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## Ecology of predator-prey and predator-predator interactions in a multi-predator context

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**Ecology of Predator-Prey and Predator-Predator  
Interactions in a Multi-Predator Context**

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## Abstract / Résumé



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## Abstract

Large carnivores' coexistence is common, the aim of that thesis is to understand how it affects predator-prey interactions. First part of the thesis is about predator's Non-Consumptive Effects (NCE hereafter) on prey. Predation risk induce costly behavioural modification for prey, that have an impact on prey population dynamics. For invertebrates these NCE can account for 85% of the total effect of predation. The first chapter is a literature review about NCE for large terrestrial mammals, it highlighted the fact studying NCE requires long term data collection, that reactive (i.e. immediate risk assessment) antipredator response have been less studied than proactive response (long term risk assessment) and that knowledge on NCE mostly come from studies taking only one predator species into account while 90% of the studies took place where several coexist.

Hence, second and third chapters focus on reactive response of prey to predators with different hunting mode in order to test the hypothesis that ambush predators (that take prey by surprise) induce higher NCE than cursorial ones (chase down prey), as it has been demonstrated for invertebrates' species. The second chapter investigate plain zebras (*Equus quagga*) spatial reactive response to encounters with spotted hyaena (*Crocuta crocuta*) a cursorial predator and African lion (*Panthera leo*) an ambush one, with data from GPS collars that were simultaneously deployed on the three species. zebras were twice as likely to leave and they left faster and further away after a lion's encounter than a hyaena's one. The third chapter was an experiment to evaluate the immediate behavioural response of the roe deer (*Capreolus capreolus*) to the Eurasian lynx (*Lynx lynx*) an ambush predator and the grey wolf (*Canis lupus*) a cursorial one. Predation risk was simulated at night with playbacks and prey's response was filmed. Roe deer were more likely to leave the experiment site if lynx vocalises were broadcasted. Results from both chapters support the hypothesis that ambush predator induce

higher antipredator response than cursorial one. Because predator not only differ by their hunting mode (body size, sociality) and that both chapters only considered one pair of predator at a time, more studies are needed in order to draw general conclusions as it has been done for invertebrates' species.

Sympatric large carnivores are linked within a web of diverse interactions (negative and positive), in a second part of the thesis with fourth chapter we evaluated spatio-temporal co-occurrence patterns at different scales, of three sympatric large carnivores: the spotted hyaena, the lion and the leopard (*Panthera pardus*), using camera trap data. We assessed the overlap in pattern of diel activities, the general spatial overlap and finer scale spatio-temporal co-occurrence patterns between the three species. The three species have an important overlap in their diel activity pattern as expected. Lions and leopards do not co-occur spatially very often (in one fourth of the camera trap stations). Time-to-event analyses suggest that carnivores tend to use areas previously used by another carnivore species very closely in time (in the 2 hours following the use of the area by the other species) but also during the consecutive nights, which led us to lay the “follower hypothesis” and the “delayed exploration hypothesis” respectively. We discussed the potential underlying interspecific interactions that take place between species such as kleptoparasitism, scavenging opportunities, interference competition and indirect interactions through prey catchability for instance.

## Résumé en français

La coexistence d'espèces de grands carnivores n'est pas rare, l'objectif de cette thèse est de comprendre comment cela affecte les interactions proie-prédateurs. La première partie de la thèse porte sur les effets non létaux (NCE, Non-Consumptive Effects) des prédateurs. Face au risque de prédation les proies peuvent modifier leur comportement, ce qui est coûteux (stress, énergie), et va avoir un effet sur la dynamique de population des proies. Chez les invertébrés les NCE contribuent jusqu'à 85% de l'effet total de la prédation. Le premier chapitre est une revue de littérature à propos des NCE chez les grands mammifères. J'ai mis en évidence qu'étudier les NCE chez les grands mammifères implique de collecter des données sur le long terme, que les réponses réactives (i.e. les réponses à un risque de prédation immédiat) ont été peu étudiées, et que les connaissances sur les NCE avaient principalement été acquises en ne prenant en compte qu'un prédateur (or pour 90% des zones d'études plusieurs espèces de prédateurs coexistent).

Ainsi, dans le deuxième et troisième chapitre, j'ai étudié la réponse réactive antiprédateur de grands herbivores à des prédateurs ayant des modes de chasses différents, afin de tester l'hypothèse que les prédateurs à l'affût (attrapent leurs proies par surprise) induisent des NCE plus importants que les prédateurs cursoriaux (coursent leurs proies) comme cela a été démontré chez les invertébrés. Le second chapitre porte sur la réponse spatiale réactive du zèbre des plaines (*Equus quagga*) après une rencontre avec la hyène tachetée (*Crocuta crocuta*) un prédateur cursorial, ou le lion d'Afrique (*Panthera leo*) un prédateur à l'affût, et ce à partir de données issues de colliers GPS, déployés simultanément sur les trois espèces. Les zèbres avaient deux fois plus de chances de fuir, ils se déplaçaient plus rapidement et plus loin après avoir rencontré un lion qu'après avoir rencontré une hyène. Dans le troisième chapitre j'ai mis au point une expérience pour évaluer la réponse comportementale immédiate du chevreuil (*Capreolus capreolus*) au lynx (*Lynx lynx*) un prédateur à l'affût et au loup gris (*Canis lupus*)

un prédateur cursorial. Le risque de prédation a été simulé la nuit avec des repasses acoustiques, et la réponse des proies a été filmée. Les chevreuils abandonnaient plus souvent le site après une repasse acoustique de lynx. Les résultats des deux chapitres tendent à supporter l'hypothèse de départ. Parce que les prédateurs ne diffèrent pas que par leur mode de chasse (masse corporelle, socialité...), et que ces chapitres ne s'intéressent qu'à une seule paire de prédateurs à la fois, il y a besoin d'autres études pour pouvoir tirer des conclusions générales comme cela a été le cas pour les invertébrés.

Les grands carnivores sympatriques sont liés par un réseau d'interactions diverses (négative et positives). Dans une seconde partie de la thèse étant le quatrième chapitre, j'ai évalué les cooccurrences spatio temporelles de trois grands carnivores sympatriques : le lion, la hyène tachetée et le léopard (*Panthera pardus*), à différentes échelles en utilisant des données de pièges photographiques. Nous avons estimé, le chevauchement de leurs patrons d'activité journalière, leur chevauchement spatial, et à une échelle plus fine les patrons de co-occurrence entre les trois espèces. Comme attendu, les trois espèces avaient des patrons d'activité temporelles chevauchants. Les lions et les léopards ne cooccuraient spatialement que très peu souvent. Les carnivores avaient tendance à visiter une zone déjà visitée par un autre carnivore, très rapidement à près celui-là (dans les 2 heures qui suivent la visite d'une précédente espèce), mais aussi durant les nuits suivantes. Cela nous a conduit à formuler « l'hypothèse du suiveur » et « l'hypothèse d'exploration tardive ». Nous avons discuté les mécanismes sous jacents potentiels, qui pouvaient avoir lieu entre les espèces, comme le kleptoparasitisme, le charognage, la compétition par interférence ou encore la facilitation indirecte via la disponibilité des proies par exemple.

# Introduction



## **Large mammals: status and ecological role**

### *Decline of large mammals in the Anthropocene*

Our impact on the planet has been so profound and rapid that the epoch we live in is now known as the Anthropocene (Crutzen & Stoermer, 2000). Since the industrial era, our impact on the planet increased greatly in terms of land use with mechanization of the agriculture and fishing, the use fossil fuels and fertilizers for instance (Ruddiman, 2013). This profound changes led to the emission of greenhouse gases with an associated raise in the global temperature, an important erosion of soils, degradation and fragmentation of habitats (Ruddiman, 2013) and biological invasion that until today are the main drivers of biodiversity loss (Fahrig, 2003; Bellard et al., 2016). Since the Earth summit on biodiversity in Rio de Janeiro in 1992, more than 20 years of research have shown that the effects of biodiversity loss on ecosystems are as important as the other effects of environmental changes (Cardinale et al., 2012).

Large terrestrial mammals are often portrayed as flagship species (Clucas, McHugh and Caro, 2008; Smith et al., 2012). However, and most importantly, their populations are facing rapid changes and the vast majority are threatened. Indeed, 61% of the large carnivore species (>15kg) are considered threatened according to the International Union for Conservation of Nature (IUCN), as they have small population sizes and their populations are declining (Ripple et al., 2014). Their main threats are habitat loss, human persecution and depletion of prey population (Ripple et al., 2014). Some of these species have undergone large range contractions as well, such as the cheetah (*Acinonyx jubatus*) and the African lion (*Panthera leo*) (they now use 17% of their historical range) (Ripple et al. 2014). Large terrestrial herbivores represent about 4000 species and 60% of the largest species (>100kg) are also considered threatened by

the IUCN (Ripple et al., 2015). Large herbivores are facing similar threats as large carnivores, i.e. land use change and associated competition with livestock, but also suffer bush meat trade, which is amplified during armed conflict (Ripple et al., 2015). Both large herbivores and carnivores are found in protected areas but also outside where they are involved in human-wildlife conflict. Large carnivores can be a threat to livestock (Ritchie et al., 2012; van Eeden et al., 2018) and sometimes to human lives (Penteriani et al., 2017). They can thus be in intense conflict with people and some species went locally extinct because of human persecution, as in France and Switzerland (Breitenmoser, 1998; Lescureux & Linnell, 2010). Large herbivores are also involved in conflicts with humans because of crop damages, road collision or disease transmission to cattle (Ripple et al., 2015).

#### Ecological role of large mammals

Large herbivores play a major role in the shaping and functioning of ecosystems (Danell et al. 2006). They are sometimes considered engineer species that can have an impact on the landscape structure through their foraging activity. For instance, large grazers help maintaining heterogeneity by maintaining patches of grassland in areas that would be recovered by woodland otherwise (Gates et al., 2010). Herbivores further influence the frequency and intensity of fire, and fire and herbivory clearly interact to shape the dynamics of vegetation (Kramer, Groen and Wieren, 2003; Sankaran, Ratnam and Hanan, 2008). For instance, the grazing activity of a megaherbivore, the white rhinoceros (*Ceratotherium simum*), reduces fuel load and so the frequency and intensity of fires in African savannas (Waldram et al., 2008). Cattle grazing can also have an influence on fires as well by reducing the probability of fire ignition (Davies et al., 2017). Following the “grazing optimization hypothesis”, herbivores can also enhance primary net production, as grazed plants compensate grazing by re-growing these parts at a speed faster than ungrazed plants (Hilbert et al., 1981; McNaughton, 1983). Some plants also rely on herbivores for seed dispersion (Blake et al., 2009). Large herbivores’ urine

and faeces affect nutrient cycling through an increase in soil nitrogen concentration and the associated microorganism concentration, which speeds the process of matter decomposition (Hobbs, 1996). Migratory herbivores are also very important for the coupling of ecosystems' functioning worldwide (Bauer & Hoyer 2014). Ultimately, the loss of large herbivores may thus lead to profound changes in ecosystem structure and functioning (Gill, 2014; Johnson et al., 2016). Conversely, very high densities of large herbivores can have negative effects on biodiversity (Foster, Barton and Lindenmayer, 2014). For instance, high densities of deer can have a negative impact on bird communities (Fuller, 2001). Overabundance of large herbivores in Europe and North America got large herbivores involved in conflicts with people, because of damages caused on crops and transmission of disease to livestock for instance (Côté et al., 2004).

The important role of herbivores in the structure, functioning and dynamics of ecosystems gives an insight on how much predation can have an impact on ecosystems, through cascading effects. In Zion canyon, USA, high levels of human disturbance induced a decrease in the density of an apex predator, the cougar (*Puma concolor*). This led to overabundance of mule deer *Odocoileus hemionus*, which affected recruitment of vegetation species close to rivers, increasing erosion dramatically and leading to decreases of biodiversity of both terrestrial and aquatic ecosystems (Ripple and Beschta, 2006). Similar patterns were found with wolf (*Canis lupus*) extinction from the Yellowstone National Park ecosystem, which led to high abundances of elk (*Cervus elaphus*). Wolf reintroduction in the ecosystem in 1995/96 is one of the most documented example of the benefits of having large carnivores in ecosystems. Wolf reintroduction in the Yellowstone ecosystem led to a reduction of herbivory pressure from elk on woody vegetation especially riparian vegetation, which had a positive impact on beaver populations, as it is an important resource for them. It also reduced bank erosion and helped stabilizing streambanks and preventing river from becoming wider and more braided (Beschta

and Ripple, 2012). The increase in woody plants affected positively bird populations, as more habitat was available for them. It also increased the production of berries, an important resource for bears. Wolf reintroduction led to reduced predatory pressure of coyotes (*Canis latrans*) on Pronghorn (*Antilocapra americana*) and other small mammals. Indeed, the absence of apex predators is often associated with the rise of the mesopredators, a phenomenon referred to as the mesopredator release (Ritchie and Johnson, 2009). Finally, wolf predation on elk led to an increase in elk carcasses that were beneficial for scavengers, such as raven (*Corvus corvax*) and bald eagles (*Haliaeetus leucocephalus*) (Ripple and Beschta, 2012). The reestablishment of the wolf in Scandinavia showed similar results, wolves increased the quantity of moose (*Alces alces*) carcasses that was beneficial for scavengers (Wikenros et al., 2013).

In natural ecosystems, a rich network of interspecific interactions connects large carnivores and herbivores. These interactions are some of the main mechanisms underlying the distribution and abundance of species in an ecosystem. Because several species of large carnivores and herbivores are facing rapid changes in their distribution and abundance worldwide, some interactions linking these species inevitably disappear or appear in some ecosystems. It is of paramount importance to understand these interactions to assess how they will change with global changes and the associated impacts on the functioning of ecosystems.

## **Interspecific interactions: towards a community perspective of these interactions**

### Interactions between two species

Historically, interspecific interactions and predation in particular were modelled with a pair of species directly interacting and the aim was to model population dynamics of the two species. The Lotka-Volterra equations have been used to model several interspecific

interactions, such as predation or competition (Volterra, 1926). For predation, the model predicted that under a deterministic environment a state of neutral stability can be reached, where population sizes of both prey and predator species fluctuate (Volterra, 1926). These equations have been revisited since then by Rosenzweig and MacArthur who introduced new notions, such as the carrying capacity of prey populations determined by resources (Rosenzweig & MacArthur, 1963).

Several types of interactions exist between species. Trophic interactions are feeding relations between a consumer species and a consumed species (Morin, 2011). Consumer species are typically carnivore species that consume herbivore species through predation and scavenging. The outcome is negative for the consumed species and positive for the consumer. Exploitative competition is the depletion of a shared resource by the most competitive species (Morin, 2011). Non-trophic interactions, such as behavioural interactions also exist. Interference competition for instance is an example of behavioural interaction. It happens when two species use a shared resource that is limited, such as space or a prey, and one (or both) species shows aggressive behaviours towards the other one. The behavioural response of prey to predator is also a type of behavioural interaction (detailed in chapter 1).

Most of the historical work on modelling interspecific interactions used a pair of species, but communities are more complex than just two sympatric species interacting. While studying simple systems has several advantages, simplification can however lead to false conclusions about the interactions between species (Morin, 2011). There is an increasing awareness of the need to take into account a more of the complexity of the systems studied in order to draw more accurate conclusions (Montgomery et al., 2019, Annexe 1).

*Predator-prey interactions: a cocktail between prey traits, predator traits and the environment*

Predator-prey interactions are multiple. For instance, the behavioural interactions between a lion pride and a buffalo (*Syncerus caffer*) herd in a grassland savanna is likely to differ from the behavioural interactions between a lone leopard (*Panthera pardus*) and a small duiker (*Raphicerus campestris*) in a wooded savanna. The nature of a predator-prey interaction is indeed influenced by the traits of the species at play and the environment where the interactions occur.

*Prey traits* - There are numerous prey traits that can modulate predator-prey interactions. Three of the most important prey traits involved in predator-prey interactions are prey body size, the degree of prey foraging specialization and prey group size (Creel, 2011). First, prey body size modulates how vulnerable a prey is to a predator, as it is a factor of prey selection by the predator (Krause & Godin, 1995; Sand et al., 2016). Very large prey, such as megaherbivores, are virtually invulnerable to predation (Ripple et al., 2015). In Kruger National Park, South Africa, where five large predator species coexist, it has been shown that each predator has a preferred range of prey body size (Owen-Smith & Mills, 2008). The degree of foraging specialization is also an important factor in predator-prey interactions. Predation risk influences the quantity of energy that prey will allocate to either foraging or antipredator behaviour, a process known as the predation risk allocation hypothesis (Lima & Bednekoff, 1999). If the situation is not risky, it is very probable that prey will allocate more time and energy to foraging than antipredator responses, whereas it will be the opposite in riskier situations (Lima & Bednekoff, 1999). Foraging specialization modulates that allocation and the magnitude of the antipredator response. Indeed, prey that have a specific diet are more likely to leave an optimal foraging area in reaction to the predator presence only and not for a long time, as this means giving up resource patches of good quality (Lima & Bednekoff, 1999; Creel, 2011). Another prey trait that can modulate interactions with predators is group size. Indeed,

studies have shown that predation risk had an influence on prey group size. For instance, when exposed to Eurasian lynx's scat, roe deer vigilance decreased as group size increased (Kuijper et al., 2015). Besides, zebras (*Equus quagga*) and wildebeests (*Connochaetes taurinus*) are found in larger groups when they are in an area where the predation risk by lions is high (Valeix et al., 2009). The underlying mechanism is a negative relationship between an individual level of risk perception and group size, which is due to the increased capacity to detect an approaching predator in large groups (the "many eyes" effect - Roberts, 1996), to a dilution effect, and in some cases to the increased ability to fight back a predator as a large group. For large mammals, prey phenology can also affect predator-prey interactions. Some species, such as wildebeests, have a calving season that is restricted in time, which lead to a too important abundance of prey for predators to consume most of it. Furthermore, wildebeest calves grow fast and can escape predation shortly after calving season (Gosling, 1969).

*Predator traits* - For a long time, the main trait considered for predators was their body size and predator-prey interactions were assessed through predator-prey size ratios. The prey had to be within a certain energy range for the predator: it had to have a sufficient body mass to meet the predator energetic needs and had to be small enough to be captured by the predator (Hirt et al., 2020). Other characteristics of the predator are at play, such as its speed capacity. For instance, the biomechanics of two pairs of predator-prey have been studied, the lion with the zebra and the cheetah with the impala (*Aepyceros melampus*), and in both cases predators had more muscle fibre power and also better capacities of acceleration and deceleration than their prey (Wilson et al., 2018). The hunting mode of the predator is also an important trait to consider. There are two main hunting modes among large carnivores: ambush and cursorial predators. Ambush predators rely on concealment to hunt by surprise prey moving within a chasing distance. Most felids use that hunting mode. Cursorial predators can chase down their prey over long distances before trying to catch them. This concerns most of the canids and

hyaenidae species. The ursidae family is aside because only one species is mostly carnivorous, the polar bear (*Ursus maritimus*). It hunts on the ice but also swims to catch its prey (Stempniewicz et al., 2013). Finally, another factor comes into account when looking at hunting strategies among large carnivores: their sociality. Social carnivores can hunt in cooperative groups. It has been observed within felidae, canidae and hyaenidae (Macdonald, 1983). While some species, such as wild dogs almost only hunt in groups (evidence for Alle effect Courchamp, Rasmussen and Macdonald, 2002), others like hyaenas get in group temporarily (up to ten individuals) for hunting parties on larger prey such as zebra or wildebeest (Macdonald, 1983). Overall, several predator characteristics are correlated. The link between one predator body size and its hunting strategy is the speed it is capable to reach (Hirt et al., 2020). Overall, cursorial predators hunt smaller prey that are also slower than they are, whereas ambush predators have no prey size preference and are more generalist but have a trophic niche close to group hunters. This niche differentiation between ambush and cursorial predators decrease competition between them when they are sympatric (Hirt et al., 2020).

