean annual rainfall is 600 mm ( $\pm$  30% coefficient of variation), with most rains falling between November and April. The surface water available to animals is found in natural waterholes, which dry up as the dry season progresses, as well as in artificially supplied waterholes pumped throughout the dry season. The study was conducted in the Main Camp region of the Park (ca. 1200 km<sup>2</sup>). There, zebra density is estimated to be around 1 individual/km<sup>2</sup> (Grange et al., 2015), lion density around 4 individuals/100 km<sup>2</sup> (Loveridge et al., 2016) and hyaena density around 9 individuals/100 km<sup>2</sup> (Périquet, 2014). Zebras are preyed upon by both predators, accounting for 8–9% of lion kill sites (Davidson et al., 2013) and 11% of hyaena scat samples (Périquet et al., 2015). Predation has

been suggested as the main ecological process causing low survival in this zebra population (Grange et al., 2015).

## Data

Thirty-two female adult zebras from different harems were equipped with GPS collars, which recorded a location every hour or 30 min (we used only one location per hour for the analyses) between August 2009 and July 2015. Zebras were equipped for a mean of 387 ( $\pm$  256 SD) days. During this 6-year period, in the area used by the studied zebras, 14 lions (from nine different prides/coalitions) and seven hyaenas (from three different clans) were also equipped with GPS collars recording hourly locations. Lions were equipped for a mean of 492 ( $\pm$  580 SD) days and hyaenas for a mean of 453 ( $\pm$  370 SD) days.

## Ethical Note

Collaring of the three species was part of three separate long-term monitoring projects. Animals from different species were not captured at the same location or at the same time. Permissions were provided by the appropriate agencies (Zimbabwe Parks and Wildlife Management Authority, Wildlife Drugs Sub-committee of the Drugs Control Council of Zimbabwe and Zimbabwe Veterinary Association, Wildlife Group, and licences to acquire, possess and administer game capture drugs/dangerous drugs) and permits were issued for each monitoring protocol (lions' monitoring permits: REF:DM/Gen/(T) 23(1) (c) (ii):713/12/01, 03/2002, 07/2003, 20/2004, 01/2005, 01/2007, 03/2008, 03/2009, 25/2010, 06/2011, 12/2012, 08/2013, 51/2014, 10/2015; spotted hyaenas' monitoring permit: ZPWMA, 23(1) (c) (ii)15/2012-2013); zebras' monitoring permit: REF:DM/Gen/(T) 23(1) (c) (ii): 03/2009, 01/2010, 25/2010, 05/2011, 06/2011, 12/2012, 15/2012, 08/2013). Relevant animal care protocols were followed during capture and collaring of all the animals, which were under chemical immobilization/anaesthesia during the collaring. Drugs were administered by trained project personnel who attended and successfully passed the Zimbabwe wildlife capture and handling course, and who held a dangerous drug licence (renewed annually through the Wildlife Veterinary Association and administered by Medicines Control Authority, Zimbabwe). Also, animal capture and collaring followed the ASAB/ABS guidelines for the Use of Animals in Research.

Lions were equipped with GPS collars from Televilt/Followit Positioning (AB, Lindesberg, Sweden, or African Wildlife Tracking, Pretoria, South Africa) or Sirtrack Ltd. (Havelock North, New Zealand). The GPS collars weighed between 600 and 900 g, which represent 0.6 and 0.9%, respectively, of the smallest individual captured (100 kg). Spotted hyaenas were equipped with GPS radiocollars with UHF download and VHF transmitter from African Wildlife Tracking (model: UHF 407). The GPS collars fitted weighed 1 kg, which represents 1.7% of adult female hyaena body weight (60 kg). Zebras were equipped with GPS radiocollars with UHF download and VHF transmitter from Africa Wildlife Tracking or Vectronics (Vectronics Aerospace GmbH, Berlin, Germany). Fitted collars always weighed less than 1 kg, which would be less than 0.5% of the body weight of a 200 kg adult female zebra.

All the animals were immobilized by chemicals. They were darted from the ground using Dan Inject J.M.SP.25 CO<sub>2</sub>-powered dart guns; hence, drugs were administered by intramuscular injection (shoulder or rump) and were species specific. For lions and hyaenas, bait was used to attract the targeted individuals to a position where they could be darted; hence, the animal was not pursued before immobilization. Zebras were darted once sighted from a vehicle. Lions

received the dissociative anaesthetic Zoletil (dosage: 0.83–0.32 (range 0.53–1.38) mg/kg; manufacturer: Virbac RSA, Centurion, South Africa) and sedative medetomidine (Zalopine/Domitor; dosage 0.05–0.01 (range 0.04–0.06) mg/kg; manufacturer: Novartis, Isando, South Africa or Orion Pharma, Turku, Finland). Hyaenas received a standard mix of 500 mg ketamine (Kyron Laboratories (Pty) Ltd, Benrose, South Africa) and 200 mg xylazine (Rompun; Bayer, Leverkusen, Germany) or of 80 mg Zoletil (Virbac RSA) and 4 mg medetomidine (Zalopine, Wildlife Pharmaceuticals, Mpumalanga, South Africa). Zebras received a standard mix of 6 mg of etorphine (Captivon, Wildlife Pharmaceuticals (Pty) Ltd., Mpumalanga, South Africa) and 48 mg of Azaperone (Wildlife Pharmaceuticals (Pty) Ltd.). It took about 7–8 min for the animals to be immobilized after the drugs were administered, then the eyes were covered and ear plugs fitted to reduce stimuli and stress and the collars were fitted. For lions, an additional safety measure was taken by using a light leg restraint in case of unexpected arousal of the animal. While animals were immobilized, blood and hair samples were collected for hyaenas and lions (not for the purpose of this specific study but to optimize the immobilization and prevent the need for other animals to be captured to answer different scientific questions). Scat samples (when possible) were collected on hyaenas. The complete procedure could take up to 1 h for all species. Then, immobilization drugs were reversed. For lions drugs were reversed with Atipamezole (dosage: 1/4 0.18–0.07 (range 0.01–0.28) mg/kg; manufacturer: Farnos; Orion Corp., Espoo, Finland or Novartis); for hyaenas drugs were reversed with 16 mg of yohimbine (Rx drug; Kyron Labs); and for zebras drugs were reversed using 18 mg of diprenorphine (Wildlife Pharmaceuticals (Pty) Ltd.). Once reversal drugs were injected, animals were monitored until their full recovery (meaning walking away normally and joining their group especially their harem for zebras). It took an average of 20 min after drug reversal injections for individuals to fully recover; zebras were even standing up within seconds. No adverse effect was recorded for any of the three species. For all the species, fully grown adults were preferentially collared and when subadults were collared, sufficient space was allowed to ensure that the collar did not become tight as the neck grew. Nonpregnant females were also preferentially collared; early-stage pregnancy cannot be determined visually but the immobilization drugs used have no known effect on unborn fetuses, are extremely safe and widely used on wildlife.

All the collared individuals were monitored by tracking from a vehicle. Collared lions were located weekly to bimonthly from a vehicle or microlight aircraft. Positional data from the GPS radiocollars were downloaded, and observations made of group composition. Collared hyaenas and zebras were tracked from a vehicle using a four-element Yagi antenna and VHF receiver (Icom IC-R20). Data from GPS collars were downloaded using a downloading console and a USB UHF modem monthly whenever possible, either directly by the observer or retrieved from automatic downloading stations (African Wildlife Tracking; range of download: ca. 300 m) located at waterholes.

Collars were removed when batteries were flat or when collars were malfunctioning or deteriorating to ensure the safety of animals. For one zebra, the collar slipped over its ears and so was removed the day after the observation. Also, collars would sometimes fall off due to deterioration. If the collar did not fall off by itself (or with the help of a drop-off system that was controlled using UHF signals for certain zebras' collars) collars were removed using the same immobilization procedure as described before.