*Environment characteristics* - Prey perception of predation risk is known as the landscape of fear (Laundré, Hernandez and Altendorf, 2001). The assessment of the predation risk is based on encounter rate with the predator, the predator lethality in the habitat and the effectiveness of vigilance (Brown, Laundré and Gurung 1999). Habitat structure modulates the hunting efficacy of a predator and environment characteristics can create refuge for prey. Predator lethality and effectiveness in a given habitat can be linked to its hunting mode. Ambush predators are thought to perform well in landscape that give them the opportunity to stay undetected, and where prey visibility is impaired (Balme, Hunter & Slotow, 2007), whereas cursorial predators are thought to perform better in opened landscape (Kauffman et al., 2007). The areas in the landscape where the predator is less efficient can be seen as refuges for prey from that predator (Sih, 1984). Predator encounter rate is linked with predator habitat selection.

Wolf for instance tend to select habitat with higher elk density in northwest Montana (Oakleaf et al., 2006). Lions in Hwange national park do select areas close to waterholes because it is where most of the prey are located (Davidson et al., 2012). Overall, prey tend to minimize their spatial overlap with predators, while predators try to maximize it in what is called a predator-prey “space race” (Sih, 2005). Human presence can as well affect predator-prey interactions and mostly help prey win the predator-prey race. High human densities are creating refuge for prey by displacing predators (Muhly et al., 2011). In Banff National Park, Canada, wolves avoided areas with high human densities that turned into refuges for prey, and survival and recruitment in herbivore populations were better than in areas low human activities (Hebblewhite et al., 2005).

Predation risk thus results from the interaction between prey characteristics, predator characteristics and the environment characteristics.

#### *An interspecific interaction embedded in a network of interactions*

As far as predation in natural ecosystems is concerned, there is a need to consider more than one prey and one predator species, as carnivore and herbivore species are embedded in complex food webs in particular (Owen-Smith & Mills 2008), and webs of interspecific interactions in general (Kéfi et al. 2012, 2015).

*Indirect interactions* - Studying indirect interactions between species in a system is also an important pathway towards a better understanding of the complexity of the functioning of interspecific interactions in general and predation in particular. This leads to investigate trophic cascades and apparent competition, two major interspecific indirect interactions (Holt 2017, Estes et al., 2011). A trophic cascade takes into account all the other species indirectly affected by one predator-prey interaction (Morin, 2011). Trophic cascades are through top-down effects, i.e. the impact of a top predator on species lower in the trophic web. Trophic cascades can

emerge in the framework of the Exploitation Ecosystem Hypothesis (EEH) or the Mesopredator Release Hypothesis (MRH). The EEH predicts that top predators will reduce herbivore abundance, and hence control herbivory (Oksanen et al., 1981; Aunapuu et al., 2008). The MRH predicts that mesopredator abundance in an ecosystem will be controlled by the presence of top predators, which suppress mesopredators (Elmhagen et al., 2010). For instance, a three-level trophic web in Finland with the Eurasian lynx, the red fox (*Vulpes vulpes*) and the mountain hare (*Lepus timidus*) showed that lynx presence reduced fox biomass, which ultimately led to an increase in hare biomass as they escape top down regulation by foxes (Elmhagen et al., 2010). This study also showed that these indirect interactions were modulated by environmental factors, as in another ecosystem the MRH effect of lynx was not strong enough to affect positively hare biomass (Elmhagen et al., 2010). Trophic cascades can be density-mediated (Ford & Goheen, 2015) or behaviourally-mediated (Schmitz, Beckerman and O'Brien, 1997).

When two prey species sharing the same predator species co-occur, predation may intensify, and prey mortality rates might be higher than when the two prey species do not co-occur. This could be interpreted as competition while in fact it is the result of a more intense predation on both species (Holt 1977, Morin, 2011). This enemy-mediated apparent competition was well demonstrated with models (Holt, 1977; Holt & Kotler, 1987; Abrams, Holt and Roth, 1998). Evidence of apparent competition in natural systems has also accumulated, mostly with parasite-host systems (Bonsall & Hassell, 1997; Tompkins, Draycott and Hudson, 2000; Morris, Lewis and Godfray, 2004) but also in predator-prey studies with introduced species (Sweitzer, Jenkins and Berger, 1997; Gibson, 2006). For instance, re-introduction of lions in a managed area (Ol Peteja Conservancy in Kenya) allowed to highlight that the main interaction between plains zebras and hartebeests (*Alcelaphus bucelaphus*) was in fact apparent competition following the reintroduction of their shared predator (Ng'weno et al., 2019). Indeed, zebras are limited by bottom-up effects of primary production and the main prey

of lions. They consequently help maintaining a healthy lion population. Hartebeests, in turn, are controlled by lions via a top-down limitation process (Ng'weno et al., 2019).

*Multi-prey and multi-predator interactions* - One way to integrate more complexity is to consider the different prey species in a study ecosystem and their interactions, as the dynamics between sympatric prey species may reduce predation risk for instance. Interspecific assemblage seems to be beneficial as it decreases the chance for an individual prey to be caught by a predator. For instance, Grant's gazelle (*Gazella granti*) and Thompson's gazelles (*Gazella thomsoni*) are often found together, and being in mixed groups reduces predation from cheetah because of an increased capacity to detect an approaching predator (many-eyes effect) and cheetah are also less likely to hunt larger groups (Fitzgibbon, 1990). Zebras also benefit from being in mixed herds with giraffes (*Giraffa camelopardalis*) as they are better at spotting predator (Schmitt, Stears and Schrader, 2016). Predator risk and impact are also prey specific as prey can have different escape tactics to a shared predator. For instance, a study showed that white-tailed deer (*Odocoileus virginianus*) flee when exposed to coyote predation risk whereas mule deer (*Odocoileus hemionus*) escape coyote predation by using active defence (Lingle, 2002). White-tailed deer relocate in a certain type of prairies when exposed to coyote predation risk, while mule deer avoid these prairies under predation risk (Lingle, 2002). Hence, these differences in escape tactics of sympatric prey are thought to affect differentially lower trophic levels such as plants communities, in this example by reducing or increasing herbivory pressure on the prairie, so predator can have a variety of indirect effects on prey and their resources (Wirsing, Cameron and Heitaus, 2010).

Considering more than one predator species is one final step to grasp the complexity of predator-prey interactions. It is a gap that has started to be filled only recently because studying large carnivores is challenging. First, large carnivores have smaller population size than prey, occur at lower densities, and roam over larger home ranges (Gittleman & Harvey, 1982; Ripple

et al., 2014). Inevitably, there are fewer opportunities of encounters for observations and/or experiments, captures with camera traps and fewer individuals to equip with GPS collars. North America and Africa are world regions that still have numerous predators co-occurring and interacting within the same ecosystem (Ripple et al., 2014). Direct negative interactions between carnivores such as interference competition, kleptoparasitism and even intraguild predation are well described in these areas (Hunter, Durant & Caro, 2007; Périquet et al., 2015). Indirect interactions between large carnivores through their respective impacts on shared prey are barely highlighted. Several mechanisms of indirect negative interaction through modification of prey anti-predator response can take place and are yet to be documented in several ecosystems. One underlying mechanism could be through the reduction of prey catchability, whereby prey make behavioural adjustments (e.g. increase in vigilance) to reduce the risk of predation by one predator, which decreases its vulnerability to another predator, a process known as behavioural resource depression (Kotler, 1992). There are also positive interactions between predators through scavenging opportunities, whereby a predator species provides carrion for other predators to feed on (Prugh & Sivy, 2020). Additionally, a prey anti-predator response to one predator can make it more vulnerable to another predator (Leblond et al., 2016). These interactions between predators can modulate the landscape of fear for a prey, via reduction or enhancement of risk, making impossible to predict prey response to risk by simply summing its response to one predator at a time (Northfield, 2017). For instance, negative interactions such as intraguild predation or interference competition between predator species can lead to a general reduction risk (Creswell & Quinn, 2013). Risk can also be enhanced when prey have large habitat domains and two sympatric carnivores avoid each other in that habitat by having narrow habitat domain, or when prey have habitat narrow domains that matches exactly predators one (Northfield, 2017). This is why there is often a difference between the predicted response of the prey and the observed ones; this is referred to as the multiple predator

effect (Sih & Wooster, 1998). Overall considering more than one predator species is important for a better prediction of prey response to risk.

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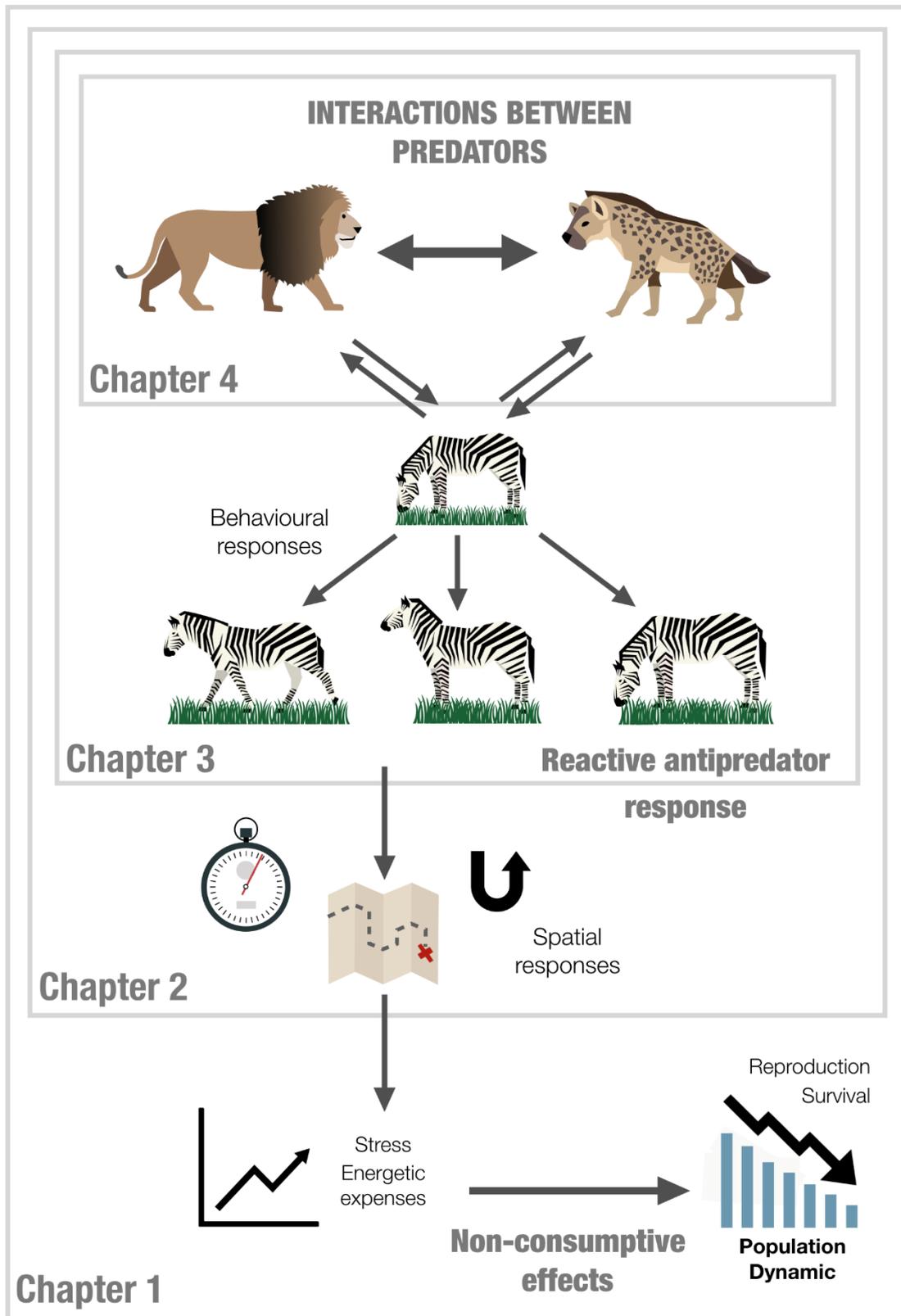
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## Thesis objectives and structure



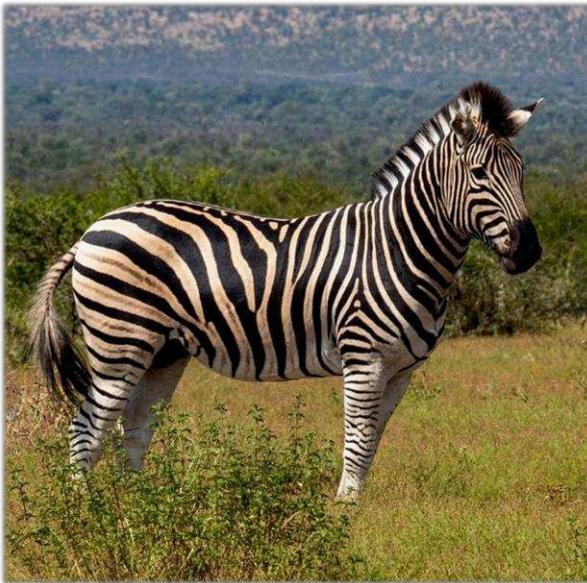
This PhD work has been thought as a contribution to pave the way towards a better understanding of interspecific interactions in a multi-species context.

The first axis of the PhD thesis focuses on predator-prey interactions through the behavioural, non-lethal effects of predators on their prey. This axis starts with a literature review (Chapter 1) of the current knowledge and gaps about the non-lethal effects of predators on prey in large terrestrial mammals. This review was closely linked with another review work that emphasizes the lack of studies taking into account several predators in studies of predation (Annexe 1). Because there is a scarcity of studies on the role of predator identity (and traits) on the behavioural anti-predator responses of prey, and because it is likely that indirect interactions between predators arise from differential behavioural responses of prey to different predators, these behavioural responses are the focus of the second and third chapters. Chapter 2 is based on the analysis of the spatial response of zebras to encounters with two predators, lions and spotted hyaenas *Crocuta crocuta*. Both are top predators of African savannas that do interact a lot already through interference competition, kleptoparasitism and intraguild predation (Périquet et al., 2015). Both predators differ in term of body size and hunting mode. Because spatial data from GPS do not provide information on the immediate response of a prey to different predators, I designed a playback experiment, which was carried out in French natural ecosystems (and is expected to be completed with the same experiment in an African savanna) to assess if the immediate reactive response of a prey, the roe deer *Capreolus capreolus*, differs when exposed to predation risk (playback sound) from different predators, the wolf and the Eurasian lynx (Chapter 3). Both predators also differ with their body mass and hunting mode.

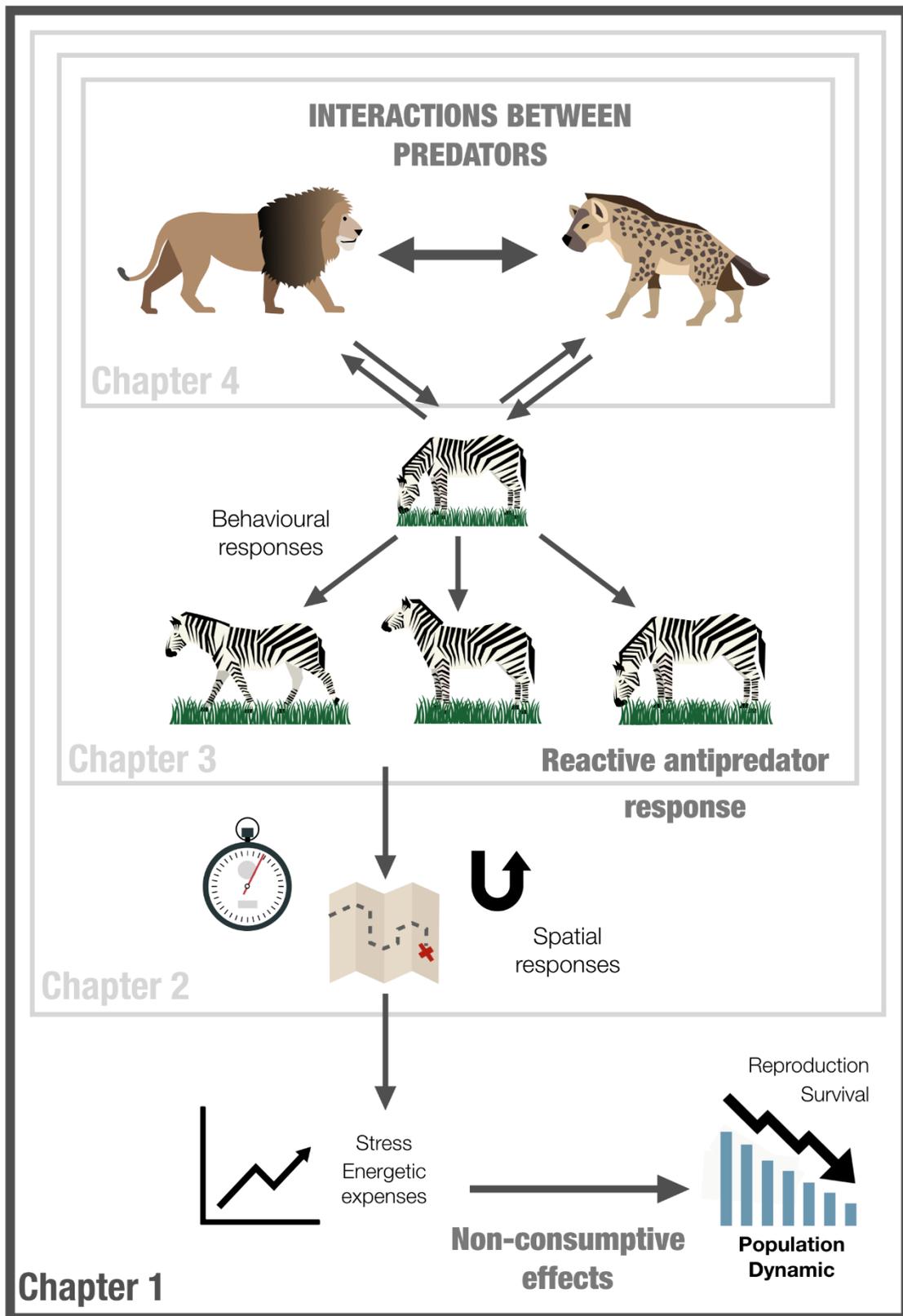
The second axis of the thesis aims to understand the interactions between sympatric predators (lions, spotted hyaenas and leopards), through the study of spatio-temporal co-occurrence patterns at different scales (Chapter 4). This chapter is based on data collected from camera traps in Hwange National Park, Zimbabwe, to understand which type of interactions

take place between the three predator species. We attempted to distinguish direct interactions - aggressive interactions, kleptoparasitism opportunities - (positive or negative associations of predators in a few hours) from indirect interactions that may operate through anti-predator behavioural responses of the prey (positive or negative associations of predators over longer periods).

# **Chapter 1: Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg**



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## Review

## Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg

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## ABSTRACT

Studies on invertebrates and small vertebrates demonstrated the underappreciated importance of the non-consumptive effects (NCE) of predators on their prey. Recently, there has been a growing interest for such effects in large vertebrates. Here, we review the empirical literature on large carnivore-ungulate systems to map our knowledge of predation NCE (from trait modification to the consequences on prey populations), and identify the gaps in our approaches that need to be fulfilled to reach a comprehensive understanding of these NCE. This review reveals (i) biases in the studies towards North American (and to a lesser extent African) ecosystems, protected areas, and investigation of NCE by wolf *Canis lupus* (and to a lesser extent African lion *Panthera leo*); (ii) a diversification of the systems studied in the past decade, which led to contrasted conclusions about the existence of NCE; (iii) that most existing work studied the effects caused by one predator only, even in ecosystems characterized by a rich carnivore community; and (iv) that the majority of the literature on NCE focused on the anti-predator behavioural responses of prey, whereas this is only the tip of the iceberg of NCE. Indeed, little is known on the other NCE components (energetic costs, stress, reproduction, survival, and population dynamics) and the links between the different components. Linking anti-predator behavioural responses to demography is thus the key challenge ahead of us to fully understand the NCE of predators on their prey in large mammals.

## 1. Introduction

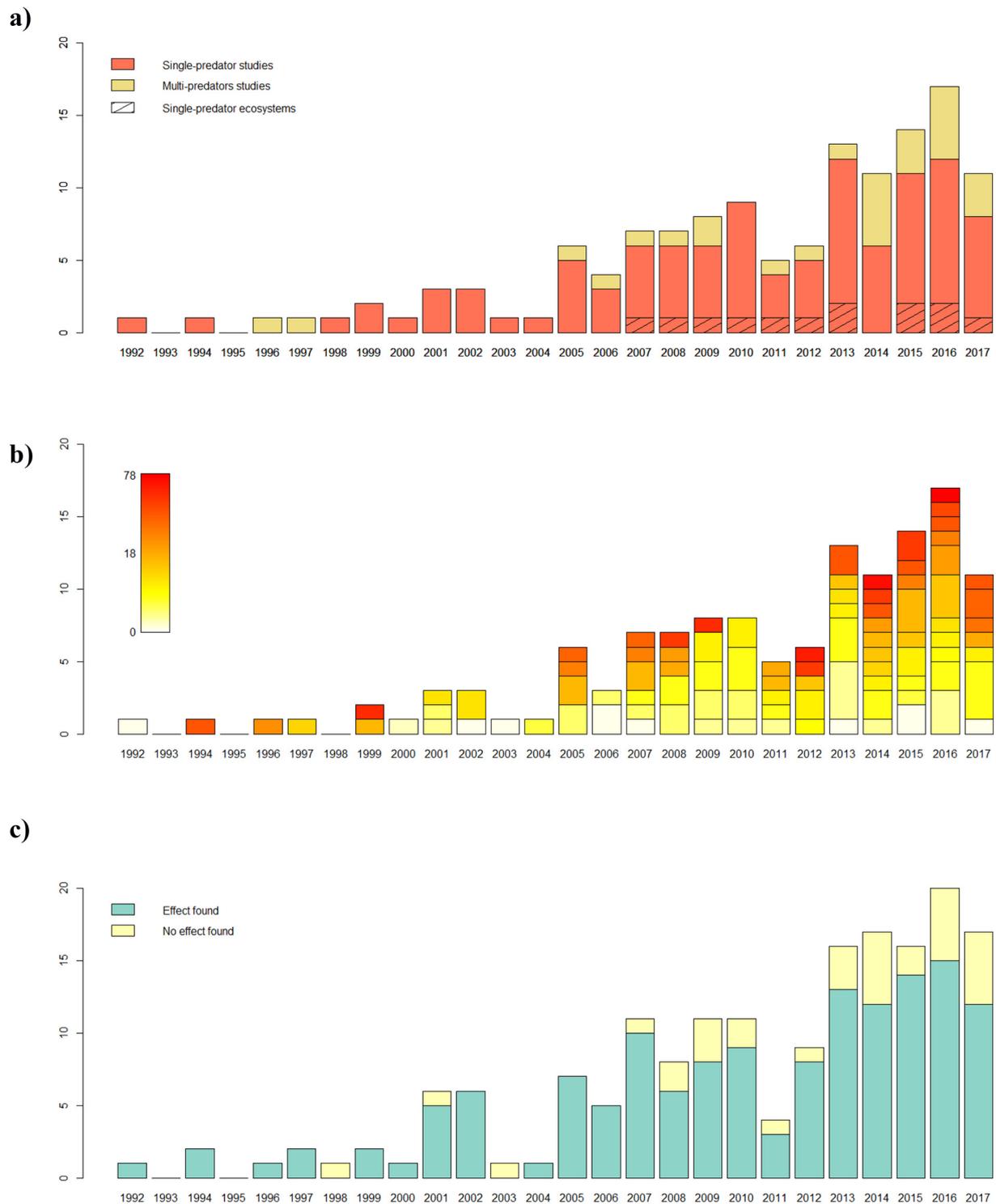
Predation is one of the most important interspecific interactions that shape communities (Paine, 1992). Predators have two kinds of effects on prey populations. First, by killing prey, predators affect the survival of prey individuals, and may ultimately affect prey population dynamics if the mortality is additive and not compensatory (i.e. predators kill individuals that are not weak or expected to die from another cause soon). This is referred to as the lethal effects or consumptive effects (this is the term we will use in this review - CE hereafter) of predators on their prey populations (Schmitz et al., 1997; Preisser et al., 2005; Creel and Christianson, 2008). Second, the mere presence of predators in the landscape represents a threat that leads prey to develop anti-

predator responses, which often entail modifications of morphological, physiological or behavioural traits (Lima and Dill, 1990; Boonstra et al., 1998). These anti-predator responses should incur costs (food-mediated or stress-mediated), which may lead to a decrease in prey performance (growth, reproduction, survival), and ultimately affect prey population dynamics. This is referred to as the non-lethal effects or risk effects or non-consumptive effects (this is the term we will use in this review - NCE hereafter) of predators on their prey populations (Schmitz et al., 1997; Preisser et al., 2005; Creel and Christianson, 2008).

Historically, CE of predation was the most studied aspect of predation. NCE were not considered (Roughgarden and Feldman, 1975; Lima, 1998) or thought to have a negligible impact on prey population dynamics (Sih et al., 1985). However, studies on the trade-off between

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**Fig. 1.** The number of publications per year according to a) whether the study was about one predator species or more (ecosystems with one predator only are represented with hatches), b) the human footprint index (index ranging from 0 to 100; from Sanderson et al., 2002), c) whether the study showed an effect of predation risk on the study NCE component. The total number of publications reviewed is 135. The length of the bars may differ as we could not extract the human footprint index for all study systems and as some studies tested several effects (all conclusions are reported in c).

foraging and predation risk avoidance in invertebrates and small vertebrates revealed that anti-predator behavioural responses lead to a reduction in activity (Peacor and Werner, 1997; Peacor, 2002) or a spatial/temporal avoidance of the predator associated with a shift to foraging areas/times where resource quality is lower (Abrams, 1984; McNamara and Houston, 1987; Lima and Dill, 1990; Peckarsky et al., 1993; Brown, 1999; Brown and Kotler, 2004; Fraser et al., 2004).

Besides, studies on stress in snowshoe hares (*Lepus americanus*) showed that exposure to high predation risk leads to chronic stress, which has an impact on variables such as the quantity of leucocytes and the body mass, and ultimately leads to smaller and lighter litter (Boonstra et al., 1998; Sheriff et al., 2009). These studies suggested that anti-predator behavioural responses carry costs for prey, and ultimately have consequences on population parameters such as survival and reproduction,

which may affect prey population dynamics similarly to the CE of predation (Peckarsky et al., 1993; Nelson et al., 2004; Preisser et al., 2005). For instance, in the Lake Erie (USA-Canada), the NCE of an invasive species (*Bythotrephes logimanus*) on its prey populations (*Daphnia mendotae* and *Daphnia retrocurva*) was ten times greater than CE (Pangle et al., 2007). This importance of NCE was made clear in a meta-analysis mostly based on invertebrate predator-prey systems, which revealed that predators can have a greater effect on prey demography through NCE than through CE, with NCE that can reach 85% of the total predator effect (Preisser et al., 2005).

In large mammals, observations and experiments are more difficult to carry out than in invertebrate and small vertebrates, and the study of the NCE of predation is more recent. However, in a context of rapidly changing large carnivore populations (Chapron et al., 2014; Ripple et al., 2014), there is a growing interest in understanding large carnivore effects on prey behaviour, physiology and abundance, as well as the cascading effects on ecosystem functioning (Estes et al., 2011). The widespread existence and diversity of anti-predator responses suggest that NCE are likely to occur in large mammals. However, there is a dearth of comprehensive studies on NCE that encompass the impact of a predator on its prey, from trait modification to the consequences on the prey population dynamics. Whether large mammalian carnivores affect their prey populations through NCE is thus debated (Creel and Christianson, 2008; White et al., 2011; Middleton et al., 2013).

In this review, we synthesize the existing knowledge on the NCE of predation in large carnivore-ungulate systems (studies on non-ungulate prey, such as kangaroos and capybaras, were excluded from this review). We review the empirical studies on large carnivore-ungulate systems to map our knowledge of the NCE of predation (from trait modification to the consequences on the prey populations), and identify the gaps in our approaches that need to be fulfilled to reach a comprehensive understanding of these NCE.

## 2. Methods

This literature review focused on large terrestrial mammalian carnivores (> 15 kg, Ripple et al., 2014) and their ungulate prey. We further included the coyote (*Canis latrans*, 7–18 kg, Way, 2007) since it is the top predator of ungulates in several ecosystems. We conducted a literature search using the Web of Science Core Collection database (WoS hereafter). We searched all publications for the following keywords: “antipredator strategy” (we also checked with the word “antipredator” throughout), “antipredator behaviour (or behavior)”, “antipredator responses”, “risk of predation”, “predation risk”, “risk effect”, “non-lethal effect”, “non-consumptive effect”, “ecology of fear”, and “landscape of fear”. All of these keywords were combined (with the Boolean connector AND) with the three following keywords: “large mammal”, “large herbivore” and “ungulate”. We then performed a search with the keyword “predation risk” combined with the 29 species of large terrestrial carnivores (Appendix A(a)). Based on titles and abstracts, we excluded publications that were not empirical studies of NCE in a large carnivore-ungulate system. 266 publications were selected for a full and comprehensive reading. Studies that were either reviews or modelling works ( $n = 55$ ) were excluded at this stage. We then excluded studies that quantified predation risk by using habitat data only ( $n = 53$ ), studies that focused on the CE of predators on juvenile prey ( $n = 9$ ), and studies that looked at the effect of prey on their predator ( $n = 14$ ). At the end of this selection process, we retained 135 publications (see Appendix B for the summary of the selection process of the publications kept for this review, and see Appendix C for the list of publications).

Only a few studies existed between 1992 and 2004, and since then the number of publications has kept increasing (Fig. 1). This increase is due to the growing interest for NCE in the study of predator-prey interactions in large mammals but also to the improved technology (e.g. GPS technology, camera trapping) that makes these studies possible to

conduct. During our literature search, we realized that most of the studies before the 1990s are not properly referenced electronically in WoS (missing keywords, abstract...). Thus, for this systematic review, we only considered studies from 1992 onwards. We are aware that a few pioneering studies took place before 1992, particularly with regard to vigilance behaviour, but we favoured maintaining a systematic approach based on the post-1992 WoS database over including pre-1992 studies that we were aware of, and therefore likely missing others. As our study shows, the study of NCE in large terrestrial mammals is relatively recent, and we believe including these few studies would not alter our conclusions.

In this review, we will use the term “NCE studies” for all studies dealing with at least one aspect of NCE, from anti-predator responses to the consequences on the prey population dynamics.

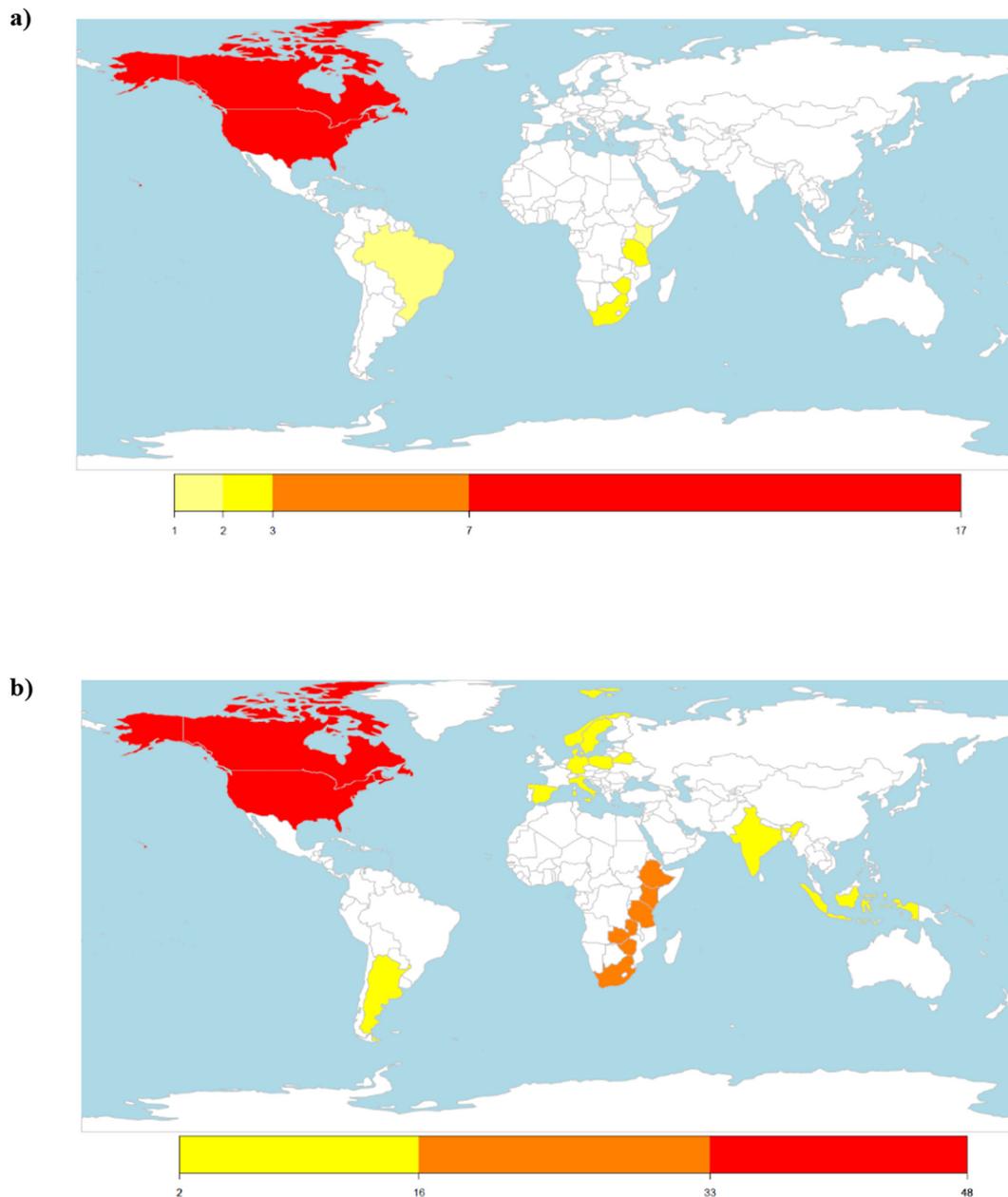
## 3. Where is our knowledge from?

### 3.1. Location of studies and species studied

Before 2007 ( $n = 33$  publications), almost all studies were carried out in North America (28 publications), with a few studies in Southern and Eastern Africa (4 publications) (Fig. 2a). This dominance of North American ecosystems led to a focus on the North American carnivores in the first NCE studies, with 20 studies on wolf (*Canis lupus*), 6 on coyote (*Canis latrans*), 3 on puma (*Puma concolor*), and 3 on grizzly bear (*Ursus arctos*; Appendix A(b)). Since 2008 ( $n = 102$  publications), we note a diversification of the locations of the studies (Fig. 2b). Most studies still come from North America (48 publications). However, African ecosystems have been the focus of a growing number of studies (33 publications), a trend also noted for Europe (15 publications) where large predators have recolonized large parts of the landscape (Chapron et al., 2014). This resulted in a diversification of the predator species studied (Appendix A(b)) even though the most studied carnivore is still the wolf (48 publications), followed by the African lion (*Panthera leo*; 28 publications) and the coyote (11 publications). Overall, the Yellowstone National Park ( $n = 19$ ; 14% of the publications) is the ecosystem the most studied for NCE in large carnivore-ungulate systems. The total number of prey species studied was high ( $n = 52$ ). Studies on elk (*Cervus elaphus*) were dominant during the period 2005–2010, and studies on plains zebra (*Equus quagga*) increasingly contributed to NCE studies in the last years, but overall the literature was very heterogeneous in terms of the prey species studied (Appendix A(c)).

### 3.2. Assessment of predation risk in the study systems

Our knowledge on NCE is clearly dominated by studies that considered one predator species only (79% of the publications;  $n = 107$ ; Fig. 1a). However, only 10% of the studies ( $n = 13$ ) were carried out in a system with one predator species (Fig. 1a). Predator communities are often composed of several predator species and predation risk faced by a prey can thus come from different predators. For the systems with two or more predator species ( $n = 122$ ), we calculated an index of predator community completeness as the number of large predators studied divided by the number of large predators present in the ecosystem (extracted from Ripple et al., 2014 – we could not extract this information for 17 studies). This index ranged from values very close to 0 (0 is excluded as it would mean that no predator species was studied and hence this is out of the scope of this review) to 1 (meaning that the study considered the whole predator community). For the 105 studies for which we could calculate the index of predator community completeness, the average index value was 0.41 (SD = 0.25) and 61% ( $n = 64$ ) of the studies had an index value lower than 0.5, highlighting that most studies focused on one or a couple of predator species in ecosystems with a richer predator community. However, 11% ( $n = 12$ ) of the studies had an index value of 1, i.e. studied the whole predator community. The studies focusing on several predator species are



**Fig. 2.** Number of publications per region a) between 1992 and 2007, b) between 2008 and 2018. The countries where the studies took place are coloured according to the number of publications per continent. The colour legends are not homogenized between the two periods not to reflect just the overall increase in the number of studies. Note that this review focuses on carnivore-ungulate systems, which explains why there is no publication in Australia.

becoming more common (Fig. 1a).

### 3.3. Level of anthropization of the study systems

Only 15% of terrestrial lands and inland water are protected areas (World Database on Protected Areas). However, 62% of the 135 studies reviewed here were in protected areas. Basing our understanding of NCE from studies conducted in protected areas only would lead to biased predictions about the strength of NCE in contexts where human and their activities may interact with predator-prey interactions (Smith et al., 2015; review in Kuijper et al., 2016). Here, we used the human footprint index (from Sanderson et al., 2002, dataset from SEDAC, WCS and CIESIN) to evaluate the level of anthropization of the systems studied. In our dataset, 96 studies (out of the 135 selected for this review) reported GPS coordinates and we were able to collect the geographic position of an additional 37 studies (we encourage future

studies to consistently report the GPS coordinates of the study systems). Studies were located in ecosystems with a human footprint index ranging from 0 (no human influence) to 78 (high level of anthropization), but a majority (73%;  $n = 99$ ) was characterized by a low human footprint index (between 0 and 20). It is interesting to note however that there is a recent diversification in the human footprint values characterizing NCE studies with several studies in ecosystems with rather high human footprint indices in the past five years (Fig. 1b).

### 3.4. Methodology used in NCE studies

A wide array of methodologies were used to assess predation risk on the one hand, and prey responses to predation risk on the other hand. The type of data used to assess predation risk can be classified into six categories: GPS or VHF telemetry, direct observation, camera trap, census (e.g. transect sampling), sign of predator presence (e.g. scat or

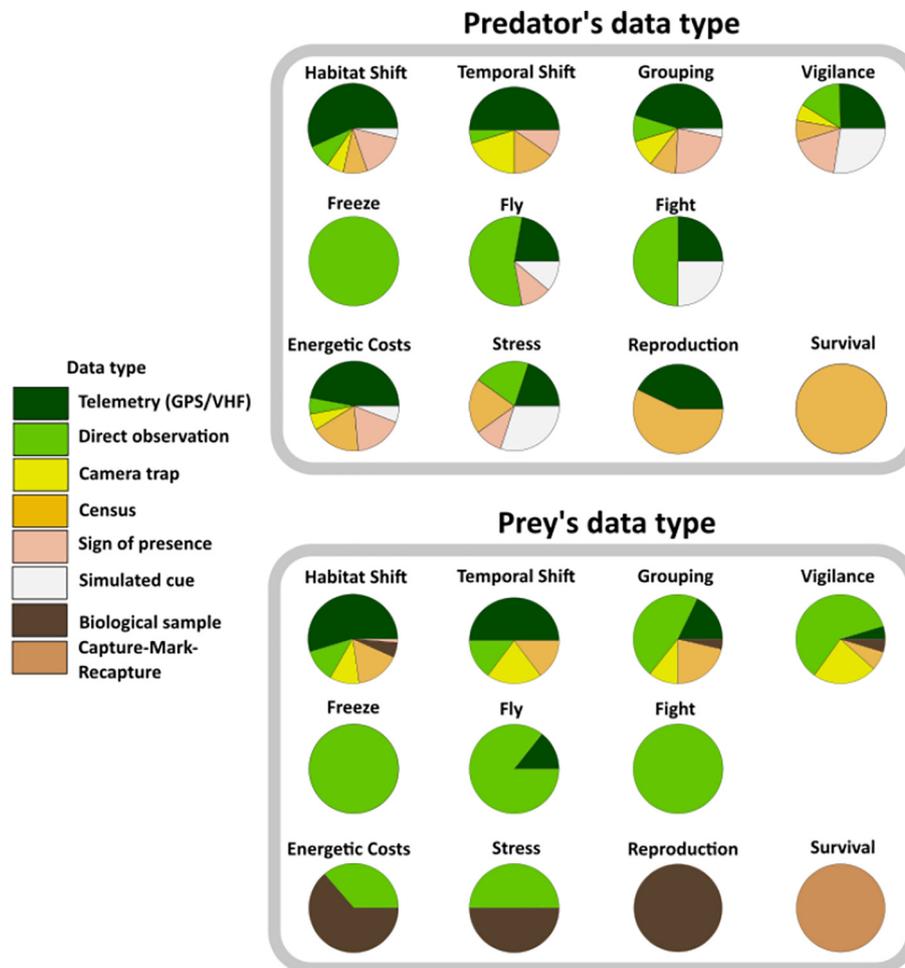


Fig. 3. Proportion of the different types of data used to assess predation risk and the prey response to predation risk depending on the NCE component studied ( $n = 135$  publications).

carcass of prey), and simulated (olfactory or auditory) cue (Fig. 3). The many ways of assessing predation risk from these different types of data are presented in details in Moll et al. (2017). The type of data used to assess prey responses to predation risk can be classified into seven categories: GPS or VHF telemetry, direct observation, camera trap, census (e.g. transect sampling), sign of prey presence, biological sample (e.g. blood or faecal sample), and capture-mark-recapture (CMR) monitoring (Fig. 3). There is a link between the type of response studied and the type of methodological approach used. For instance, telemetry data, camera trap data and census data were mainly used for studying the proactive responses of prey (when prey modify their behaviour in response to an a priori assessment of the risk level), such as shifts in habitat use or in temporal patterns of activity. Direct observations were mainly used for studying the reactive responses of prey (when prey modify their behaviour as a response of the detection of an immediate threat), such as freeze, fly, fight responses (Fig. 3). Biological samples, such as blood or faecal samples, were the main source of information for the study of energetic costs, stress and reproduction (Fig. 3). CMR was the only approach used to assess prey survival (Fig. 3).