## Analyses

### *Definition of encounters*

We assumed that a zebra encountered a predator when they were simultaneously located less than 500 m apart (as in Courbin et al., 2016; this distance threshold appears a good balance between a biologically meaningful threshold for this study and a cutoff point that allows reasonable sample sizes; we preliminarily checked that the results of this study were qualitatively robust using a shorter distance, and that there was no effect of the distance between the zebra and its predator on the results). For consecutive pairs of simultaneous locations less than 500 m apart, the first pair was considered as the encounter. We only considered night encounters (between 1800 and 0600) since this is when lions and hyaenas are active and likely to be hunting (Hayward & Slotow, 2009). In the subsequent analyses, we included only individual zebras that encountered both predators during the period they were tracked ( $N = 15$ ). We identified 68 encounters between a zebra and a lion and 90 encounters between a zebra and a hyaena.

### *Definition of controls*

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

### *Description of environmental variables*

For each encounter and control location, we extracted three variables: distance to the closest waterhole, vegetation type and period of the night. (1) Waterhole areas are considered hotspots of predator–prey interactions in the Hwange ecosystem (Valeix et al., 2009; Périquet, 2014). We were interested in contrasting zebra responses in the vicinity or away from waterholes, and thus used a simple dichotomy for the variable ‘distance to water’ (referred to as ‘water’ in the equations below): ‘close’ ( $\leq 1$  km from a waterhole) versus ‘distant’ ( $> 1$  km from a waterhole). (2) For the variable ‘vegetation type’ (referred to as ‘vegetation’ in the equations), we used the vegetation structure map in Arraut et al. (2018). We contrasted two types of vegetation: ‘open vegetation’ (corresponding to the class ‘grassland’ in the original map) and ‘dense vegetation’ (corresponding to the classes ‘bushed grassland’, ‘bushland’, ‘woodland’, ‘mopane woodland’ and ‘woodland evergreen’ in the original map). (3) The period of the night (referred to as ‘night’ in the equations) was classified as either the ‘beginning’ (between 1800 and midnight) or ‘end’ (between midnight and 0600) of the night. At the ‘beginning’ of the night, prey, if they do not respond to the predator, will have to cope with its presence for most of the night. In contrast, at the ‘end’ of the night prey only have to deal with the presence of the predator for a few hours before it becomes much less dangerous after dawn, as both predators are mainly active at night (Hayward & Slotow, 2009). We therefore predicted that prey would be more likely to leave an encounter area at the ‘beginning’ of the night than at the ‘end’.

We preliminarily assessed whether encounters occurred in a specific subset of circumstances (environmental conditions or time), compared to those generally experienced by zebras during the night to assess whether characteristics of the encounters varied between the two predators.

We detected no major difference. Details of the analyses and results are available in the Appendix, Table A1 and Fig. A1.

### ***Describing the variability of the reactive spatial response***

For each encounter with a predator (a lion or a hyaena) and for each control, we calculated the distance between these locations and each zebra's location during the next 24 h. Plotting the data revealed a high variability of how zebras moved away from the locations with time (Fig. A2), which led us to decompose the spatial response of zebras to understand this variability (Fig. 1). Building upon Courbin et al. (2016), who performed an unsupervised model-based clustering analysis to classify the immediate response of zebras after an encounter with lions and found that the best model was a two-cluster model (superior to the model with only one model), we first identified two types of immediate spatial responses depending on whether zebras were further than 900 m from the encounter location 2 h after the encounter ('immediate flight') or not ('initial stay'). This 900 m threshold distance defines the 'encounter area' hereafter and was the distance that best discriminated the two types of immediate responses in Courbin et al. (2016). To assess whether the choice of the 2 h time window affected the results, we ran the subsequent analyses with a 1 h and a 3 h time window to preliminarily check that the results were qualitatively the same. As this was the case, we present the results for the 2 h window only. This corresponds to step (1) in Fig. 1. We assessed whether this immediate response was influenced by the predator species and the environmental variables. We then investigated whether there were longer-term spatial responses. We specifically calculated, for zebras that left the encounter area, the speed with which they left and the distance they moved away over 24 h (step (2) in Fig. 1), and we compared whether this dynamic of the flight was influenced by the predator species. We further assessed how long it took zebras that initially displayed a flight response to come back to an encounter area (step (3) in Fig. 1). For zebras that initially stayed in the encounter area, we assessed whether predator species or environmental variables influenced the time zebras ultimately spent in the encounter area after the encounter (step (4) in Fig. 1).

### **Statistical Analyses**

#### ***Short-term response of zebras after a predator encounter***

We used a mixed logistic regression to assess the probability that an encounter led to an 'immediate flight' response (coded 1) versus an 'initial stay' response (coded 0) and whether this probability was affected by the predator species and the environmental variables (step (1) in Fig. 1):

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

Where  $P_{ij}$  is the probability of an 'immediate flight',  $i$  being the  $i$ th observation and  $j$  the  $j$ th zebra.  $B_0$  is the intercept,  $B_p$  is the estimated coefficient for the explanatory variable 'predator species encountered' (abbreviated 'predator'; a categorical variable with three levels: hyaena, lion and control), the other  $B$  are the estimated fixed regression coefficients for the environmental variables, and  $\gamma_{0j}$  is the random effect on the intercept  $B_0$  for zebra  $j$ .

### ***Temporal dynamics after an ‘immediate flight’***

For ‘immediate flight’ responses ( $N = 19$  after an encounter with a hyaena and  $N = 31$  after an encounter with a lion), we assessed whether the predator species encountered influenced (1) the speed with which the zebra left the encounter area, and (2) how far the zebra went following the ‘immediate flight’ response (step (2) in Fig. 1). The controls included in this analysis (and the next) are controls when zebras moved further than 900 m in 2 h, i.e. comparable to an ‘immediate flight’. For each encounter or control location, we calculated, for each hourly interval from 5 h before to 24 h after the location, the speed (m/h) of the zebra. To assess how far zebras moved after a predator encounter, we calculated the net displacement from the encounter or control location for each location over the same period (5 h before to 24 h after the encounter or control location). We then compared the mean difference in speed over each hourly interval (for all the encounters) and the mean difference in net displacement between situations corresponding to encounters with a lion, encounters with a hyaena and controls by using multiple means comparisons (Herberich et al., 2010). Including data 5 h before the encounter allowed us to compare zebras' trajectories before and after the encounter.

### ***Avoidance of the encounter area after an ‘immediate flight’***

‘For ‘immediate flight’ responses, we calculated the time elapsed before coming back to the encounter area (Fig. A3, step (3) in Fig. 1). We chose to study this response only within a 72 h window after the encounter, to ensure that we were studying the actual antipredator response of the prey. Indeed, the longer the time gap since the encounter, the less likely it is that zebras' trajectories are influenced by the predator encounter. For returns within 72 h (which happened for 38% of the ‘immediate flight’ responses; Fig. A3), we further studied the drivers of this temporal dynamics of avoidance of the encounter area by using a Poisson regression:

$$T_{ij} = \exp(\beta_0 + \beta_p \text{predator}_{ij} + \beta_w \text{water}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij}) \quad (2)$$

### ***Time spent in the encounter area***

For ‘initial stay’ responses ( $N = 71$  after an encounter with a hyaena and  $N = 36$  after an encounter with a lion; one lion encounter was removed from the analysis as the lion killed the zebra), and for controls where zebras initially stayed in the encounter area, we calculated the time spent there (Fig. A4; step (4) in Fig. 1) and investigated whether some factors influenced it using a mixed negative binomial regression as it fitted the data better than the Poisson regression model:

$$S_{ij} = \exp(\beta_0 + \beta_p \text{predator}_{ij} + \beta_w \text{water}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij}) \quad (3)$$

The goodness of fit of every model was assessed using the Hosmer–Lemeshow test (Hosmer & Lemeshow, 2000; see goodness-of-fit (gof)  $P$  value in the Results). All the statistical analyses were performed with the R software (version 3.6.1; R Core Team, 2021). We considered explanatory variables with a  $P$  value lower than 0.05 statistically significant.



## Results

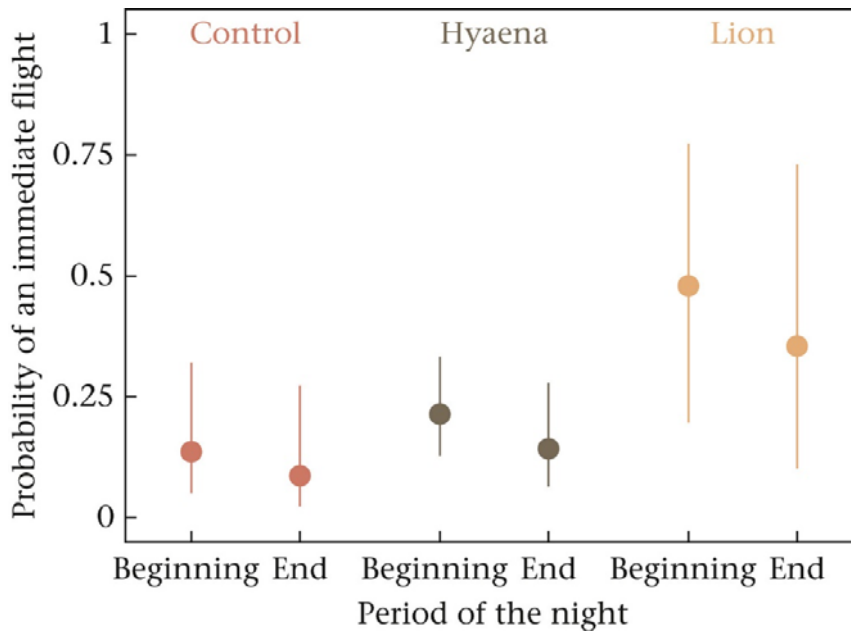
### Short-term Response of Zebras after a Predator Encounter

The probability of observing an ‘immediate flight’ response was higher after an encounter with a lion (0.48 on average) than after an encounter with a hyaena (0.21 on average), both being higher than for control situations (0.14 on average; Table 1, Fig. 2). After an encounter with a predator, zebras went mostly in the direction opposite from the predator location during the encounter (Figure A5, Figure A6). The probability of an ‘immediate flight’ response was lower at the end of the night (Table 1, Fig. 2), but was not significantly affected by distance to water or the vegetation type where the encounter occurred (Table 1;  $\text{gof } P = 0.07$ ).

**Table 1.** Estimates of the variables explaining the probability of a zebra engaging in an ‘immediate flight’ response within 2 h after an encounter with a predator

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

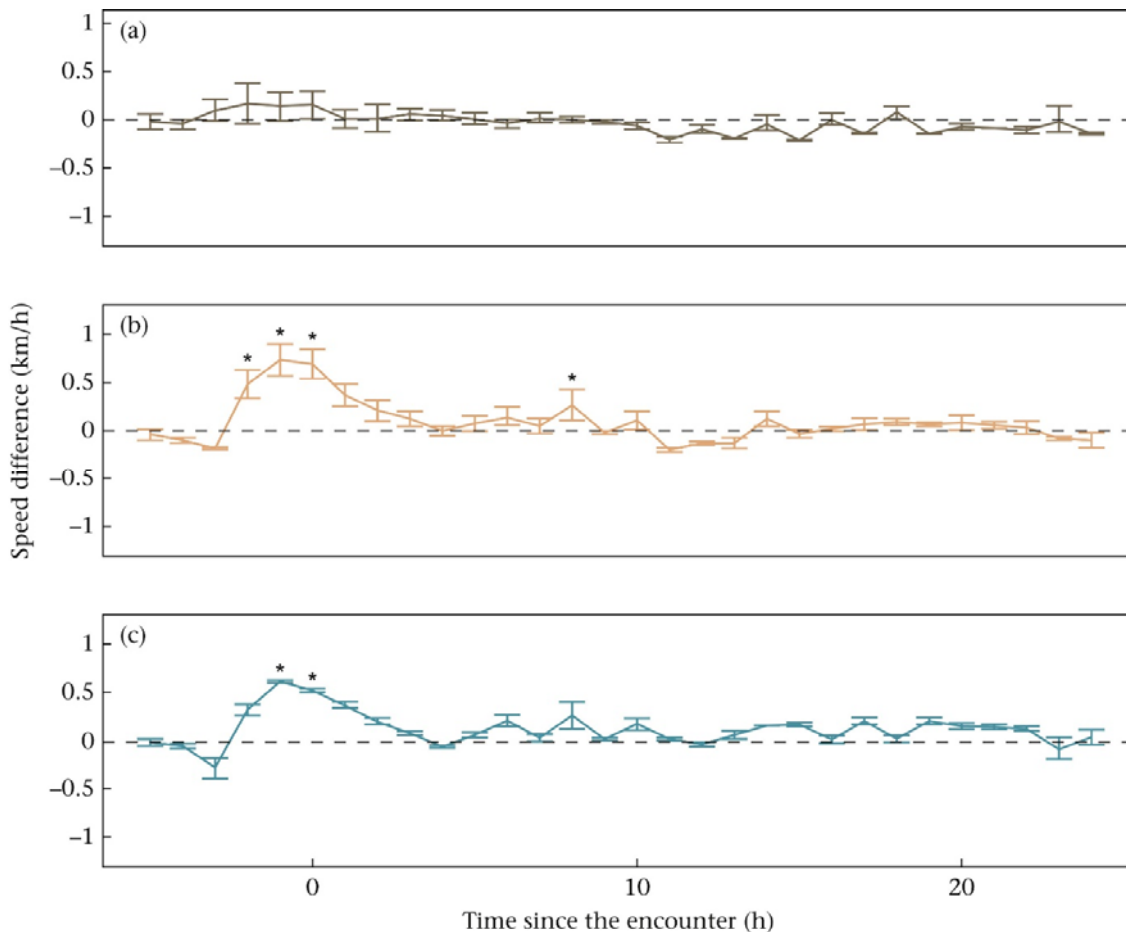
Hyaena is the reference level for the predator variable. Significant values are in bold.



**Figure 2.** Probability (calculated from the model estimates, with error bars representing the 95% confidence intervals) of a zebra leaving the encounter area in the 2 h following an encounter with a predator (‘immediate flight’) according to the period of the night (‘beginning’ or ‘end’). Probabilities were calculated for the default values of the other variables (i.e. when close to water and in dense vegetation).