#### 4. What have we learnt?

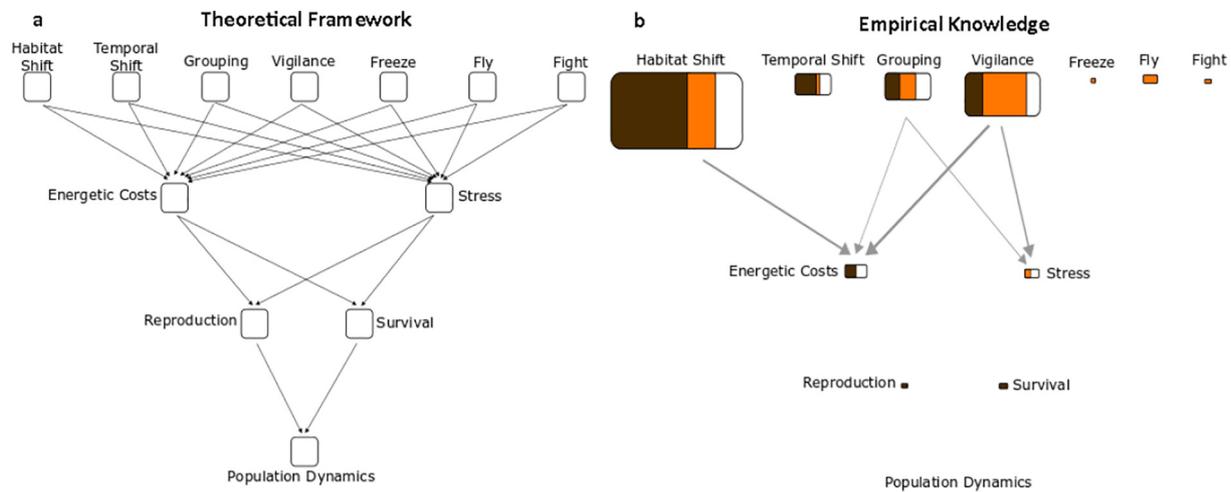
In this review, we decomposed the different components of NCE (Fig. 4; see also Creel, 2018), and quantified to which extent each component of NCE has been studied so far.

#### 4.1. Behavioural responses of prey to predation risk

Fig. 4 reveals that the behavioural responses of prey to predation risk are, and by far, the most studied NCE components (85% of the publications reviewed,  $n = 115$ ). Both proactive and reactive anti-predator responses were relatively well represented (82 and 63 publications respectively; with some publications investigating both), and we identified seven behavioural responses to predation risk: habitat shift, temporal shift, grouping, vigilance, freeze, fly, and fight (Fig. 4).

The most studied behavioural response was habitat shift (either a shift to a different geographical area or a shift to a different vegetation type) (Fig. 4, 67 publications), whereby prey relocate from a habitat that they perceive risky to a safer habitat when exposed to an increase in predation risk. The majority of the publications on habitat shift took into account past variations in the presence of the predator so habitat shift was mainly studied as a proactive response (48 publications; e.g. Atwood et al., 2009; Valeix et al., 2009b). Habitat shift can also be an efficient reactive response (16 publications; e.g. Valeix et al., 2009b; Courbin et al., 2016). Courbin et al. (2016), for instance, demonstrated that a few hours after an encounter with a lion, zebras move several kilometres away from the location of the encounter.

The second most studied anti-predator response is the increase of prey vigilance level (Fig. 4, 38 publications; e.g. FitzGibbon, 1994; Laundré et al., 2001; Creel et al., 2014). Indeed, vigilant prey have a better chance to detect an approaching predator before it launches an attack, which will often lead the predator to abort the hunt. This response has been mainly investigated as a reactive mechanism (25



**Fig. 4.** a) Conceptual diagram of NCE components and the links between the different components. b) Representation of our empirical knowledge. Rectangle size and link width are proportional to the number of studies that focused on the different NCE components and on the links between the different components. Brown colour represent the proportion of studies that found a proactive effect of predation risk, orange colour represents the proportion of studies that found a reactive effect of predation risk, and white colour represents the proportion of studies that investigated the component and found no effect. Anti-predator behavioural responses can be induced by stress but in this figure, we simplified and focused on stress as a consequence of anti-predator responses. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

publications), even though proactive vigilance in response to a priori knowledge of long-term variations in risk exists too (11 publications; Fig. 4).

Another well-studied aspect of anti-predator behaviour is how individuals modify their social dynamics when faced with increased predation risk (Fig. 4, 23 publications; e.g. Lima, 1995; Roberts, 1996; Creel and Winnie, 2005; Creel et al., 2014). Most studies ( $n = 18$ ) found an increase of the group size due to predation risk. Indeed, larger groups are often associated with a reduced predation risk because of an improved detection of approaching predators thanks to collective detection (the “many eyes effect” (Powell, 1974)), and because of a “dilution effect” whereby the probability of an individual to be targeted by the predator decreases as group size increases (Bertram, 1978). However, a few studies found a negative correlation between predation risk and group size. This could arise because smaller groups are more difficult to detect for predators (Creel and Winnie, 2005), or because of interactions between vigilance and other anti-predator behaviours (Patin et al., 2019). The numbers of publications that looked at changes in group size as a proactive and reactive response are balanced.

Temporal shift in activity is the fourth anti-predator response investigated (Fig. 4, 18 publications; e.g. Creel et al., 2008; Valeix et al., 2009a; Courbin et al., 2018). Risky places cannot always be avoided and their use during safer periods (when the predator is the least active) is an anti-predator strategy that has been commonly reported. For instance, Valeix et al. (2009a) demonstrated that, when lions are in the vicinity of a waterhole, buffaloes avoid drinking at that waterhole at times when lions are known to be active and hunting (a case of short-term proactive response). The majority of the publications (13 publications) looked at prey temporal shift as a proactive response (Fig. 4).

The three other anti-predator responses are exclusively reactive responses: freezing, flying and fighting (Fig. 4). They are the anti-predator responses that have been the least studied (Fig. 4). However, the study of prey fighting when exposed to a predator is a growing part of the literature (Mukherjee and Heithaus, 2013), especially because the dangerousness of prey influences prey preference by predators (Tallian et al., 2017).

#### 4.2. A focus on the studies that went beyond anti-predator behavioural responses

This literature review reveals that very little is known on (i) the

components of NCE other than the anti-predator behavioural responses of prey, and (ii) the links between the different components of NCE (Fig. 4). In order to grasp the full picture of NCE, it is interesting to look at the few publications that studied components of NCE other than anti-predator behavioural responses (17% of the publications reviewed; 23 publications in total including 15 publications that found an effect, all are listed in Table 1). Seventeen studies looked at the costs of predation risk on prey individuals, through the study of stress (anti-predator behavioural responses can be induced by stress but in Fig. 4 we simplified and focused on stress as a consequence of anti-predator responses as in Creel, 2018) and energetic costs (6 and 11 publications respectively). No publication studied both effects at the same time.

Three studies on stress used experiments simulating predator's presence and concluded that prey stress level strongly increased as a response to an immediate predation risk (reactive response; Chabot et al., 1996; Christensen and Rundgren, 2008; Cooke et al., 2013). However, the three other studies measured fGCM (faecal Gluco-Corticoid Metabolite) in natural environments to investigate how prey stress levels vary with longer-term variations in predation risk (proactive response), and concluded that prey do not have higher baseline stress hormone level in risky areas (Creel et al., 2009; Périquet et al., 2017; Zbyryt et al., 2018).

Eleven publications attempted to assess the energetic costs of predation risk through prey foraging behaviour (Altendorf et al., 2001; White and Feller, 2001; Kluever et al., 2009; Creel et al., 2014), foraging patch quality (Harvey and Fortin, 2013), measures of prey body condition (body fat: Middleton et al., 2013; chest size: Bourbeau-Lemieux et al., 2011), or faecal samples to evaluate diet quality (Hernández and Laundré, 2005; Christianson and Creel, 2008; Creel and Christianson, 2009; Christianson and Creel, 2010; Barnier et al., 2014). Most studies demonstrated correlations between the level of predation risk and the proxies used to assess energetic costs (Table 1). Of these 11 publications, four were associated with the study of habitat shift (Altendorf et al., 2001; White and Feller, 2001; Hernández and Laundré, 2005; Middleton et al., 2013) and two found an effect of habitat shift when predation risk was higher: reduction in diet quality (Hernández and Laundré, 2005) and reduction in browsing activity (White and Feller, 2001). Five publications on the energetic costs of predation risk were associated with the study of vigilance (Altendorf et al., 2001; White and Feller, 2001; Kluever et al., 2009; Middleton et al., 2013; Creel et al., 2014). Four of these studies found that an

**Table 1**  
Publications that studied NCE components other than anti-predator behavioural responses.

Predator species	Prey species	Outcome	Reference
<b>Stress</b>			
Wolf	Elk	Cougar and wolf faeces increased significantly the heart rate and oxygen consumption.	Chabot, D., Gagnon, P., Dixon, E. A. (1996). Effect of predator odors on heart rate and metabolic rate of wapiti ( <i>Cervus elaphus canadensis</i> ). <i>Journal of Chemical Ecology</i> , 22(4), 839–868.
Puma			
Coyote			
Wolf	Horse	There is an increased of heart rate when exposed to wolf urine only if prey simultaneously exposed to an additional stimulus such as a plastic bag.	Christensen, J. W., Rundgren, M. (2008). Predator odour per se does not frighten domestic horses. <i>Applied Animal Behaviour Science</i> , 112(1–2), 136–145.
Lion			
Wolf	Elk	There is no correlation between faecal glucocorticoid concentrations and predator-prey ratios.	Creel, S., Winnie, J. A., Christianson, D. (2009). Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. <i>Proceedings of the National Academy of Sciences</i> , 106(30), 12,388–93.
Wolf	Cattle	The exposure to wolf urine and sounds increased cow temperature and plasma cortisol concentration.	Cooke, R. F., Bohnert, D. W., Reis, M. M., Cappelozza, B. I. (2013). Wolf presence in the ranch of origin: Impacts on temperament and physiological responses of beef cattle following a simulated wolf encounter. <i>Journal of Animal Science</i> , 91(12), 5905–5911.
Lion	Zebra	Zebras did not have higher stress hormone levels in area with lions.	Périquet, S., Richardson, P., Cameron, E. Z., Ganswindt, A., Belton, L., Loubser, E., Dalerum, F. (2017). Effects of lions on behaviour and endocrine stress in plains zebras. <i>Ethology</i> , 123(9), 667–674.
Wolf	Roe deer	Faecal glucocorticoid metabolites levels were lower and less variable in areas with carnivore than in areas without.	Zbyryt, A., Bubnicki, J. W., Kuijper, D. P. J., Dehnhard, M., Churski, M., Schmidt, K. (2018). Do wild ungulates experience higher stress with humans than with large carnivores? <i>Behavioural Ecology</i> , 29(1), 19–30.
Eurasian Lynx	Red deer		
<b>Energetic costs</b>			
Mountain lion	Mule deer	Mule deer had higher GUDs in riskier habitats.	Altendorf, K. B., Laundré, J. W., Pez, C. A. L., Lez, G., Brown, J. S. (2001). Assessing effects of predation risk on foraging behaviour of mule deer. <i>Journal of Mammalogy</i> , 82(2), 430–439.
Wolf	Elk	Elk decreased their browsing on aspen in high predation risk areas.	White, C. A., Feller, M. C. (2001). Predation risk and elk-aspen foraging patterns. <i>Sustaining Aspen in Western Landscapes: Symposium Proceedings</i> ,
Wolf	Elk	The faecal concentration of nitrogen for elk was significantly lower in areas where wolves were present than in areas without wolves.	Hernández, L., Laundré, J. W. (2005). Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk <i>Cervus elaphus</i> and <i>Bison bison bison</i> . <i>Wildlife Biology</i> , 11(3), 215–220.
Wolf	Bison	Both sexes decreased their grazing when wolf were present.	Christianson, D., Creel, S. (2008). Risk effects in elk: sex-specific responses in grazing and browsing due to predation risk from wolves. <i>Behavioural Ecology</i> , 19(6), 1258–1266.
Wolf	Elk	Willow consumption was more strongly affected by snow conditions than by the presence of wolves.	Creel, S., Christianson, D. (2009). Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. <i>Ecology</i> , 90(9), 2454–2466.
Wolf	Cattle	Wolf stimuli significantly decreased cattle foraging rate but had no effect on giving up densities and time spent on high quality forage locations. Mountain lion had no significant effect on any cattle variable.	Cluever, B. M., Howerly, L. D., Breck, S. W., Bergman, D. L. (2009). Predator and heterospecific stimuli alter behaviour in cattle. <i>Behavioural Processes</i> , 81(1), 85–91.
Mountain Lion			
Wolf	Elk	Urine analysis of nitrogen:creatinine ratios showed a reduction of energy intakes and deficiencies of nitrogen when wolves were present.	Christianson, D., Creel, S. (2010). A nutritionally mediated risk effect of wolves on elk. <i>Ecology</i> , 91(4), 1184–1191.
Wolf	Bison	Bison foraged less in areas of high predation risk.	Harvey, L., Fortin, D. (2013). Spatial heterogeneity in the strength of plant-herbivore interactions under predation risk: the tale of bison foraging in wolf country. <i>PLoS ONE</i> , 8(9), e73324.
Wolf	Elk	Elk body fat did not correlate with wolf predation risk.	Middleton, A. D., Kauffman, M. J., McWhirter, D. E., Jimenez, M. D., Cook, R. C., Cook, J. G. et al. (2013). Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. <i>Ecology Letters</i> , 16(8), 1023–1030.
Lion	Zebra	Zebra that foraged in areas with lions around had a lower diet quality (measure of faecal crude protein).	Barnier, F., Valeix, M., Duncan, P., Chamailé-Jammes, S., Barre, P., Loveridge, A. J. et al. (2014). Diet quality in a wild grazer declines under the threat of an ambush predator. <i>Proceedings of the Royal Society B</i> , 281(1785), 20,140,446–20,140,446.
Lion	Zebra	Increased vigilance caused a large reduction in foraging for some species (but not all). There was no clear relationship between predation rates and the foraging costs of anti-predator responses.	Creel, S., Schuette, P., Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. <i>Behavioural Ecology</i> , 25(4), 773–784.
Spotted hyaena	Wilbebeest		
	Gazelle		
	Impala		
	Giraffe		
<b>Reproduction</b>			
Wolf	Elk	Lactation rates (indicator of calf survival) decreased as the grizzly bear:elk ratio increased.	Proffitt, K. M., Cunningham, J. A., Hamlin, K. L., Garrott, R. A. (2014). Bottom-up and top-down influences on pregnancy rates and recruitment of northern Yellowstone elk. <i>The Journal of Wildlife Management</i> , 78(8), 1383–1393.
Grizzly bear			
Wolf	Elk	Faecal progesterone concentration were negatively correlated with higher predation risk, as well a calf recruitment of the following year that was correlated with faecal progesterone concentrations.	Creel, S., Christianson, D., Liley, S., Winnie, J. A. (2007). Predation risk affects reproductive physiology and demography of elk. <i>Science</i> , 315(5814), 960.
Coyote	White-tailed deer	Lactation (indicator of reproductive success) and ovulation (indicator of fecundity) increased with the diminution of predation risk from coyote (declining population).	Cherry, M. J., Morgan, K. E., Rutledge, B. T., Conner, L. M., Warren, R. J. (2016). Can coyote predation risk induce reproduction suppression in white-tailed deer? <i>Ecosphere</i> , 7(10), e01481.
Wolf			

(continued on next page)

Table 1 (continued)

Predator species	Prey species	Outcome	Reference
	Woodland caribou Moose Dall sheep	The pregnancy rate of woodland caribou was not correlated with the diminution of wolf abundances.	Hayes, R.D., Farnell, R., Ward, R.M.P., Carey, J., Dehn, M., Kuzyk, G.W., Baer, A.M., Gardner, C.L., Donoghue, M.O., 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. <i>Wildlife Monographs</i> 67, 1–35.
Survival Puma	Bighorn sheep	Lamb survival decreased with years of high predation rates through a decrease of individual growth rate (reduced chest size in years of high predation).	Bourbeau-Lemieux, A., Festa-Bianchet, M., Gaillard, J.-M., Pelletier, F. (2011). Predator-driven component Allee effects in a wild ungulate. <i>Ecology Letters</i> , 14(4), 358–363.
Puma Wolf Black bear Coyote	Elk	Mountain lion predation risk has a negative effect on calf survival (this includes both CE and NCE)	Eacker, D. R., Hebblewhite, M., Proffitt, K. M., Jimenez, B. S., Mitchell, M. S., Robinson, H. S. (2016). Annual elk calf survival in a multiple carnivore system. <i>The Journal of Wildlife Management</i> , 80(8), 1345–1359.

increase in prey vigilance level was linked to a decrease in the prey foraging rate (or higher giving-up densities) under high predation risk (Altendorf et al., 2001; White and Feller, 2001; Kluever et al., 2009; Creel et al., 2014). However, one study found no change in prey body condition associated to increased vigilance levels (Middleton et al., 2013). Finally, one study focused on the link between group size changes and energetic costs, but found no effect (Creel et al., 2014).

Only six publications looked at the effects of predation risk on prey individual performance: reproduction (4 publications that showed an effect; Table 1) or survival (2 publications that showed an effect; Table 1). The effect of predation risk on prey reproduction was assessed through the pregnancy status of individuals harvested by people (Proffitt et al., 2014; Cherry et al., 2016), blood concentration of progesterone (Hayes et al., 2003) or concentration of progesterone from faecal samples (Creel et al., 2007). Two publications studied the effect of predation risk on survival (Bourbeau-Lemieux et al., 2011; Eacker et al., 2016). For the first time in large mammals, Bourbeau-Lemieux et al. (2011) showed that during years of high puma predation, bighorn sheep *Ovis canadensis* lambs also suffered mortality through reduced growth (lambs would have been larger without predation and survival is a function of lamb body size), contributing a third of the total impact of predation on lamb survival (NCE: 8% decrease of survival; CE: 20%). Eacker et al. (2016) looked at the effect of predation risk by multiple carnivores on wapiti (*Cervus canadensis*) calf survival and showed that different predator species have contrasted effects and that season matters. However, they could not disentangle the role of CE and NCE. No study investigated the consequences of NCE for prey population dynamics. Overall, the links between the different components of NCE have been seldom studied (Fig. 4).

## 5. Discussion

### 5.1. The importance of diversifying the systems studied

The geographical repartition of NCE studies on large mammals is tightly linked to the presence of emblematic species and good research opportunities (e.g. reintroductions, protected areas), as suggested by the dominance of studies from the Yellowstone ecosystem (wolves) and African protected areas (lions). Yellowstone in particular has been the most studied ecosystem as it offered a unique opportunity to study NCE due to the reintroduction of wolves in certain parts of the park in 1995–1996. This allowed for spatial and temporal comparisons between risk-free and risky periods/areas (e.g. Ripple and Larsen, 2000; Laundré et al., 2001; Fortin et al., 2005; Mao et al., 2005; Lung and Childress, 2007; Creel and Christianson, 2009; Creel et al., 2009; Barnowe-Meyer et al., 2010; Middleton et al., 2013). It is noteworthy that the population-level effects of NCE are still debated in this well-studied ecosystem (Creel and Christianson, 2008; White et al., 2011; Middleton et al., 2013). These studies have been key in our awareness of the role of the NCE of predation in large mammals and in our

understanding of these NCE. However, conducting studies in a diversity of systems is critical to assess whether we can generalize the findings from studies on predation risk by wolves in the Yellowstone, and whether NCE are generally an important aspect of predator-prey relationships. As shown in this review, this is slowly being achieved (Figs. 1, 2, Appendix A), and this correlates with an increase in the proportion of studies that reported no effect of predation risk on prey (Fig. 1c). This suggests that, as the study systems diversify, there are more contexts where NCE are not operating. The challenge is now to identify the factors that can modulate the strength of NCE.

One important future direction relies on comparative approaches across different predator and prey characteristics to identify which species characteristics are important for the strength of NCE in large mammals (Creel, 2011; Creel et al., 2019; Owen-Smith, 2019). For example, in invertebrates, general rules about the role of the predator hunting mode have emerged, with sit-and-wait and sit-and-pursue hunters causing stronger NCE than active hunters (Preisser et al., 2007; Schmitz, 2008). Wolves are cursorial predators (i.e. they chase down their prey over long distances). It will thus be important to accumulate evidence on the NCE of other cursorial predators (e.g. spotted hyaenas (*Crocuta crocuta*)) but also of ambush predators (i.e. predators that rely on concealment to hunt by surprise prey moving within a chasing distance; this is the case of most Felids) to assess whether the predator hunting mode influences the strength of NCE in large mammals too. Recent works have also suggested that prey characteristics may play the most important role for the strength of NCE in large mammals (Creel et al., 2019; Owen-Smith, 2019). Diversifying the systems studied will also allow covering a range of densities of predator and prey populations. This is important as prey density-dependent mechanisms will affect the trade-off between food and safety, and predator and prey population densities are key proxies for the frequency of predator-prey encounters, a key parameter to understand the magnitude of NCE (Middleton et al., 2013).

Other important factors that can modulate the strength of NCE are the characteristics of the environment where predator-prey interactions occur (Brown and Kotler, 2004; Laundré et al., 2014). In a context of increasing overlap between human-dominated and carnivores' habitats (Chapron et al., 2014; Ripple et al., 2014), it is of particular importance to understand how people and their activities may interact with predator-prey interactions (see Kuijper et al., 2016 for a review of the mechanisms involved). For example, carnivores may increase their kill rate when they approach human settlements because of the fear of people (Smith et al., 2015), or prey may use human infrastructures as a shield against carnivores (Berger, 2007). Hence, human presence may influence the perceived predation risk by prey and hence affect the level of their anti-predator responses.

### 5.2. The importance of considering the complexity of the systems studied

By considering one prey and one predator only in often multi-prey

multi-predator systems, interspecific interactions other than the predator-prey interaction studied are omitted. However, these interactions can modulate the NCE of predation on prey (Wootton, 2002; see also Montgomery et al., 2019). For example, in the Madison Valley (Montana, USA), it has been shown that elk shift to habitats that have more complex structure to reduce predation risk from wolves, but this significantly increases the predation risk from puma (Atwood et al., 2009). In that case, considering wolves only would minimize the overall NCE of predation suffered by elk. In natural ecosystems, it is difficult to study all large carnivore species but the development of GPS-technology, animal-borne video, and camera trapping in ecological studies provides increased possibilities to address this complexity (Prugh et al., 2019). This review has revealed a growing number of studies focusing on multiple predators when studying NCE. This effort needs to continue to understand how species interactions can modulate NCE. It is an important corner stone in future research of NCE to grasp the full picture of NCE in natural ecosystems. The role of interactions between prey or of dilution effects in multi-prey systems, even though not addressed in this review, is important to consider when assessing the NCE of predation (Montgomery et al., 2019).

### 5.3. Anti-predator behavioural responses of prey: the tip of the iceberg

Fig. 4 clearly shows that behavioural responses are the most studied NCE components in large mammals, and that little is known on the other NCE components (energetic costs, stress, reproduction, survival, and population dynamics) and the links between the different components. We acknowledge that there could be studies on NCE using a different terminology than the key words selected for our literature search, and that are consequently missing from this review.

It is easier to measure stress, energetic costs, reproduction and survival and to design experiments to disentangle the role of CE and NCE of predation in invertebrates or small vertebrates, which are short-lived species often easy to manipulate. In such systems, we have learnt a lot from experiments where predators were caged (e.g. Peacor, 2002) or the presence of the predator was simulated over critical periods for the reproduction and survival of prey (e.g. Zanette et al., 2011). In large mammalian systems, where species are long-lived and difficult to manipulate, this is more challenging. It is possible to carry out experiments where the presence of the predator is simulated (visual, olfactory or auditory cues). So far, this has been done over short periods to assess prey behavioural responses or stress responses. However, this will need to be done over much longer periods (if this is ethically possible) to assess the impact of predation risk on prey population dynamics. In any case, in natural ecosystems, it will be impossible to exclude the CE of predators that roam naturally in the landscape. The best way forward therefore lies in approaches similar to the one used by Bourbeau-Lemieux et al. (2011) who studied the impact of contrasting periods of puma predation on bighorn sheep body condition and survival over 27 years to disentangle the impacts of CE and NCE. The unique insights provided by this study rely on two important aspects: the long-term monitoring of the prey population and the handling of prey individual to measure individual performance proxies. Long-term studies are indeed crucial to assess the effect of predation on a prey population dynamics and the scarcity of such studies explains the knowledge gap on the effect of predation risk on prey reproduction and survival. Additionally, the capture of individual prey is needed to take biological

## Appendices

### Appendix A.

a) Number of publications per large carnivore species (body weight > 15 kg as defined in Ripple et al., 2014), and according to the taxonomic group. The graph shows that NCE studies focused on a small proportion of large predator species. b) Number of publications per year according to the predator species studied (the “other species” category refers to the carnivore species listed in (a) and not detailed in (b)). c) Number of publications per year according to the prey species studied. The length of the bars in (b) and (c) is sometimes different from that of the corresponding bars in

samples and body measurements. People around the world harvest wild ungulate populations, and this could be considered as a useful source of information to evaluate the NCE of predators on prey population parameters. The studies that estimated energetic costs and stress due to predation risk made the implicit assumption that it would affect survival and reproduction of prey and that it would ultimately affect prey population dynamics. Even though this has been demonstrated in invertebrates (Peckarsky et al., 1993; Peacor and Werner, 2004), nearly nothing is known for large terrestrial mammals and this is a major challenge for future studies if we want to comprehensively understand NCE, from the behavioural responses of prey individuals to the modification of prey population dynamics. Behavioural anti-predator responses are just the tip of the NCE's iceberg.

## 6. Implications for conservation

Populations of large carnivores are characterized by major changes in their abundance and distribution worldwide with declines in many ecosystems (Ripple et al., 2014), recolonization of human-dominated habitats in Europe (Chapron et al., 2014), and reintroduction in many reserves (Hayward and Somers, 2009). These changes mean the loss or appearance of CE but also NCE of predators on ungulate populations, which will have cascading effects down the food chain and for the whole ecosystem functioning (Estes et al., 2011). While CE are well understood and can be easily quantified, our review reveals that, in spite of the widespread evidence of anti-predator behavioural responses in ungulates, current knowledge prevents us for predicting the population-level consequences of NCE in large mammals (Fig. 4). Studies on invertebrates and small vertebrates demonstrated the underappreciated importance of NCE. For example, Zanette et al. (2011) demonstrated that predation risk (simulated with predators calls) reduced by 40% the number of offspring produced per year by songbirds. In large mammals, evidence of population-level consequences of NCE is extremely scarce. Bourbeau-Lemieux et al. (2011) were the first to demonstrate that NCE can account for a third of the total impact of predation on prey population survival. If NCE can have such an important impact, they need to be taken into account and anticipated in the management of large mammal populations (e.g. for the reintroduction of large carnivores; see also Allen et al., 2019 for animal welfare considerations). However, in natural environments, many factors may affect the strength of NCE (predator and prey attributes, landscape characteristics, and the complexity of large mammal communities) and NCE may be negligible under some circumstances (Fig. 1c; e.g. Middleton et al., 2013). Linking anti-predator behavioural responses to demography in different contexts is thus the key challenge ahead of us to fully understand the NCE of predators on their prey in large mammals. This information is crucial for a sound management and conservation of large mammals worldwide.

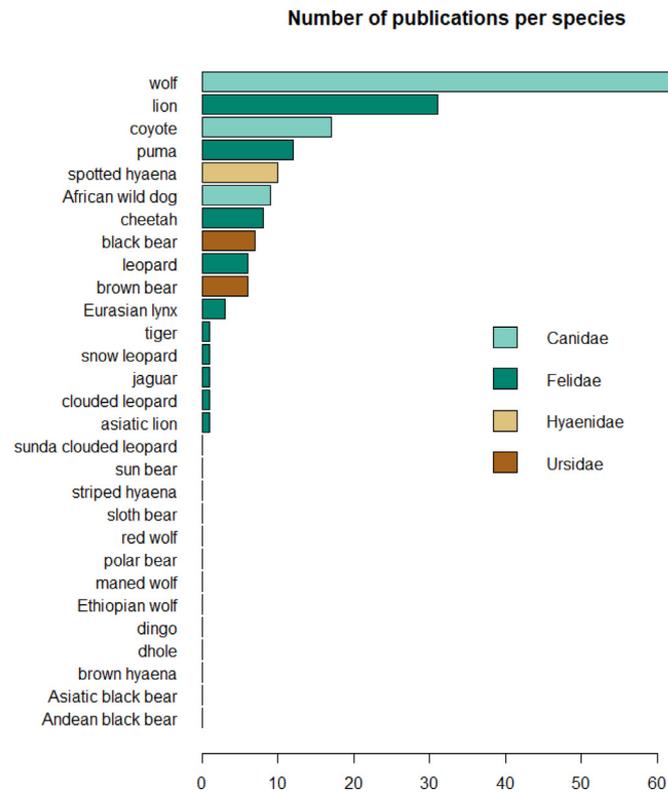
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Fig. 1 because of the multi-predator or multi-prey species studies.

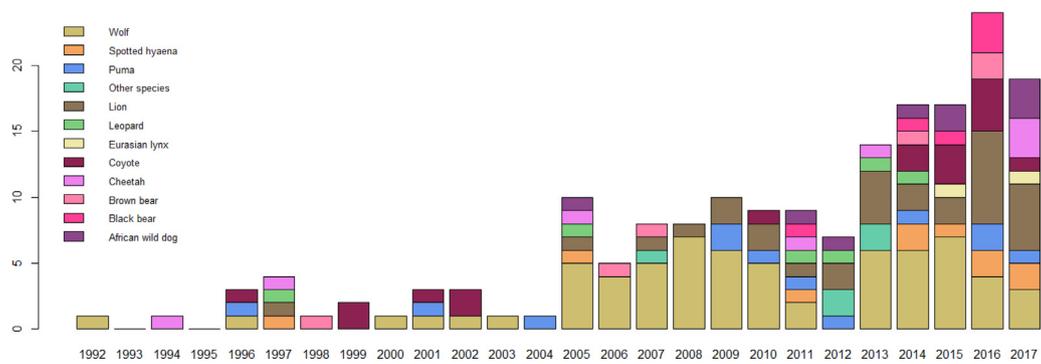
a)

a)



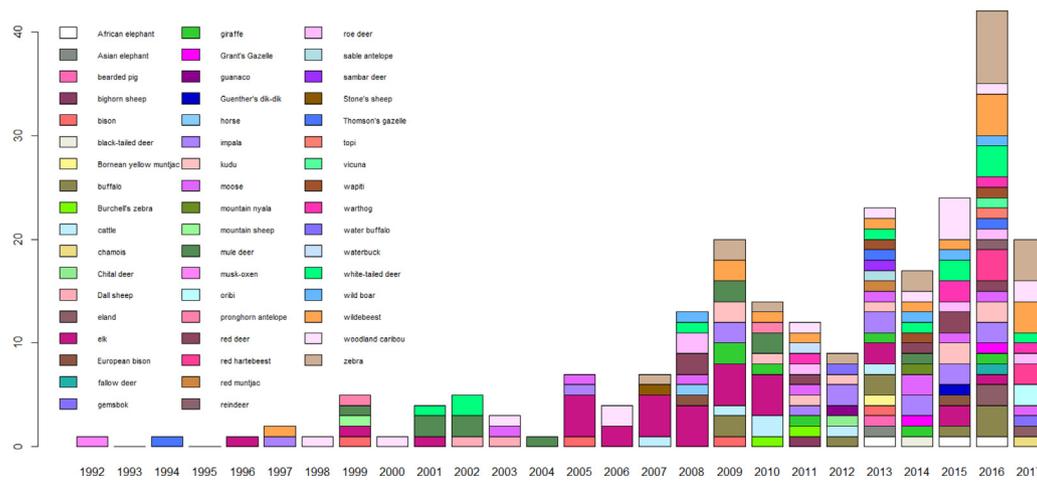
b)

b)

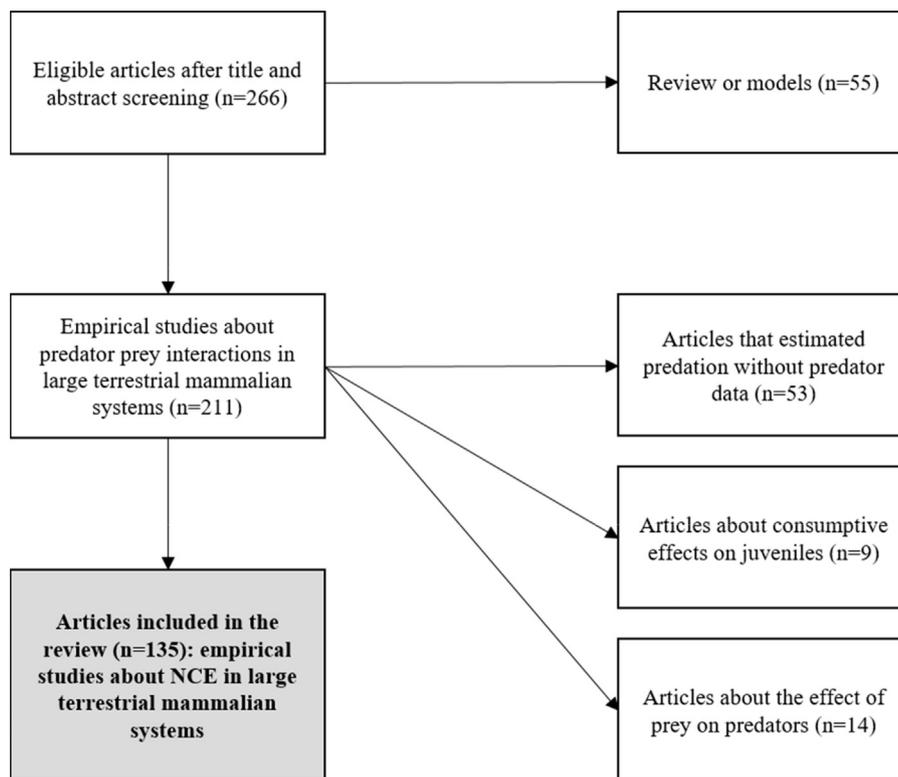


c)

c)



Appendix B. Schema of the literature reviewing process. The research process was done with Web of Science Core Collection database, and was stopped the 12th of April 2018



Appendix C. Data sources

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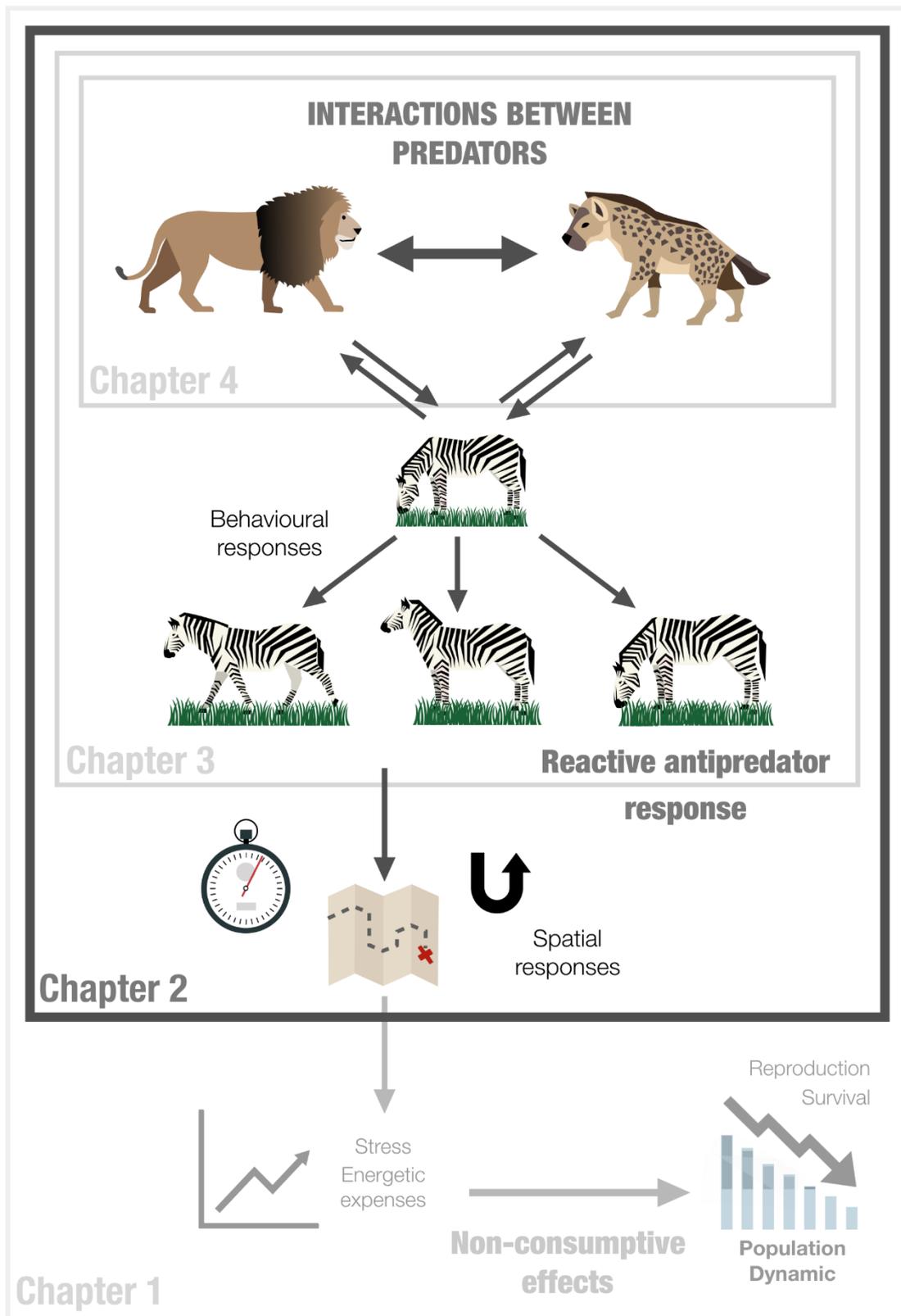
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## **Chapter 2: Predator hunting mode affects the nature and the strength of the reactive spatial response of prey to predation risk in large mammals**



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**Predator hunting mode affects the nature and the strength of the reactive spatial response of prey to predation risk in large mammals**

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## Abstract

Predator-prey interactions rely on prey characteristics and habitat type as well as predator characteristics. Literature on invertebrate species has demonstrated that according to their hunting mode, predator would induce antipredator response of different magnitudes for prey. The goal of this study was to test this hypothesis on large terrestrial mammalian species. We assessed if zebras' (*Equus quagga*) spatial antipredator reactive response differed when exposed to lion (*Panthera leo*, ambush predator) compared to spotted hyaena (*Crocuta crocuta*, cursorial predator). We expected lions to induce a higher reactive antipredator response than hyaenas. Using data from GPS collars (deployed on the three species), we studied the spatial reactive responses of zebras after being exposed to both predators. We found that zebras responded more to lions more than to hyaenas. Indeed, zebras were twice as likely to flee after an encounter with a lion than a hyaena and, immediately after an encounter, with lions, zebras moved on average twice as fast than after an encounter with a hyaena. As expected, lion induce a stronger reactive spatial antipredator response than hyaenas on zebras, it seems that the hunting mode does affect the reactive response of prey and this is consistent with literature from invertebrate species.