### Temporal Dynamics After an ‘Immediate Flight’

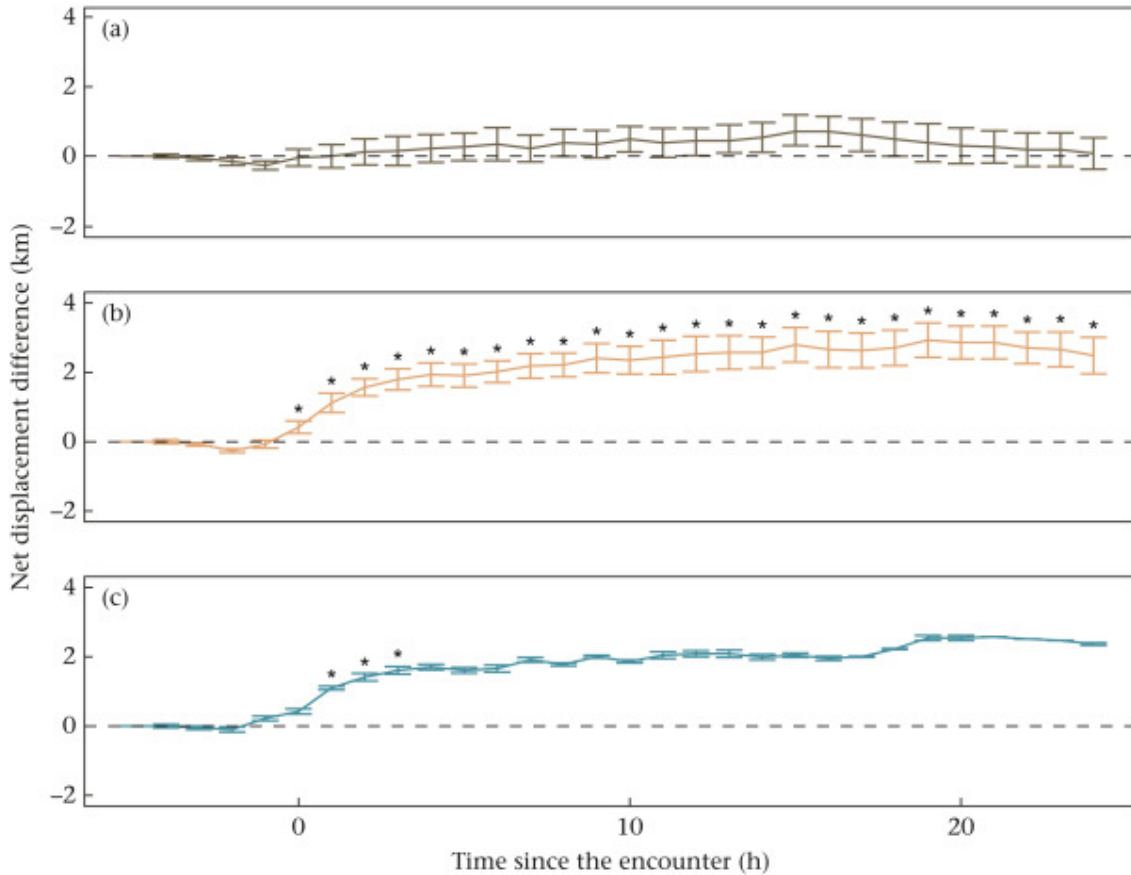
Zebras that fled immediately after an encounter with a hyaena did not move on average faster than during control situations as no mean speed difference at any time period was significant (mean speed  $\pm$  SD =  $1010 \pm 838$  m/h and  $854 \pm 741$  m/h, respectively;  $P = 0.87$ ; Fig. 3a). After an encounter with a lion, zebras immediately moved on average faster (mean speed  $\pm$  SD =  $1544 \pm 1198$  m/h) than after a control (mean speed  $\pm$  SD =  $854 \pm 741$  m/h; Fig. 3b;  $P = 0.4e-05$ ) or than after an encounter with a hyaena (mean speed  $\pm$  SD =  $1010 \pm 838$  m/h; Fig. 3c;  $P = 0.03$ ). We also detected a significant mean speed difference for the hour preceding the encounter (Fig. 3b and c). This is most probably because an encounter is defined from simultaneous hourly GPS fixes and the actual encounter may have occurred within the hour preceding the acquisition of these fixes. Afterwards, mean speed differences between lion encounters and hyaena encounters or controls were not significant, indicating that a higher mean speed characterized only the hour following the encounter (Fig. 3).



**Figure 3.** Difference in mean speed (between time  $t$  and  $t + 1$ ) between pairs of situations: (a) hyaena encounters versus controls, (b) lion encounters versus controls and (c) lion encounters versus hyaena encounters for zebras that performed an ‘immediate flight’ response. The bars represent standard errors. Asterisks indicate significant ( $P < 0.05$ ) differences from the multiple mean comparisons tests. Dashed lines indicate the value 0.

We detected no significant difference between mean net displacements after an encounter with a hyaena and after a control (Fig. 4a;  $P = 0.89$ ). Zebras moved further away after an encounter

with a lion (mean net displacement  $\pm$  SD = 6.2  $\pm$  4.4 km 24 h after; Fig. 4b) than after a control (mean net displacement  $\pm$  SD = 4.1  $\pm$  3.8 km 24 h after;  $P = 0.004$ ; Fig. 4b). In the 3 h following an encounter, zebras moved further away after a lion encounter (mean net displacement  $\pm$  SD = 4.8  $\pm$  2.5 km 3 h after; Fig. 4c) than after a hyaena encounter (mean net displacement  $\pm$  SD = 3.2  $\pm$  2.4 km 3 h after  $P = 0.004$ ; Fig. 4c).



**Figure 4.** Difference in mean net displacement between pairs of situations: (a) hyaena encounters versus controls, (b) lion encounters versus controls and (c) lion encounters versus hyaena encounters, for zebras that performed an ‘immediate flight’ response. The bars indicate the standard errors. Asterisks indicate significant ( $P < 0.05$ ) differences from the multiple mean comparisons tests. Dashed lines indicate the value 0.

### **Avoidance of the Encounter Area After an ‘Immediate Flight’**

Zebras returned sooner to an encounter area after an encounter with a hyaena (mean = 7.17 h; confidence interval, CI = 3.74–13.74) or after a control (mean = 10.81; CI = 3.10–37.71) than after a lion encounter (mean = 14.90 h; CI = 4.22–52.46; Table 2, Fig. A7;  $\text{gof } P = 0.99$ ).

**Table 2.** Estimates of the variables explaining the time spent by a zebra that performed an ‘immediate flight’ response before returning to the encounter area within 72 h

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

Hyaena is the reference level for the predator variable. Significant values are in bold.

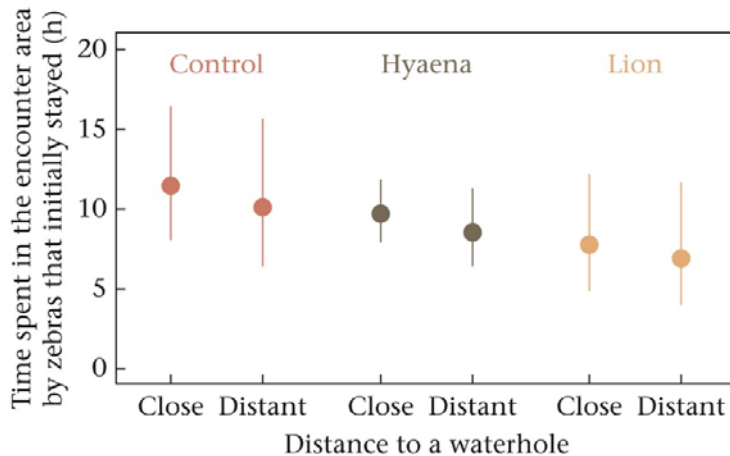
### Time Spent in the Encounter Area

The time zebras stayed in the encounter area did not differ between encounters with lions or hyaenas (Table 3, Fig. 5;  $gof P = 1.00$ ) and was ca. 10 h on average (CI = 8.25–12.31), but was a couple of hours shorter than under control situations (mean = 12 h; CI = 8.01–17.29; Table 3, Fig. 5). Zebras stayed longer (2 h more on average) in the encounter area when they were close to a waterhole (Table 3, Fig. 5).

**Table 3.** Estimates of the variables explaining the time spent by a zebra in the encounter area before leaving the encounter area for zebras that performed an ‘initial stay’ response

	Estimates	SE	z	P	Confidence interval	
					2.5%	97.5%
Intercept	<b>2.27</b>	<b>0.10</b>	<b>22.58</b>	<b>&lt;2e-16</b>	<b>2.06</b>	<b>2.47</b>
Control (predator)	<b>0.17</b>	<b>0.08</b>	<b>2.12</b>	<b>0.03</b>	<b>0.02</b>	<b>0.33</b>
Lion (predator)	-0.22	0.13	-1.68	0.09	-0.49	0.03
End (night period)	0.06	0.04	1.73	0.08	-0.01	0.12
Open (vegetation type)	0.001	0.05	0.02	0.99	-0.10	0.10
Distant (distance to water)	<b>-0.13</b>	<b>0.05</b>	<b>-2.73</b>	<b>0.01</b>	<b>-0.22</b>	<b>-0.05</b>

Hyaena is the reference level for the predator variable. Significant values are in bold.