**Key-words:** African lion, antipredator response, ecology of fear, plains zebra, predator-prey interactions, risk effects, spotted hyaena.

## Introduction

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 (FitzGibbon, 1994), altered grouping strategies (Creel & Winnie, 2005), relocation to safer areas (Fortin et al., 2005), changes in diel activity rhythms (Valeix et al., 2009a), and combination of these (Creel, Schuette and Christianson, 2014; Courbin et al., 2019). While prey antipredator behavioural responses have been well described for a variety of predator-prey systems and their interactions theoretically investigated (Mitchell & Lima, 2002; Patin et al., 2019), less is known about the factors underlying the variations in the nature and strength of these responses in natural ecosystems. Prey may not respond the same way to different predators, as not all predators are associated to the same level of predation risk, and a response efficient toward a particular predator may not serve as an efficient defence against another one (Relyea, 2001).

In invertebrates, experimental evidence showed the importance of the predator hunting mode to understand the nature and strength of the antipredator response of a given prey species (Miller et al., 2014). A meta-analysis of experimental studies also showed that prey exposed to cues from sit-and-pursue (ambush) predators experienced greater reductions in growth, fecundity and density than when exposed to cues from actively hunting (cursorial) predators, suggesting stronger antipredator responses to sit-and-pursue predators (Preisser et al., 2007). The underlying mechanism would be that sit-and-pursue predators tend to spend longer periods in the same area, and hence cues of their presence should be more indicative of imminent predation risk, and therefore evoke stronger prey responses. Such a mechanism makes perfect sense when considering the proactive response of prey to predation risk, i.e. when prey modify their behaviour in response to an a priori assessment of the level of risk, for which cues of the

presence of the predator are important. However, the role of hunting mode is less clear when considering the reactive response of prey, i.e. when prey have detected an immediate threat.

Of the few recent empirical studies investigating the role of the predator species and hunting mode on prey proactive antipredator responses in large mammals, most were at the proactive level and supported the hypothesis that ambush predators provoke stronger behavioural responses than cursorial predators (with the noticeable exception of Dröge et al., 2019). For instance, in Tswalu Kalahari Reserve, South Africa, herbivores were more vigilant, and used waterholes less at dawn, dusk and night in areas where African lions *Panthera leo* (ambush predators) were present than in areas where cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus* (both cursorial predators even though they characterize the two extremes of cursorial hunting strategies – cf. Hubel et al., 2016) were present (Makin et al., 2017). In Karongwe Game Reserve, South Africa, herbivores consistently avoided the activity areas of ambush predators (lions and leopards *Panthera pardus*), but not those of cursorial predators (cheetahs and wild dogs; Thaker et al., 2011). In the Bialowieza Primeval Forest, Poland, lynx *Lynx lynx* (ambush predator) olfactory cues influenced the visitation rate of sites by red deer *Cervus elaphus* (Wikenros et al., 2015), whereas wolf *Canis lupus* (cursorial predator) olfactory cues had no impact (Kuijper et al., 2014). These pioneering results at the proactive response scale corroborate the idea that cues from ambush predators induce stronger antipredator responses than cues from cursorial predators.

Most studies on the antipredator responses of prey in large mammals focused on one predator species only, whereas most were carried out in ecosystems where several predator species actually occur (Montgomery et al., 2019; Say-Sallaz et al., 2019). Studies considering several predator species are therefore needed to assess the role of predator species and predator attributes in the behavioural responses of prey to predation risk if we want to be able to understand the variability of responses reported in the literature and derive general rules. In

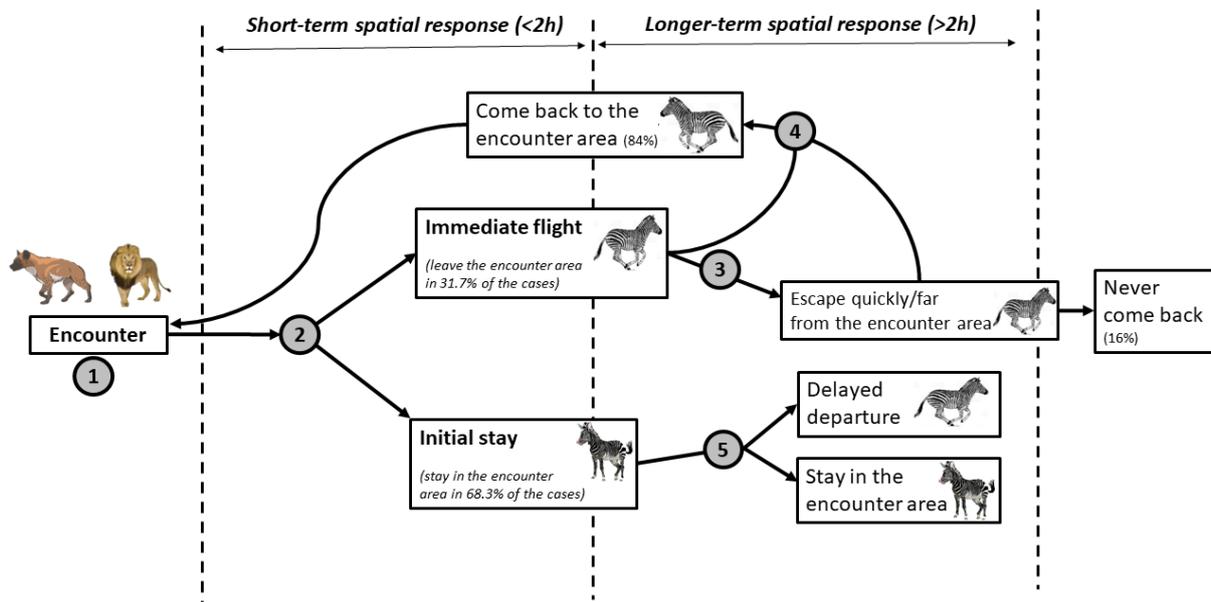
particular, more studies are needed in natural systems where sympatric predators have contrasted hunting modes with ambush predators (mostly felids) that need concealing cover to wait and/or approach their prey undetected, and cursorial (or coursing) predators (mostly canids and hyaenids) that attack from the open and can chase down their prey over long distances.

In this work, we studied the reactive spatial response of plains zebras *Equus quagga* to encounters with lions (ambush predators) and spotted hyaenas *Crocuta crocuta* (cursorial predator), using GPS data acquired simultaneously on zebras and the two predators. We explored whether predator hunting mode is an important driver of their reactive antipredator spatial response by testing 2 hypotheses:

*Hypothesis 1 - Consistent importance of the predator hunting mode* - Following the same logic as the one developed in the existing literature on the role of predator cues for proactive responses (Preisser et al., 2007; Miller et al., 2014), we can make the assumption that an ambush predator is more likely to stay in an encounter area than a cursorial predator, and hence the detected presence of an ambush predator is more associated to the probability of presence of this predator in the near future. Based on this assumption, we hypothesize that prey should leave more often an area after an encounter with an ambush predator than with a cursorial predator.

*Hypothesis 2 - Habitat-dependent importance of the predator hunting mode* - Because habitat affects the hunting success of ambush and cursorial predators differently (ambush predators need cover to launch their attack whereas cursorial predator need open habitat to chase efficiently), the spatial reactive response of prey should be habitat-dependent: ambush predators should induce stronger reactive responses than cursorial predators in closed habitats but weaker reactive responses in open habitats.

To test these hypotheses, we assessed the environmental characteristics of encounters with lions and with hyaenas and studied different steps in the reactive spatial response of zebras (Fig. 1, see “Material and Methods” for details).



**Figure 1:** Temporal dynamics of the reactive spatial response of zebras after an encounter with a predator. Once an encounter with a predator has occurred at a specific location (1), a zebra has two options for its short-term spatial response (<2h): it either leaves the encounter area or it stays (2). At a longer time scale, a zebra that left the encounter area can go more or less far from the encounter area (3) and either never return to the encounter area or come back to the encounter area (4). For a zebra that initially stayed in the encounter area, it can either stay for a long period in the encounter area or initiate a delayed departure (5). Percentages in the boxes indicate the percentages of the study cases (for encounters with lions, with hyaenas and for controls) concerned by the different spatial behaviours described here.

## Material & Methods

### *Study area*

The general study area is Hwange National Park, a large unfenced protected area (~15 000 km<sup>2</sup>) located in western Zimbabwe (19°00’S, 26°30’E). This ecosystem is

characterized by a dystrophic (low nutrient soil) semi-arid savanna 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. (Rogers, 1993). The long-term mean annual rainfall is 600mm  $\pm$  30%CV, 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, which are pumped throughout the dry season. The study was conducted in the Main Camp region of the Park ( $\sim$ 1 200 km<sup>2</sup>). There, zebra density is estimated to be around 1 indiv./km<sup>2</sup> (Grange et al., 2015), lion density around 4 indiv./100 km<sup>2</sup> (Loveridge et al., 2016), and hyaena density around 9 indiv./100 km<sup>2</sup> (Périquet 2014). Zebras are predated upon by both predators, accounting for 8-9% of lion diet (Davidson et al., 2013) and 11% of hyaena diet (Périquet et al., 2015).

### Data

Thirty-two female adult zebras from different harems were equipped with GPS collars, which recorded a location every hour or every 30 minutes (we only kept a location per hour for the analyses) between August 2009 and July 2015. Zebras were tracked for 387 ( $\pm$  256 SD) days on average. During this 6-year period, in the area used by the studied zebras, 14 lions (from 9 different prides/coalitions) and 7 hyaenas (from 3 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. The capture and collaring of zebras, lions and hyaenas were performed by qualified personnel, under permits from Zimbabwe Parks and Wildlife Management Authority, using standard protocols for these species.

### *Definition of encounters*

We assumed that a zebra encountered a predator when they were simultaneously located less than 500m apart, the first pair of locations under 500m are considered as the encounter (as in Courbin et al., 2016). We only considered encounters occurring at night (between 6pm and 6am) since this is when lions and hyaenas are active and likely to be hunting (Kruuk, 1972; Schaller, 1972). In the subsequent analyses, we included only individual zebras that encountered both predators in order to reduce asymmetry in our dataset (more lions were equipped with GPS collars than hyaenas and data were collected for a longer period of time so there are more encounters of zebras and lions). This was the case for 15 zebras. We identified 68 encounters between a zebra and a lion, and 90 encounters between a zebra and a hyaena.

### *Analyses*

#### *1. Environmental characteristics and timing of encounters*

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. 2009a, 2010). This habitat selection process can be considered as the proactive spatial behaviour of zebras to the risk of predation by nocturnal predators (Courbin et al., 2016, 2019). Here, we used selection functions (Manly et al., 2002) to assess if 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. For each encounter and random location, we extracted (1) the distance to the closest waterhole. Waterhole areas are considered hotspots of predator-prey interactions in the Hwange ecosystem (Valeix et al., 2011; 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 as ‘distance’ in equations 1,2,3,4): ‘close’ (less than 1km of a waterhole) vs “distant” (> 1km of a waterhole); (2) the vegetation type (referred as ‘vegetation’ in equations 1,2,3,4). Based on the vegetation structure map by Arraut et al. (2018), we contrasted two types of vegetation: ‘open vegetation’ (corresponding to the class ‘grassland’ in the original map) and ‘closed 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 as ‘night’ in equations 1,2,3,4), classified as either the ‘beginning’ (between 6pm and midnight) or ‘end’ (between midnight and 6am). At the ‘beginning’ of the night, prey, if not responding, will have to cope with the presence of the predator 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 predator species are mainly active at night-time (Hayward & Slotow, 2009). We therefore predicted that prey would be more likely to leave at the ‘beginning’ of the night than at the ‘end’. 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 1s, random locations as 0s):

$$x_{ij} = \exp(\beta_0 + \beta_w distance_{ij} + \beta_v vegetation_{ij} + \beta_n night_{ij} + \gamma_{0j})$$

(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 others  $\beta$  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 calculated the variance inflation factor (VIF) for all the estimates of fixed effects (Dormann et al., 2013). All VIFs were  $<1.5$ , indicating that inference was not affected by collinearity. We conducted this analysis for the zebra-lion encounters and for the zebra-hyaena encounters to assess if the characteristics of the encounters varied between the two predators (step (1) in Fig. 1).

## 2. *Spatial response of zebras after a predator encounter*

*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 (for the random draw in section 1, the time was not constrained as we selected night locations independently from the time of the encounter) 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. We were unable to detect if zebras encountered predators that were not GPS-collared during these controls, as not all lions and hyaenas were equipped with a GPS collar, but we reduced the impact of that uncertainty by choosing 10 controls for every encounter. Further, the effect of undetected predators should mainly reduce our capacity to detect differences in zebra spatial response between encounters and controls.

*Describing the variability of the spatial reactive 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 location of the zebra during the next 24h. Plotting the data revealed a high variability in how zebras moved away from the locations with time (Appendix A), which led us to decompose the spatial response of zebras to understand this variability (Fig. 1). We first focused on the short-term spatial response. Building upon Courbin et al. (2016), we identified

two types of immediate spatial responses, linked to whether zebras were further than 900m from the encounter location 2 hours after the encounter ('immediate flight') or not ('initial stay'). This 900m threshold distance will define what we will refer to as the 'encounter area' hereafter. This threshold distance was the distance that best discriminated two type of immediate responses in Courbin et al. (2016). This corresponds to step (2) in Fig. 1. We assessed whether this immediate response was influenced by the predator species and the habitat. We then investigated whether there were longer-term spatial responses, which are likely more costly. We specifically calculated, for zebras that left the encounter area, the speed (meters/hour) with which they left the area and at which distance they moved away over 24hours (step (3) in Fig. 1), and compared whether this dynamics of the flight was influenced by the predator species. We further assessed how long it took zebras to come back to an encounter area if they did return (step (4) in Fig. 1). For zebras that initially stayed in the encounter area after a predator encounter, we assessed whether predator species or habitat type at the encounter influenced the time ultimately zebras spent in the encounter area after the encounter (step (5) in Fig. 1).

*2.1 Short-term response of zebras after a predator encounter* - We calculated the proportion of encounters that led to an 'immediate flight' response and the proportion of encounters that led to an 'initial stay' response. We then used a mixed logistic regression to assess whether the probability of observing an 'immediate flight' response (coded 1) vs. an 'initial stay' response (coded 0) was affected by the study variables:

$$P_{ij} = \frac{\exp(\beta_0 + \beta_p \text{predator}_{ij} + \beta_w \text{distance}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij} + \gamma_{0j})}{1 + \exp(\beta_0 + \beta_p \text{predator}_{ij} + \beta_w \text{distance}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij} + \gamma_{0j})} \quad (2)$$

Where  $P_{ij}$  is the probability of an ‘immediate flight’,  $i$  being the  $i^{\text{th}}$  observation and  $j$  the  $j^{\text{th}}$  zebra. We used the same explanatory variables as in the eq. 1 and we added the explanatory variable ‘predator species encountered’ (abbreviated ‘predator’), which is a categorical variable with three levels: hyaena, lion, and control. Sample sizes were too small to allow us testing for interactions between the predator variable and the environmental variables.

*2.2. Temporal dynamics of zebra response for zebras that performed 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 if the predator species encountered influenced (i) the speed with which the zebra left the encounter area, and (ii) how far zebra went following the ‘immediate flight’ response (step (3) in Fig. 1). For each encounter or control location, we calculated, for each hourly interval from 5h before to 24h after the location, the speed (meters/hour) of the zebra. We then compared the mean difference of speed over each hourly interval between encounters with a lion, encounters with a hyaena and controls by using multiple means comparisons (Herberich et al., 2010). To assess how far zebras moved after a predator encounter, we estimated the net displacement of individuals away from the encounter at increasing time-lags after the encounter (hourly time stamps) and then the difference for each pair of species and compared, using multiple means comparisons, net difference of displacement between encounter with lions, hyaenas and controls.

*2.3. Temporal dynamics of the avoidance of the encounter area by zebras that performed an ‘immediate flight’* – For ‘immediate flight’ responses, we studied the time elapsed before coming back to the encounter area (data are shown in Appendix B). For returns (which happened for 84% of the ‘immediate flight’ responses, step (4) in Fig. 1), we further studied the drivers of this temporal dynamics of avoidance of the encounter area by using a negative binomial regression (to avoid issues of overdispersion of the model):

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

where  $T_{ij}$  is the time before returning to the encounter area for the  $i$ th observation of the  $j$ th animal, and  $\varepsilon_j$  is the error term that is uncorrelated with the model's variables and has a gamma distribution. All the explanatory variables are the same as above.

*2.4. Time spent in the encounter area for zebras that initially stayed* – For ‘initial stay’ situations (n=71 after an encounter with a hyaena and n=37 after an encounter with a lion), we calculated the time spent in the encounter area (data are shown in Appendix C; step (5) in Fig. 1) and investigated if some factors influenced it using a mixed negative binomial regression:

$$S_{ij} = \exp(\beta_0 + \beta_p \text{predator}_{ij} + \beta_w \text{distance}_{ij} + \beta_v \text{vegetation}_{ij} + \beta_n \text{night}_{ij} + \varepsilon_j) \quad (4)$$

Where  $S_{ij}$  is the time spent by a zebra in the encounter area. All the explanatory variables and the error are the same as above.

All the statistical analyses were performed with the R software (version 3.6.1, Team, R core, 2021). We considered explanatory variables with p-value lower than 0.05 statistically significant.

## Results

### *1. Environmental characteristics and timing of encounters*

Encounters between zebras and lions were located closer to waterholes than random zebra night locations (Table 1, Appendix D). This was not the case for encounters between zebras and hyaenas (Table 1). Encounters with both predators did not occur in specific vegetation type

compared to those generally used by zebras at night (Table 1). Encounters also did not occur at a specific period of the night (Table 1).

Table 1: Estimates of the variables explaining the relative probability of encounter between a zebra and a predator (see Appendix D for the figure relevant to the result on the effect of distance to water on the relative probability of encounter with a lion). Significant values (< 0.05) are in bold.

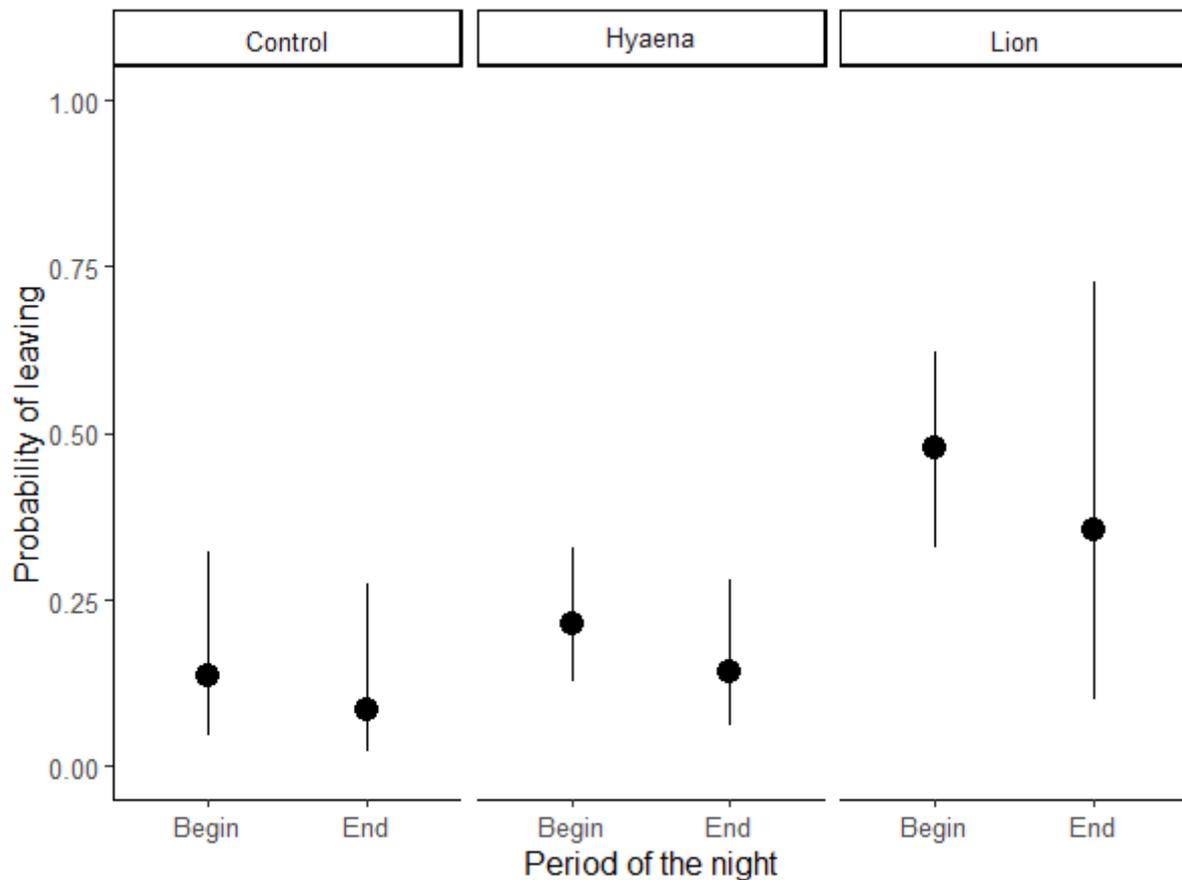
Predator species	Variables	Estimates	Std. Error	z	pr(> z )	Confidence Interval	
						2.5%	97.5%
Hyaena	<b>Intercept</b>	<b>-1.98</b>	<b>0.26</b>	<b>-7.52</b>	<b>5.43e-14</b>	<b>-2.52</b>	<b>-1.49</b>
	Distant (distance to water)	-0.33	0.27	-1.21	0.23	-0.84	0.22
	Open (vegetation type)	-0.15	0.34	-0.42	0.68	-0.85	0.50
	End (night period)	-0.11	0.22	-0.50	0.62	-0.55	0.33
Lion	<b>Intercept</b>	<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>
	<b>Distant (distance to water)</b>	<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

## 2. Short-term spatial response of zebras after a predator encounter

The probability of observing an ‘immediate flight’ response was higher after an encounter with a lion (45% on average) than after an encounter with a hyaena (21% on average), both being higher than for control situations (16% on average, Table 2, Fig. 2). The probability of an ‘immediate flight’ response was lower at the end of the night (Table 2, Fig. 2), but was not significantly affected by distance to water or the vegetation where the encounter occurred (Table 2).

Table 2: Estimates of the variables explaining the probability for a zebra to do an ‘immediate flight’ response in the 2 hours following an encounter with a predator (hyaena being the default for the predator variable). Significant values are in bold.

	Estimates	Std. Error	z	pr(> z )	Confidence Interval	
					2.5%	97.5%
<b>Intercept</b>	<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>
<b>Control (predator)</b>	<b>-0.55</b>	<b>0.27</b>	<b>-2.04</b>	<b>0.0410</b>	<b>-1.07</b>	<b>-0.03</b>
<b>Lion (predator)</b>	<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>
<b>End (night period)</b>	<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

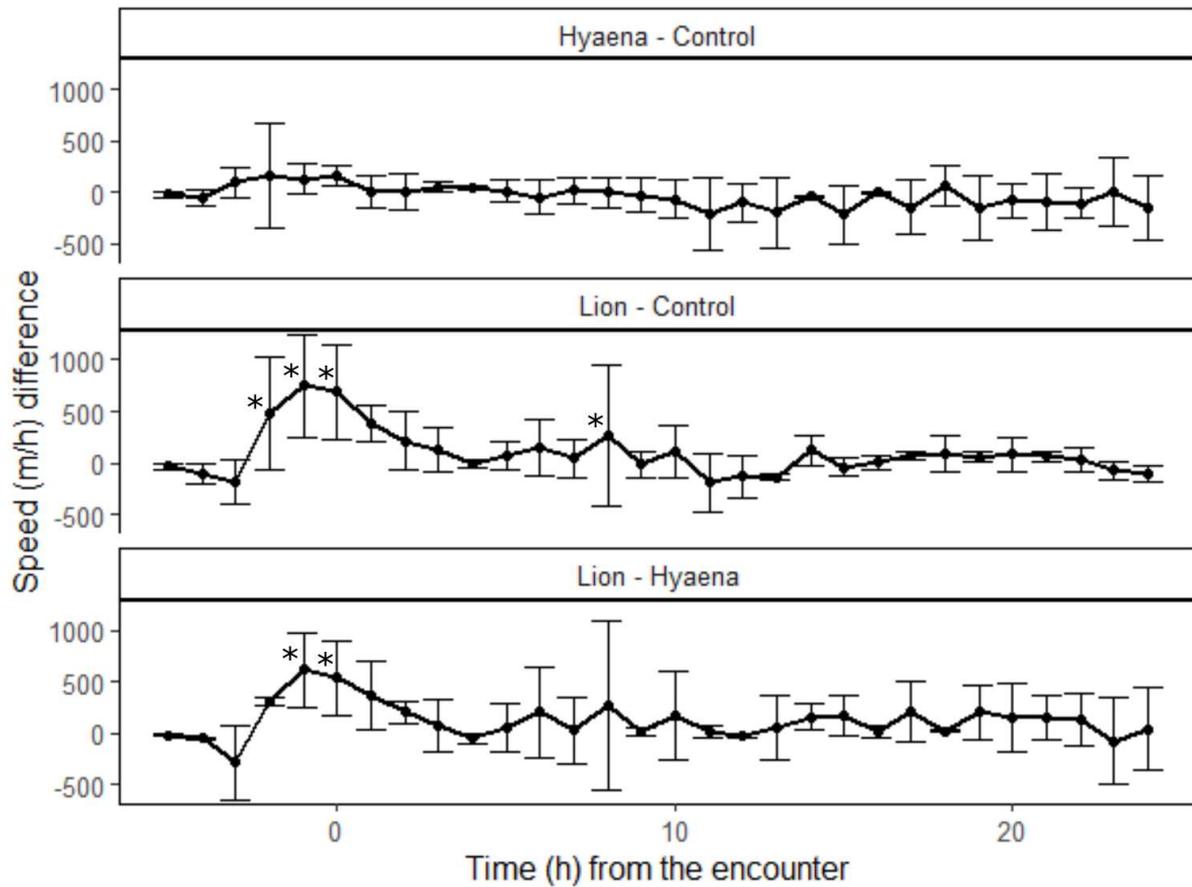


**Figure 2:** Probability (calculated from the model estimates, and with error bars representing the 95% confidence interval) for a zebra to leave the encounter area in the 2 hours following an encounter with a predator ('immediate flight') according to the period of the night (Begin or End). Probabilities were calculated for the default values of the other variables (i.e. when close to water and in a closed habitat).

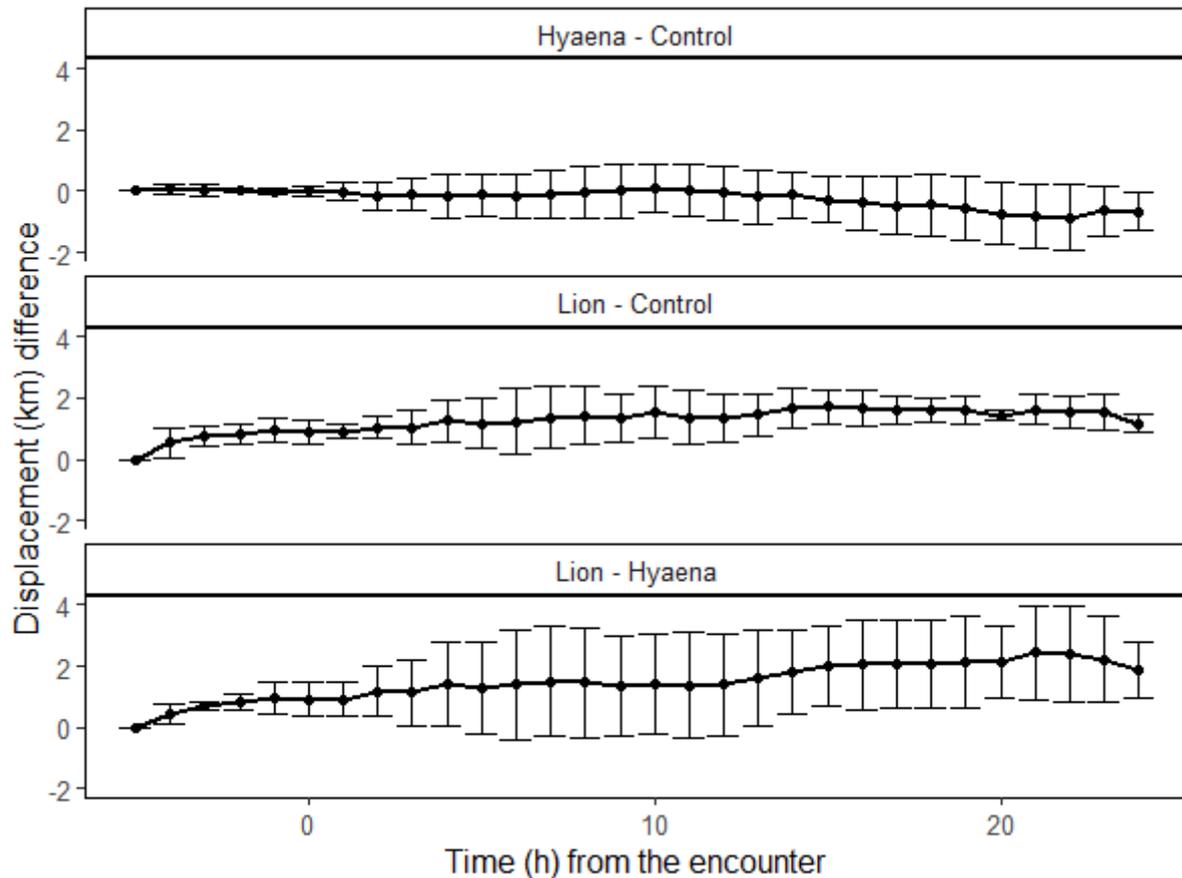
### 3. *Temporal dynamics of zebra spatial response for zebras that performed an 'immediate flight'*

Immediately after an encounter with lions, zebras moved on average faster than after an encounter with a hyaena (Fig. 3, p-value = 0.03), or than after a control (Fig. 3, p-value = 0.4e-05). Afterward mean speeds are not significantly different between lion encounter and hyaena encounters or controls (Fig. 3). Zebras that fled immediately after an encounter with a hyaena did not move faster than during control situations as no mean speed at any time period is

significantly different (mean speed  $\pm$  SD =  $1011 \pm 838$  m/h and  $854 \pm 741$  m/h respectively; p-value=0.87; Fig. 3). It is noteworthy that, with an encounter area defined by a radius of 900m, zebras needed to have travelled at least this distance in 2 hours even in control cases (as can be seen in Fig. 3). There was a tendency for zebras to have longer net displacements after an encounter with a lion (mean net displacement  $\pm$  SD =  $5.5 \pm 4.0$  kilometres 24 hours after; Fig. 4) than after a control (mean net displacement  $\pm$  SD =  $3.3 \pm 2.5$  kilometres 24 hours after; p-value=0.06; Fig. 4). A similar tendency of longer net displacements after an encounter with a lion than after an encounter with a hyaena can be noticed although a high variability is depicted. We detected no significant difference between zebra mean net displacements after an encounter with a hyaena and both zebra mean net displacements in control situations (Fig. 4, p-value=0.99) or after an encounter with a lion (Fig. 4, p-value=0.28).



**Figure 3:** Difference of mean speed between pairs of situations (hyaena encounter *vs.* controls, lion encounters *vs.* controls, and lion encounters *vs.* hyaena encounters) for zebras that performed an ‘immediate flight’ response. The bars indicate the 95% confidence intervals. The stars indicate significant ( $p < 0.05$ ) differences from the multiple mean comparisons’ tests.



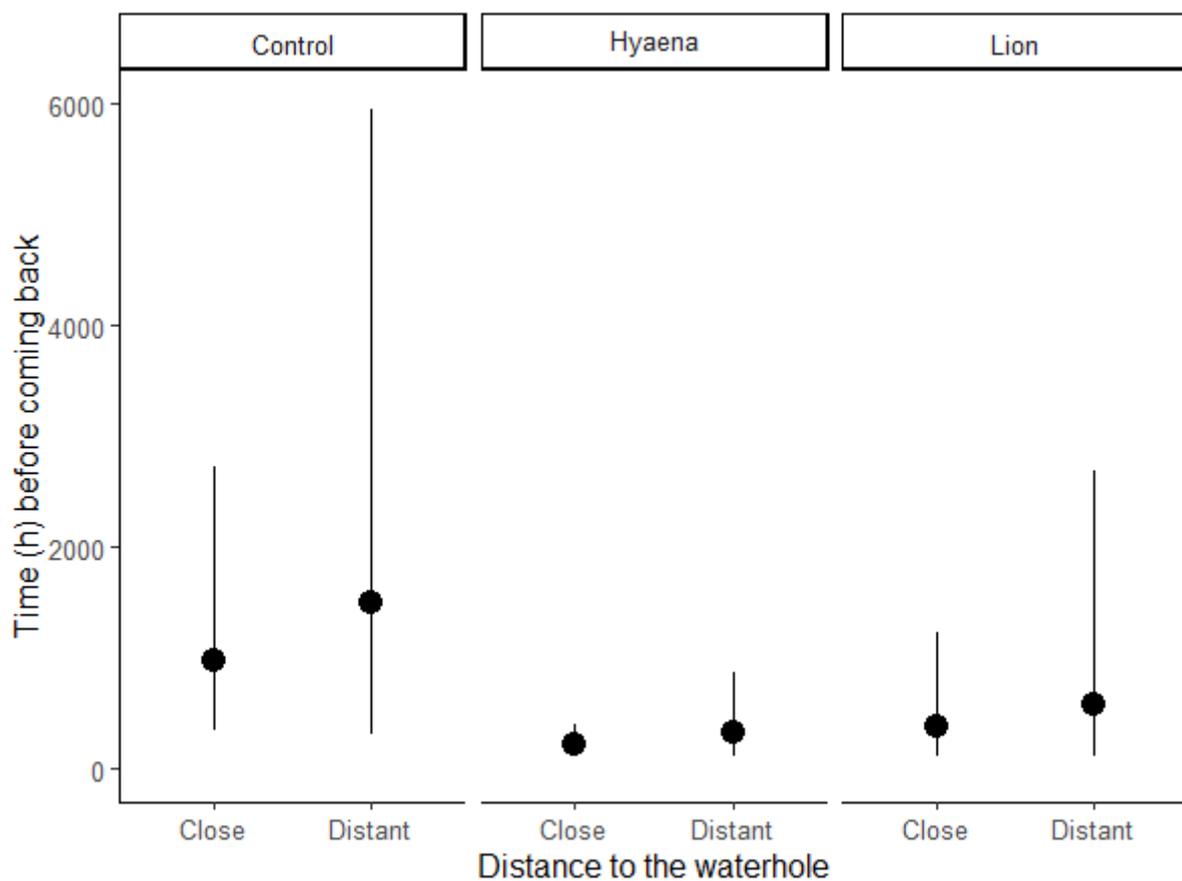
**Figure 4:** Difference of mean displacement speed between pairs of situations (hyaena encounter vs. controls, lion encounters vs. controls, and lion encounters vs. hyaena encounters) for zebras that performed an ‘immediate flight’ response. The bars indicate the 95% confidence intervals. The stars indicate significant ( $p < 0.05$ ) differences from the multiple mean comparisons tests.

4. *Temporal dynamics of the avoidance of the encounter area by zebras that left after a predator encounter*

Zebras returned sooner to an encounter area after an encounter with a predator (hyaena or lion) than after a control situation, with shorter times after an encounter with a hyaena than after an encounter with a lion (Table 3, Fig. 5, Appendix B). Furthermore, we found that zebras came back sooner when they had encountered the predator close to a waterhole (Table 3, Fig. 5).

Table 3: Estimates of the variables explaining the time spent by a zebra that performed an ‘immediate flight’ response before returning to the encounter area (hyaena being the default for the predator variable). Significant values are in bold.

	Estimates	Std. Error	z	pr(> z )	Confidence Interval	
					2.5%	97.5%
<b>Intercept</b>	<b>5.37</b>	<b>0.31</b>	<b>17.27</b>	<b>&lt;2e-16</b>	<b>4.78</b>	<b>5.98</b>
<b>Control (predator)</b>	<b>1.51</b>	<b>0.22</b>	<b>6.74</b>	<b>1.56e-11</b>	<b>1.05</b>	<b>1.93</b>
<b>Lion (predator)</b>	<b>0.58</b>	<b>0.29</b>	<b>2.00</b>	<b>0.045</b>	<b>0.01</b>	<b>1.14</b>
End (night period)	-0.02	0.13	-0.19	0.850	-0.27	0.22
Open (vegetation type)	0.25	0.18	1.38	0.168	-0.10	0.61
<b>Distant (distance to water)</b>	<b>0.43</b>	<b>0.17</b>	<b>2.56</b>	<b>0.010</b>	<b>0.10</b>	<b>0.78</b>



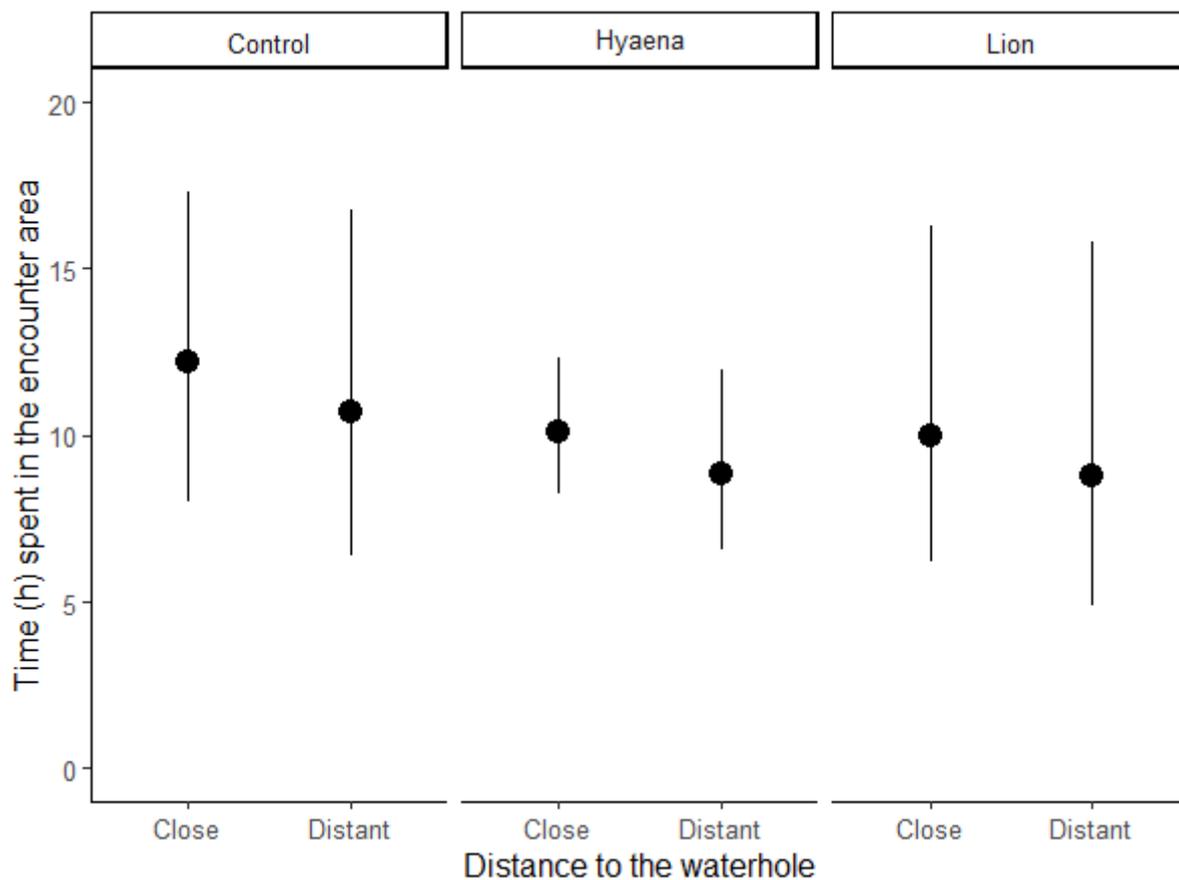
**Figure 5:** Time spent by zebras that performed an ‘immediate flight’ response before returning to the encounter area (calculated from the model estimate, and with 95% confidence interval, error bars) according to the distance to water (Close or Distant). Times were calculated for the default values of the other variables (at the beginning of the night and in a closed habitat).