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

## Discussion

### Spatial Response and Predator Dangerousness

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

Overall, our results are consistent with antipredator responses of prey strengthening as the dangerousness of the predator increases. The differences observed in the zebras' reactive spatial response between encounters with both predators can be intuitively explained by the difference in body size between lions and hyaenas, as the larger body size of lions gives this predator an obvious advantage over hyaenas to capture zebras. More originally, our results are also consistent with the hypothesis originating from the invertebrate literature that prey exposed to cues from sit-and-pursue predators (equivalent to ambush predators) should display stronger antipredator responses than prey exposed to cues from actively hunting predators (Preisser et al., 2007; Miller et al., 2014). The underlying mechanism would be that because sit-and-pursue predators tend to spend longer periods in the same area, cues of their presence should be more indicative of imminent predation risk, and therefore should elicit stronger prey responses. The idea that predator hunting mode can affect antipredator responses this way has started to appear in the literature on large mammals, with support for the above hypothesis at the scale of the proactive responses of prey (Thaker et al., 2011; Moll et al., 2016; Makin et al., 2017). Furthermore, the hunting success of ambush predators, such as lions, benefits from a surprise effect, as they can run at a very high speed but over short distances. Hence, once a prey has detected an ambush predator and leaves the encounter area, the probability that it will be pursued is low. This is different for cursorial predators, such as hyaenas, which can chase down prey over long distances and thus remain dangerous once detected. Hence, upon an encounter with a cursorial predator, leaving the area might not decrease the probability that the predator will pursue the prey. It has been shown that cursorial predators, such as hyaenas or wild dogs, *Lycaon pictus*, are often more successful hunters when prey flee right after the encounter (Creel & Creel, 2002; Mills, 1990). It is therefore possible that zebras do not leave the area immediately after encountering a hyaena, as this may be the most effective antipredator response, in particular if they increase their vigilance level. Our findings thus complement the other studies that found that lions elicited stronger proactive antipredator responses in African herbivores than hyaenas (Thaker et al., 2011; Moll et al., 2016; Makin et al., 2017), and suggest that this may hold for reactive antipredator spatial responses too. However, more studies covering other pairs of large carnivores are clearly needed to rigorously assess the role of the predator hunting mode.

Our study focused on the reactive spatial response, but prey can invest in other types of reactive responses, such as exclusive vigilance (Creel et al., 2017), resistance display such as bunching (Dannock et al., 2019) or fighting behaviours (Lingle & Pellis, 2002). This illustrates the limits of studies based on GPS data only, for which detailed information on nonspatial behaviour of prey is missing. Furthermore, GPS data that records hourly locations miss spatial response at a

finer timescale, as zebras might also move away for a few minutes only. Tackling the full complexity of the role of behaviour in predator–prey interactions will likely require a suite of data that new technologies can now provide (Suraci et al., 2022).

### **Context Dependence of Predator–Prey Interactions**

One important finding from our work is the high variability in the zebras' spatial responses, as zebras did not always leave an encounter area after a predator encounter and there was a high variability in the speed of movement after the encounter. In some cases, it is possible that predation risk was wrongly assessed, or assessed as not warranting a response, or that another antipredator response was more appropriate. The ecology of predator–prey interactions is context dependent and influenced by attributes of the predator, the prey and the environment (Wirsing et al., 2021). First, the behaviour of the predator, its group size and its hunger state can influence the antipredator behaviour of prey. For instance, an ‘immediate flight’ response might be the most appropriate to a hunting predator with a thin belly, likely hungry, while an ‘initial stay’ response might be the most appropriate to a walking predator with a fully distended belly that suggests that the predator is satiated. For instance, gerbils, *Gerbillus andersoni allenbyi*, adjust their foraging behaviour to the hunger state of owls, *Tyto alba*, (Berger-Tal et al., 2010). Prey attributes may affect the perception of predation risk and the associated antipredator responses such as group size (Childress & Lung, 2003), presence of young (Gochfeld & Burger, 1994), hunger state (Berger-Tal et al., 2010) and personality (Belgrad & Blaine, 2016). Another prey attribute is diet and, more precisely, the importance of their diet in their habitat selection. For instance, by having a selective diet for patches of short grass, wildebeests are less likely to leave a short grass patch after an encounter with a lion, while zebras, which are generalists, are less constrained and thus more likely to leave (Martin & Owen-Smith, 2016). Finally, the assessment of predation risk and the associated antipredator response may be influenced by the habitat configuration at the landscape level with an important role of the relative abundance and distribution of safe and risky areas (Laundré et al., 2014; Smith et al., 2019). In our study, habitat (vegetation structure and distance to water) at the encounter location did not play an important role in zebras' immediate spatial response. The probability of a zebra initiating an ‘immediate flight’ response increased at the beginning of the night, suggesting that encounters occurring at that time are riskier or that the costs associated with staying in the same area as their predator is too high when they need to monitor the predator for the whole night (‘risky times’ and ‘risky place’ hypotheses; Dröge et al., 2017).

### **Predator Influence on Prey Space Use**

In our study, we further explored how far a zebra went after an encounter with a predator and how long it avoided an encounter area (already studied for encounters with lions in Courbin et al., 2016). We believe such results provide useful insights into the predator–prey space game at the landscape scale (Sih, 2005). Our results show that lions influenced zebra space use over larger spatial scales than hyaenas. Indeed, zebras performed an ‘immediate flight’ more often after an encounter with a lion; they also moved further away when they encountered a lion (>6 km away on average 24 h after the encounter) than a hyaena (ca. 4 km on average). The immediate flight response is therefore associated with a missed opportunity cost in terms of foraging, as zebras forage a lot at night (Chamaillé-Jammes, n.d.), and prematurely leave their foraging patch for ‘immediate flight’ responses, but also with travelling costs (higher when zebras encounter lions because they move faster immediately after the encounter and cover longer distances). Additionally, our results mirror previous findings on lions leaving a kill area, probably because of the prey's behavioural depression after locating the lions and moving to a

different area (>5 km away; Valeix et al., 2011). This illustrates the predator–prey space game at the landscape scale. However, note that zebras that performed an ‘immediate flight’ had often returned to the encounter area by the next night, which may indicate a strong but nonlasting avoidance.

Zebras that initially stayed in the encounter area stayed longer in a control situation than when they encountered a predator, especially when close to water. Waterholes are important drivers of zebras' habitat selection, as zebras are water dependent and need to drink daily (Redfern et al., 2003). Furthermore, open grassland areas where zebras mainly forage are scarce and often associated with waterhole areas in the study ecosystem (Arraut et al., 2018). This result is consistent with a scenario whereby zebras in control conditions left the area because they had finished exploiting the resource patch (Searle et al., 2005), whereas zebras disturbed by a predator likely had to leave their resource patch prematurely. Zebras that had left immediately returned sooner to an encounter area after a hyaena encounter than after a lion encounter. This result suggests that zebras may perceive the environment risky for a longer period after a lion encounter and is again consistent with the hypothesis that ambush predators induce a stronger antipredator response.

### **Emergent Multiple Predator Effects?**

Different predators may affect prey's landscape of fear in complex ways (Sih et al., 1998). They can interfere directly by chasing each other (Périquet et al., 2021). They can interfere indirectly by reducing their hunting efficiency leading to risk reduction for the prey (Hoset et al., 2009). They can also facilitate each other if the prey's response to one predator makes the prey more vulnerable to the other (Leblond et al., 2016). At a small spatial scale (the encounter area), our results suggest that lion presence may lead to fewer prey for hyaenas, while at a larger spatial scale, hyaenas may benefit from lions that force zebras to move across the landscape at night. Indeed, in Hwange National Park, where hyaena density is high, hyaenas show no strong habitat selection pattern (Périquet, 2014), and their distribution is rather homogeneous across the landscape (Loveridge, n.d.). Therefore, hyaenas are likely to represent a uniform risk of predation over the landscape and lions may increase the probability that a zebra will encounter a hyaena by increasing zebra movements at night.

Our study builds upon and completes the study on the reactive spatial response of zebras to encounters with lions by Courbin et al. (2016). The controlled comparison with the reactive spatial response to encounters with hyaenas is a first step towards a better understanding of the role of the predator's identity and overall dangerousness on the nature and strength of this antipredator response. Our work further emphasizes that the immediate flight response is not that frequent, even after an encounter with a lion. It also highlights the limits of knowledge exclusively based on GPS information regarding the biological context of the encounter (predator behaviour, predator group size, prey context). Our study calls for further studies on other pairs of large mammalian predator species to be able to draw general conclusions on the impact of different predator attributes (e.g. body size, hunting mode) on the antipredator response of prey.

### **Author Contributions**

**Elise Say-Sallaz:** Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Simon Chamaille-Jammes:** Conceptualization (equal); Supervision (supporting); Data curation (equal); Funding

acquisition (equal); Project administration (equal); Investigation (equal); Methodology (equal); Writing – review and editing (supporting). **Stéphanie Périnet**: Data curation (equal); Writing – review and editing (supporting). **Andrew J. Loveridge**: Data curation (equal); Funding acquisition (equal); Project administration (equal); Writing – review and editing (supporting). **David W. Macdonald**: Funding acquisition (equal); Writing – review and editing (supporting). **Antony Antonio**: Data curation (equal); Writing – review and editing (supporting). **Hervé Fritz**: Data curation (equal); Funding acquisition (equal); Project administration (equal); Writing – review and editing (supporting). **Marion Valeix**: Conceptualization (equal); Supervision (lead); Methodology (equal); Investigation (equal); Writing – original draft (supporting); Writing – review and editing (equal).

## **Data Availability**

The data used in this study are archived and available from Mendeley Data: <https://data.mendeley.com/datasets/3yfn2jb6p8>

## **Declaration of Interest**

The authors declare that they have no conflict of interest.

## **Acknowledgments**

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## Appendix.

The diel shifts in habitat selection of zebras (i.e. GPS locations of zebras compared to random locations in zebras' home ranges) in the study area have already been investigated (Courbin et al., 2016, 2019): during the day, zebras strongly select for open grasslands located near waterholes; at night, zebras keep selecting the open vegetation patches but tend to move away from waterhole areas, which are heavily utilized by lions while hunting (Valeix et al., 2009, 2010). Here, we used selection functions (Manly et al., 2002) to assess whether encounters between a zebra and a lion or a hyaena occurred in a specific subset of circumstances (environmental conditions or time), compared to those generally experienced by zebras during the night. We did so by randomly selecting, for each encounter, 10 night-time locations from the trajectory of the zebra involved in the encounter. We then modelled the relative probability that a location could be an encounter given the distance to water, vegetation type and night period, by using a generalized linear mixed model with a binomial distribution for errors (encounters coded as 1 s, random locations as 0 s):

$$x_{ij} = \exp(\beta_0 + \beta_w \text{water}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij} + \gamma_{0j}) \quad (1)$$

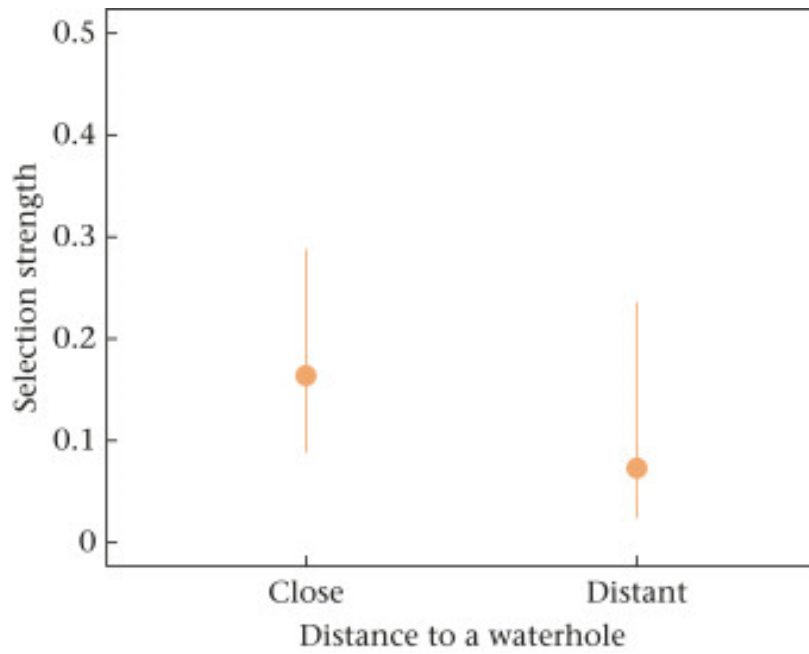
where  $i$  is the  $i$ th observation,  $j$  the  $j$ th individual zebra,  $x_{ij}$  is the selection strength,  $\beta_0$  is the intercept, the other  $\beta$  are the estimated fixed regression coefficients for the explanatory variables, and  $\gamma_{0j}$  is the random effect on the intercept  $\beta_0$  for zebra  $j$ . We conducted this analysis for the zebra–lion encounters and for the zebra–hyaena encounters to assess whether the characteristics of the encounters varied between the two predators.

Encounters between zebras and lions were located closer to waterholes than random zebra night locations (Table A1, Fig. A1). This was not the case for encounters between zebras and hyaenas (Table A1), but the difference between encounters with a lion and with a hyaena was not significant (overlapping CI; Fig. A1). Encounters with both predators did not occur in any specific vegetation type compared to those generally used by zebras at night (Table A1). Encounters also did not occur at a specific period of the night (Table A1).

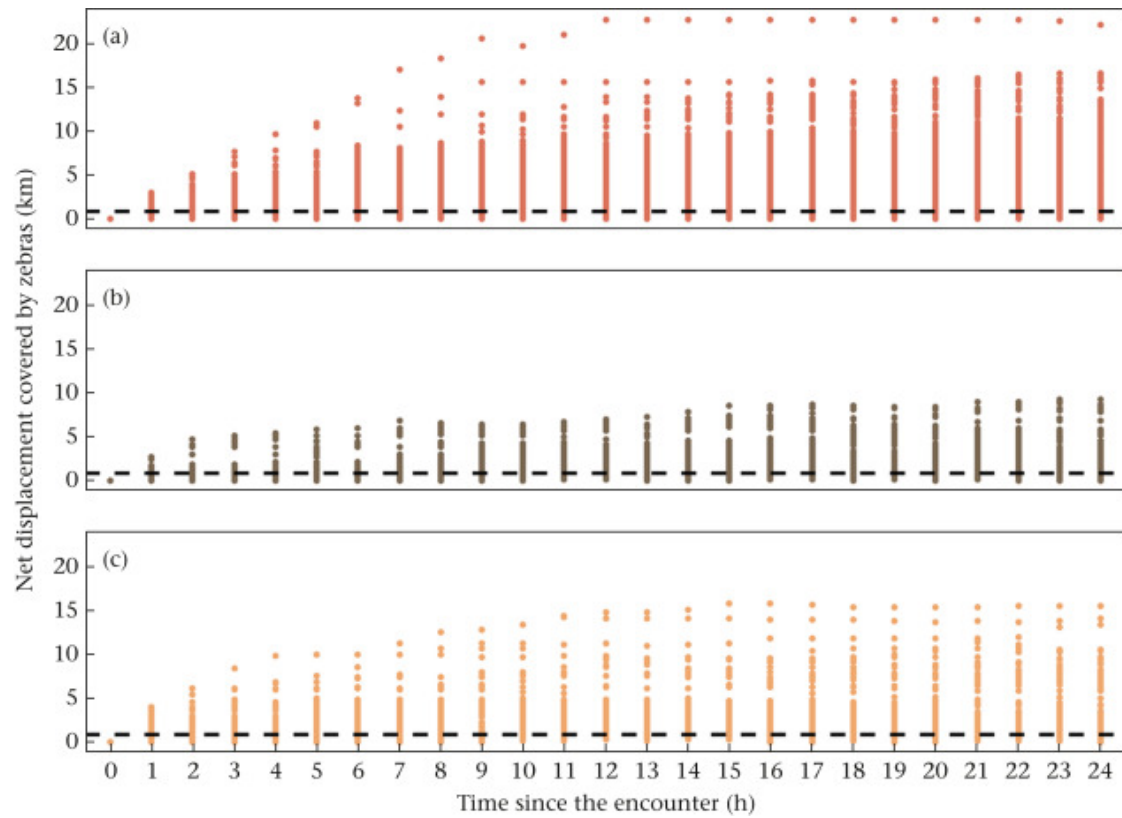
**Table A1.** Estimates of the variables explaining the relative probability of encounter between a zebra and a predator

Predator species	Variables	Estimates	SE	z	P	Confidence interval	
						2.5%	97.5%
Hyaena	Intercept	<b>-1.98</b>	<b>0.26</b>	<b>-7.52</b>	<b>5.43e-14</b>	<b>-2.52</b>	<b>-1.49</b>
	Distant (distance to water)	-0.33	0.27	-1.21	0.23	-0.84	0.22
	Open (vegetation type)	-0.15	0.34	-0.42	0.68	-0.85	0.50
	End (night period)	-0.11	0.22	-0.50	0.62	-0.55	0.33
Lion	Intercept	<b>-1.82</b>	<b>0.31</b>	<b>-5.94</b>	<b>2.92e-09</b>	<b>-2.45</b>	<b>-1.25</b>
	Distant (distance to water)	<b>-0.83</b>	<b>0.31</b>	<b>-2.67</b>	<b>0.008</b>	<b>-1.43</b>	<b>-0.20</b>
	Open (vegetation type)	-0.04	0.40	-0.10	0.928	-0.85	0.70
	End (night period)	0.27	0.26	1.05	0.294	-0.23	0.79

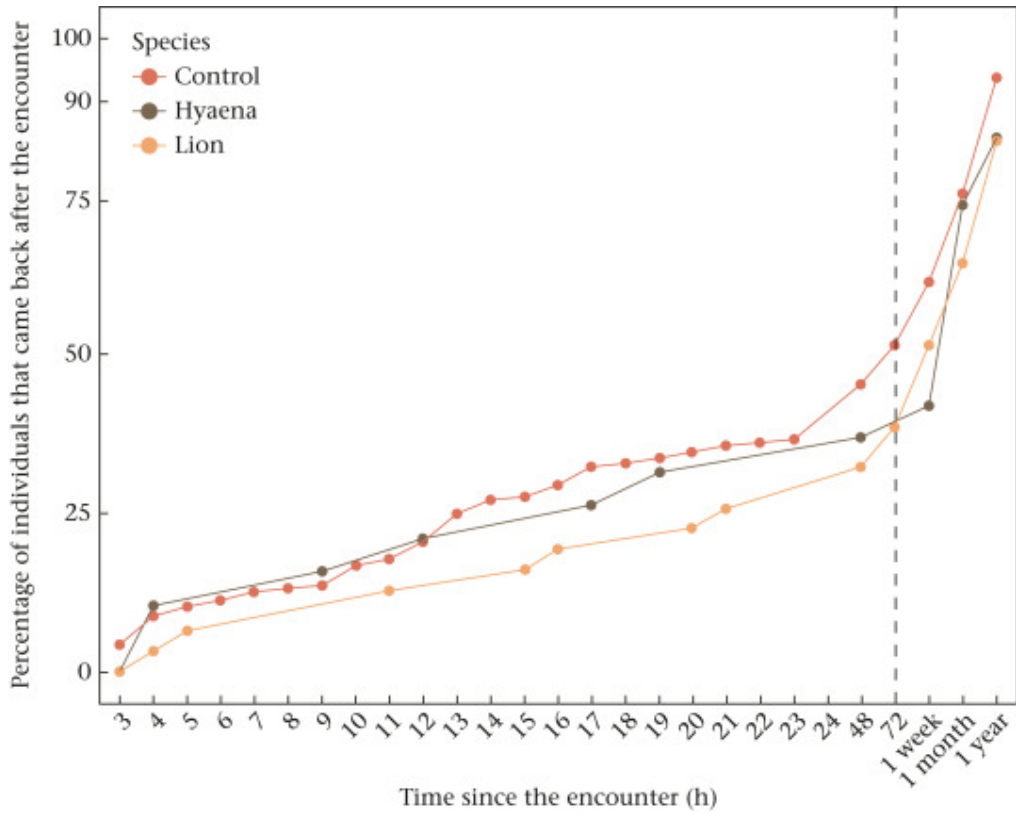
Significant values are in bold.



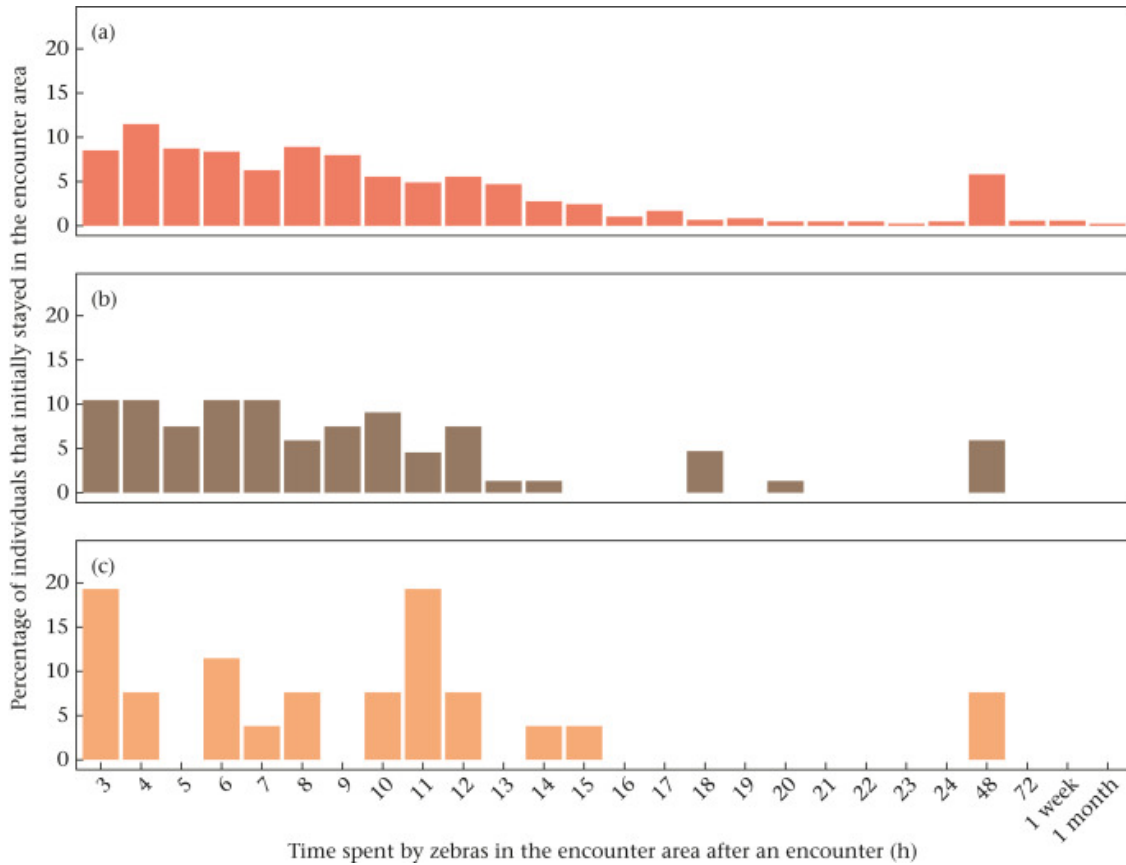
**Figure A1.** Relative probability (calculated from the model estimates, with error bars representing the 95% confidence intervals) that an encounter between a zebra and a lion would occur (selection strength) according to the distance to water. The distance to water is represented by a discrete variable of two classes: ‘close’ ( $\leq 1$  km) and ‘distant’ ( $> 1$  km). The selection strength was calculated for the default values of the other variables (in dense vegetation and at the beginning of the night).



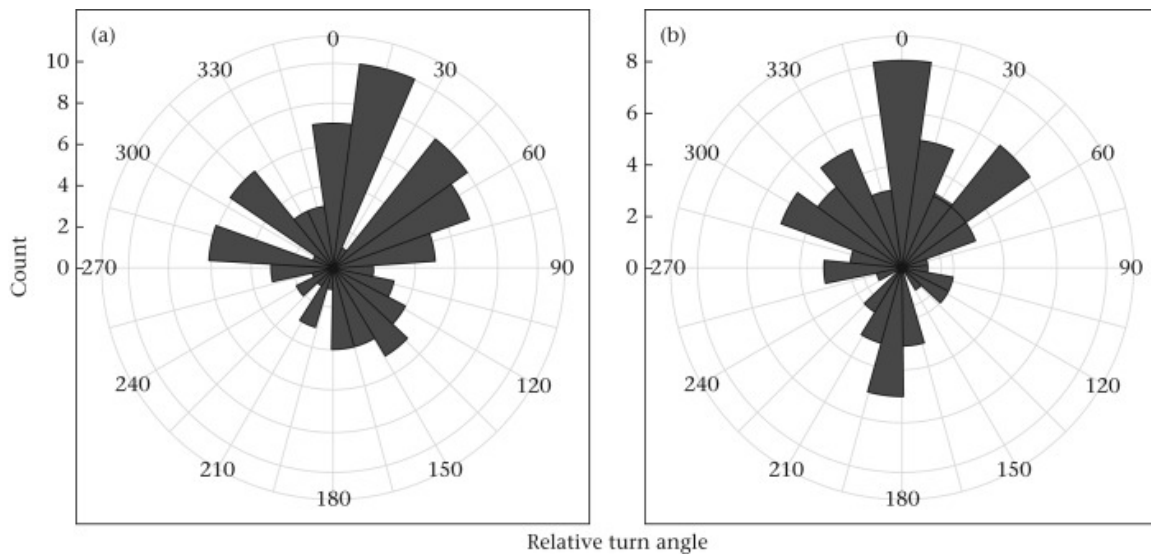
**Figure A2.** Net displacement (km) covered by zebras according to the time in (a) a control situation and the time since an encounter with (b) a hyaena or (c) a lion. The dashed black line represents the 900 m threshold used to characterize immediate flight responses.



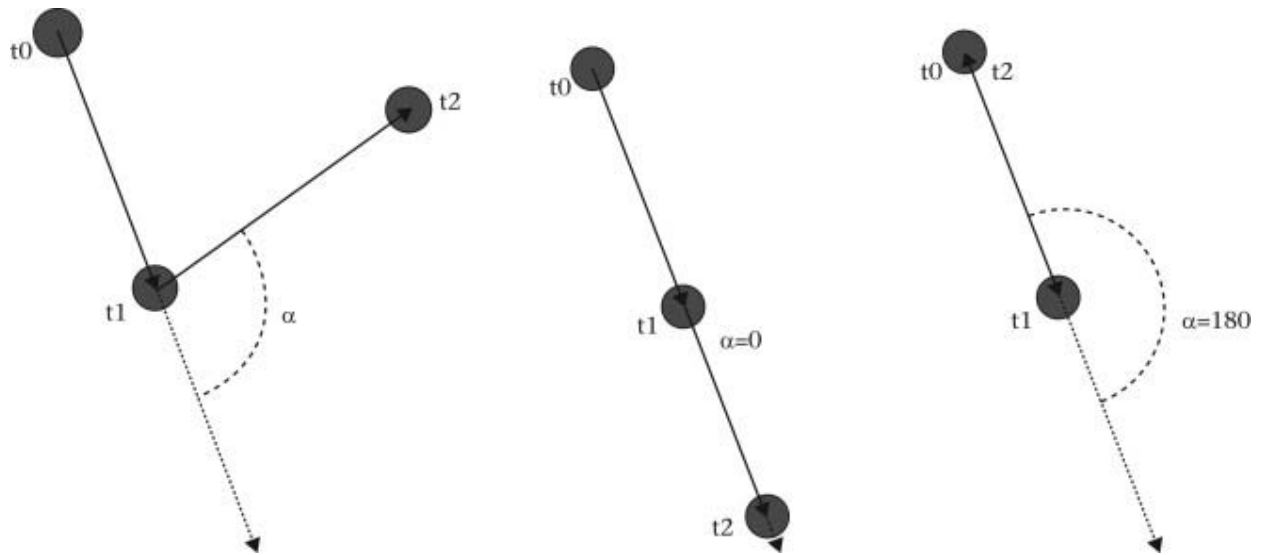
**Figure A3.** Percentage of individuals that came back after predator encounters and in control situations according to the time since the encounter for zebras that fled immediately after an encounter with a lion ( $N = 31$ , 26 came back and five did not come back within 72 h), an encounter with a hyaena ( $N = 19$ , 16 came back and three did not come back within 72 h) and a control situation ( $N = 213$ , 200 came back and 13 did not come back within 72 h). The dashed line represents the time interval used (72 h) to study the return of zebras to the encounter area. Note the change in the size of the temporal window over which percentages are calculated after the window size of 24 h.



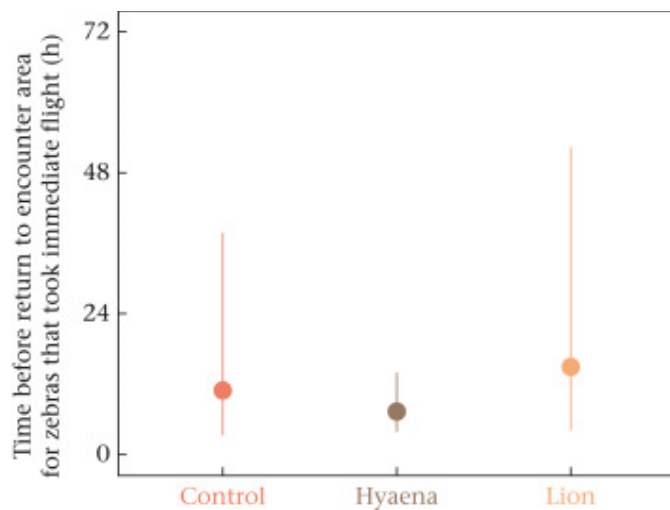
**Figure A4.** Distribution of the time spent by zebras in the encounter area in (a) a control situation ( $N = 1346$ ), after an encounter with (b) a hyaena ( $N = 71$ ) and (c) a lion ( $N = 36$ ), for zebras that did not initiate an ‘immediate flight’ response after an encounter. Note the change in the size of the temporal window over which percentages are calculated after the window size of 24 h.



**Figure A5.** The distribution of turning angles for zebras that encountered (a) hyaenas and (b) lions. Relative turn angles of zebras' trajectories were compared to the predator's (lion or hyaena) location by using the package ‘adehabitatLT’ in Rstudio (Calenge, 2006). See also Fig. A6.



**Figure A6.** Schematic representation of the relative turning angle ( $\alpha$ ). It is calculated within consecutive points of a trajectory ( $t_0, t_1, t_2$ ) and is a measure of the change in direction between the consecutive points of a trajectory. Relative turning angle values at 180 degrees suggest that zebras went in the direction of the predator location, whereas a relative turn angle of 0 degrees suggests that the zebra went away from the predator location.



**Figure A7.** For zebras that performed an ‘immediate flight’ response, time spent before returning to the encounter area (calculated from the model estimate, with error bars for the 95% confidence interval) within 72 h. Times were calculated for the default values of the other variables (at the beginning of the night, close to the water and in dense vegetation).

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