5. *Time spent in the encounter area for zebras that initially stayed*

The duration of zebra stay in the encounter area did not differ between encounters with lions or hyaenas (Table 4, Fig. 6, Appendix C) and was ~10 hours on average. This duration differed in control situations when zebras stayed slightly longer (~12h, Table 4, Fig. 6). Environmental variables had no effect on the duration of the stay in the area, except for the distance to water, with zebras staying longer (2 hours more on average) in the encounter area when it was close to a waterhole (Table 4, Fig. 6).

Table 4: 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	Std. Error	z	pr(> z )	Confidence Interval	
					2.5%	97.5%
<b>Intercept</b>	<b>2.31</b>	<b>0.10</b>	<b>22.87</b>	<b>&lt;2e-16</b>	<b>2.11</b>	<b>2.51</b>
<b>Control (predator)</b>	<b>0.19</b>	<b>0.08</b>	<b>2.32</b>	<b>0.02</b>	<b>0.03</b>	<b>0.34</b>
Lion (predator)	-0.01	0.15	-0.07	0.95	-0.29	0.28
End (night period)	0.06	0.04	1.79	0.07	-0.01	0.14
Open (vegetation type)	-0.004	0.06	-0.07	0.94	-0.11	0.11
<b>Distant (distance to water)</b>	<b>-0.13</b>	<b>0.05</b>	<b>-2.61</b>	<b>0.01</b>	<b>-0.23</b>	<b>-0.03</b>



**Figure 6:** For zebras that initially stayed, time spent in the encounter area (calculated from the model estimates, and with error bars indicating 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 a closed habitat).

## Discussion

*Zebras' immediate spatial response to predation risk differs according to the predator species encountered* – Zebras were clearly much more likely to leave the encounter area when they encountered a lion than when they encountered a hyaena, to which zebras showed little sign of responding. They also fled faster and further away after encountering a lion. The nature and strength of the reactive spatial response of zebras was thus influenced by the species of predator encountered. Altogether, these results tend to support hypothesis 1 on the importance of the predator hunting mode in prey antipredator reactive response, with ambush predators (lions) eliciting a stronger reactive response than cursorial predators (hyaenas). A presence cue from an ambush predator tends to be associated with a high probability of the predator being in the vicinity at the time of the cue detection but also in the near future. Consequently, it is logical that a prey detecting an ambush predator leaves the encounter area to decrease the time spent near this predator. Contrarily, cursorial predators explore the landscape for potential prey over large areas and their presence (or a cue of their presence) at a given time is not correlated to their presence in the near future. Additionally, ambush predators, such as lions, rely on concealment to approach their prey undetected and their hunting success benefits from a surprise effect as they can run at a very high speed but over short distances. Hence, once a prey detects an ambush predator and leaves the encounter area, the probability that the ambush predator will pursue the prey is almost nil. This is different for cursorial predators, such as hyaenas, which can chase down their prey over long distances and thus remain dangerous once detected. Hence, upon an encounter, leaving the encounter area with a cursorial predator might not decrease the probability that the predator will pursue the prey. Altogether, these mechanisms may explain why in large mammals ambush predators elicit a stronger reactive spatial response than cursorial predators.

Lions and hyaenas differ also by other characteristics, such as body size or speed, which clearly play a role in predator-prey interactions (Cuthbert et al., 2020; Hirt et al., 2020; Wei et al., 2020). In the future, it will thus be important to compare our results with similar studies on different pairs of large carnivores with contrasting hunting modes to assess if hunting mode is the right predator attribute that matters to explain the variability of prey antipredator responses, as it was done for invertebrate species (Preisser et al., 2007). Furthermore, our study focused on the spatial reactive response only (with reactive movements expected to reduce exposure to risks assessed to be acute) and prey can also invest (in addition to or in replacement of the spatial response) in other reactive behavioural responses, such as exclusive vigilance (Creel et al. 2017, Dannock et al. 2019), resistance display such as bunching (McComb et al. 2011, Dannock et al. 2019) or fighting behaviours (Lingle & Pellis 2002). For example, moose can effectively repulse wolves by counterattacking them and show little spatial response to wolf presence (Nicholson et al., 2014). Finally, it seems that cursorial predators, such as hyaenas or wild dogs *Lycaon pictus*, are often more successful hunters when prey flee right after the encounter (Mills 1990, Creel & Creel 2002). Even though our data do not allow assessing the very fine scale response of prey, it is therefore possible that zebras do not leave the area immediately after encountering a hyaena, as this may actually be the most effective antipredator response. Future research will need to study jointly the different types of reactive responses if we want to grasp the full picture of the role of predator hunting mode. Nonetheless, African ungulates in general do not tend to be more vigilant after an encounter with a hyaena than after an encounter with a lion (Creel et al., 2014; Creel et al., 2017). Hence, lions may overall induce stronger reactive antipredator responses than hyaenas (hypothesis 1). This is consistent with 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).

*The behavioural ecology of predator-prey interactions is context-dependent* – One important finding from our work is the high variability in the zebra spatial responses. In particular, our results show that zebras do not leave an encounter area; even after encountering a lion, they performed an ‘immediate flight’ response in only 45% of the situations, which means that either the predation risk was assessed as not acute enough or another antipredator response was more appropriate. 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 (attacking, looking for prey, walking nonchalantly or other) and its hunger state (which can be assessed from the belly distension of the predator – Bertram, 1975, Packer et al. 2011) can strongly influence prey behaviour. For instance, an ‘immediate flight’ response might be the common and most appropriate response to a hunting predator with a thin belly while an ‘initial stay’ response might be the common and most appropriate response to a walking predator with a fully distended belly. Regarding prey attributes, because our study focused on one prey species only, the prey attributes that may affect antipredator responses are prey group size (Creel & Christianson., 2008; Périquet et al., 2012), presence of young (Gochfeld & Burger, 1994), prey hunger state (Berger-Tal et al., 2010), and prey personality (DiRienzo et al., 2013; Belgrad & Griffen, 2016). This illustrates the limits of studies based on the analysis of GPS data only, for which detailed information on the context of predator-prey encounters is missing. In addition, different prey species can be expected to have a different answer to the same predator. By having a selective diet for patches of short grass, blue wildebeests (*Connochaetes taurinus*) are less likely to leave a short grass patch after an encounter with a lion, while zebras, which are generalists, are less constrained and more likely to leave (Martin & Owen-Smith, 2016). Finally, the assessment of risk level by prey and the associated antipredator response may be influenced by the characteristics of the surrounding environment, but also the habitat complexity 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, the habitat (vegetation structure and distance to water) did not play an important role in zebra immediate spatial response, which overturns hypothesis 2. The probability of a zebra initiating an ‘immediate flight’ response was accentuated at the beginning of the night. This suggests that encounters occurring earlier in the night are riskier than the ones occurring later in the night. This may arise from the fact that both hyaenas and lions are the most active at the beginning of the night (Cozzi et al., 2012) making it the riskiest period for prey (‘risky times’ hypothesis – Dröge et al., 2017). This may also be because if a prey encounters a predator at the beginning of the night and stays in the encounter area, it will have to adjust to the presence of the predator and the associated high level of risk for a long period of night-time when predators are active (‘risky place’ hypothesis – Dröge et al., 2017). The variability of the contexts associated to the encounters studied (predator behaviour, prey context, and environmental characteristics) may underlie the variability of the responses studied.

*Predator influence on prey space use at the landscape level and on a longer temporal scale* – In our study, we did not focus on the immediate spatial response of zebras only. We further explored how far a zebra went after an encounter with a predator and how long a zebra avoided an encounter area with a predator (already studied but only 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, not only did zebras performed an “immediate flight” more often after an encounter with a lion, but they also moved further away when they encountered a lion (> 5 km away on average 24h after the encounter) than a hyaena (~ 3 km on average 24h after the encounter). The immediate flight response is therefore associated not only to a missed opportunity cost in terms of foraging as zebras forage a lot at

night (unpublished data) and prematurely leave their foraging patch for ‘immediate flight’ responses, but also to travelling costs (higher when zebras encounter lions because of higher speed just after the encounter and longer distances covered). Additionally, our results mirror previous findings on lions leaving a kill area, probably because of prey behavioural depression after prey have located the lions and moving to a different area (> 5km away – Valeix et al., 2011). This illustrates the predator-prey space game at the landscape scale.

Furthermore, we investigated whether there were longer-term spatial responses, which are likely costlier, to provide insights into the potential fitness consequences of the studied reactive spatial responses as there is current debate on the implications of anti-predator behavioural responses at the prey population level (Say-Sallaz et al., 2019; Zanette & Clinchy, 2020; Sheriff et al., 2020). Zebras that had left immediately returned sooner to an encounter area after a true predator encounter than when zebras left the area in control situations. 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 prematurely their resource patch, explaining why they came back to the encounter area shortly, most probably as soon as the environment was less risky. This was true especially for encounter areas close to a waterhole. Zebra showed the same type of response in Courbin et al., (2016): zebra tend to rapidly go back to an area close to a waterhole after an encounter with a lion. Waterholes are important drivers of zebra habitat selection as zebras are water dependant and need to drink daily (Redfern et al., 2003), and open grassland areas where zebras mainly forage are scarce and often associated with waterhole areas in the study ecosystem (Arraut et al., 2018).

*Emergent multiple predator effects* – Our results, by supporting the first hypothesis that prey reactive antipredator responses is affected by predator hunting mode, underlines that different predators may affect each other and prey’s landscape of fear in complex ways (Sih et

al, 1998). Multiple predators can affect predation risk for a prey species in two ways: (i) they interfere directly by chasing each other (Périquet et al., 2021) or indirectly by reducing their hunting efficiency leading to risk reduction for the prey (Hoset et al., 2009), or (ii) they facilitate each other if the prey response to one predator makes the prey more vulnerable to the other (Cresswell & Quinn, 2013, Atwood et al., 2009; Leblond et al., 2016). In our study, zebras often stayed in the area where they encountered a hyaena. Contrarily, zebras that encountered a lion tend to fly from the encounter area. Encounters with both predators did not occur in a specific vegetation type compared to those generally used by zebras at night (open habitats - Courbin et al., 2016), and zebras encountered lions (but not hyaenas) closer to water than compared to sites generally used by zebras at night (Courbin et al., 2016). Altogether, our results therefore suggest that a zebra fleeing from an encounter with a lion will leave at a rather high speed an open area, having to move across wooded areas, to reach a different area > 5 km away 24 hours after. This may have two implications for hyaenas. At a small spatial scale (the encounter area), lion presence leads to a depression of prey as prey do not stay in the encounter area. However, at a larger spatial scale, hyaenas may benefit from lions that force zebras to move across the landscape at night. Indeed, hyaena density is higher than lion density and hyaenas show no strong habitat selection pattern (Périquet, 2014). Consequently, hyaenas are expected to be spread more evenly through the landscape (a pattern confirmed by camera-trap data - unpublished data). Therefore, hyaenas are likely to represent a uniform risk of predation over the landscape contrarily to lions (Valeix et al. 2009b). Hence, 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 addition of the spatial reactive spatial response to encounters with hyaenas is a first step towards a better understanding of the role of the predator hunting mode 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 emphasizes the limits of our knowledge exclusively based on GPS information regarding the biological context of the encounter (predator behaviour, predator group size, prey context). In large mammals, this calls for further studies on other pair of predator species with contrasting hunting modes covering a wide range of contexts to be able to draw general conclusions on the impact of the hunting mode on prey antipredator response as it has been done for invertebrate species.

### **Authors' contributions**

Marion Valeix and Simon Chamaillé-Jammes conceived and designed the study. Simon Chamaillé-Jammes, Antony Antonio, Hervé Fritz, Andrew Loveridge, David Macdonald and Stéphanie Périquet collected the data in the field or coordinated field data collection. Elise Say-Sallaz analysed the data. Elise Say-Sallaz, Marion Valeix and Simon Chamaillé interpreted the results. Elise Say-Sallaz and Marion Valeix drafted the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

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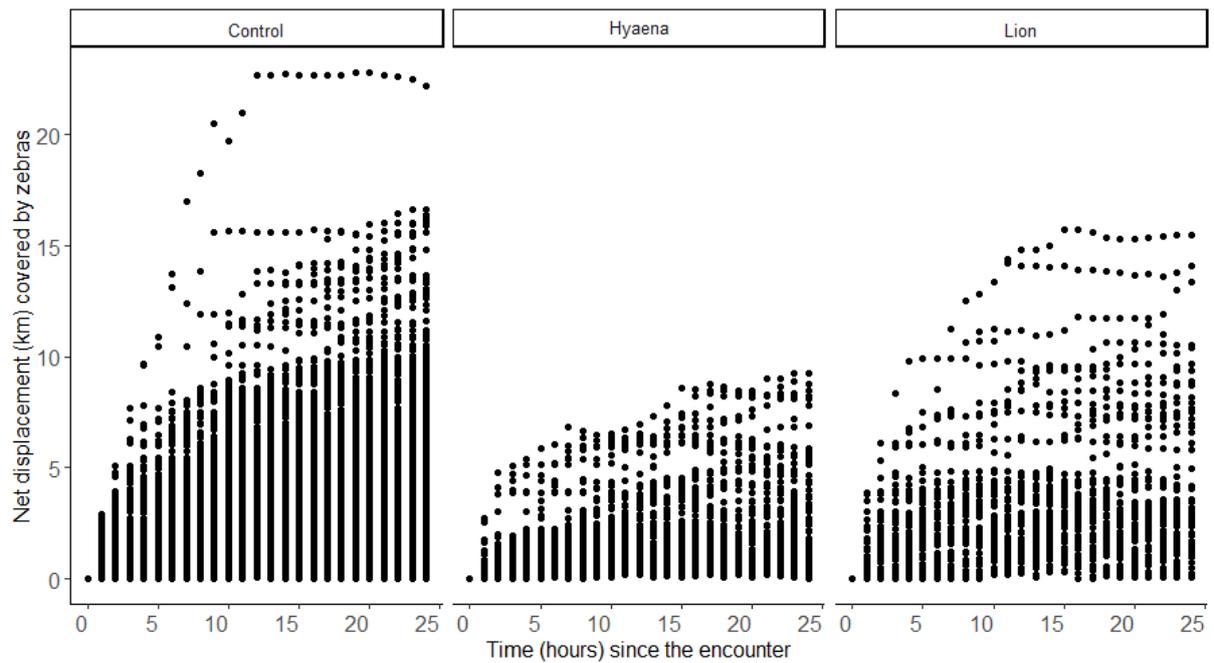
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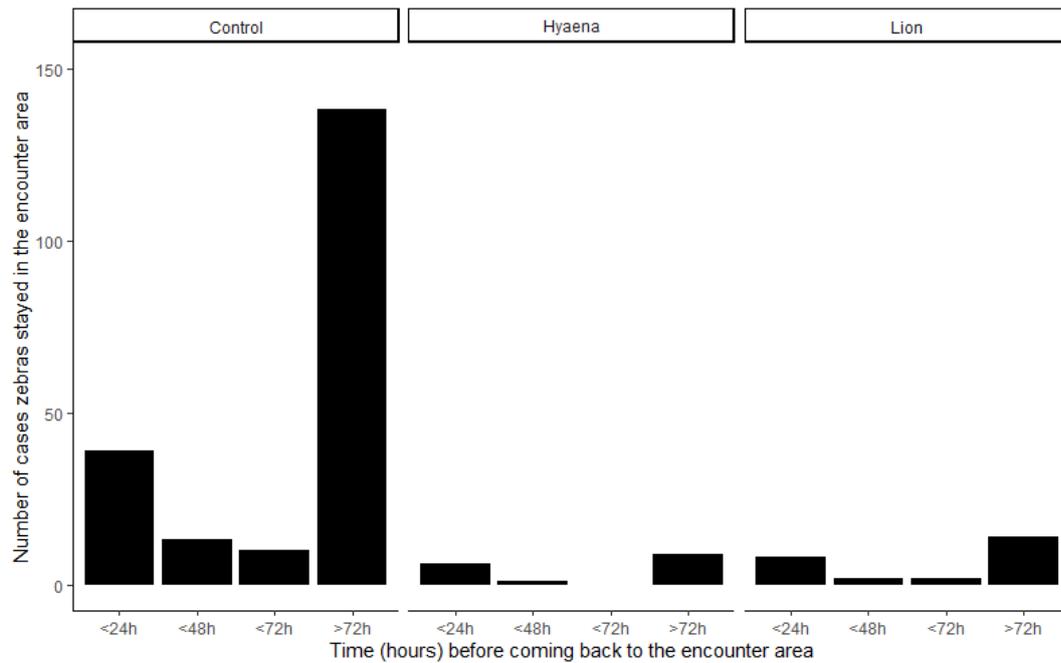
*Appendices***Appendix A.**

Net displacement (kilometers) covered by zebras according to the time since the encounter with a hyaena, a lion, or after a control locations).



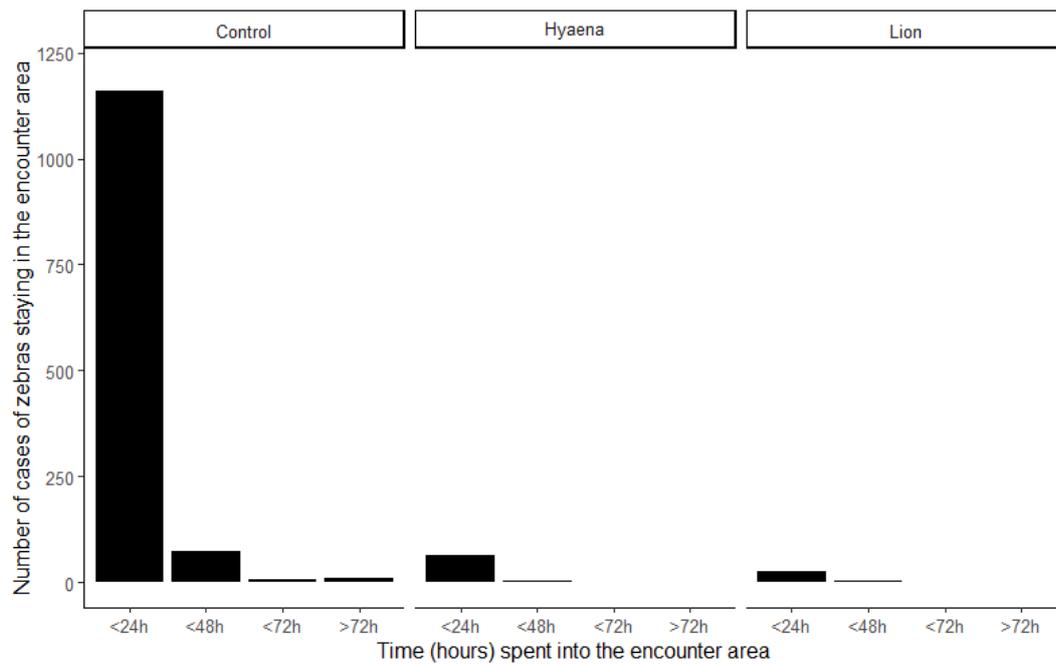
**Appendix B.**

Distribution of the time spent by zebras before coming back to an encounter area for zebras that fled immediately after an encounter with a lion, an encounter with a hyaena, and a control situation.



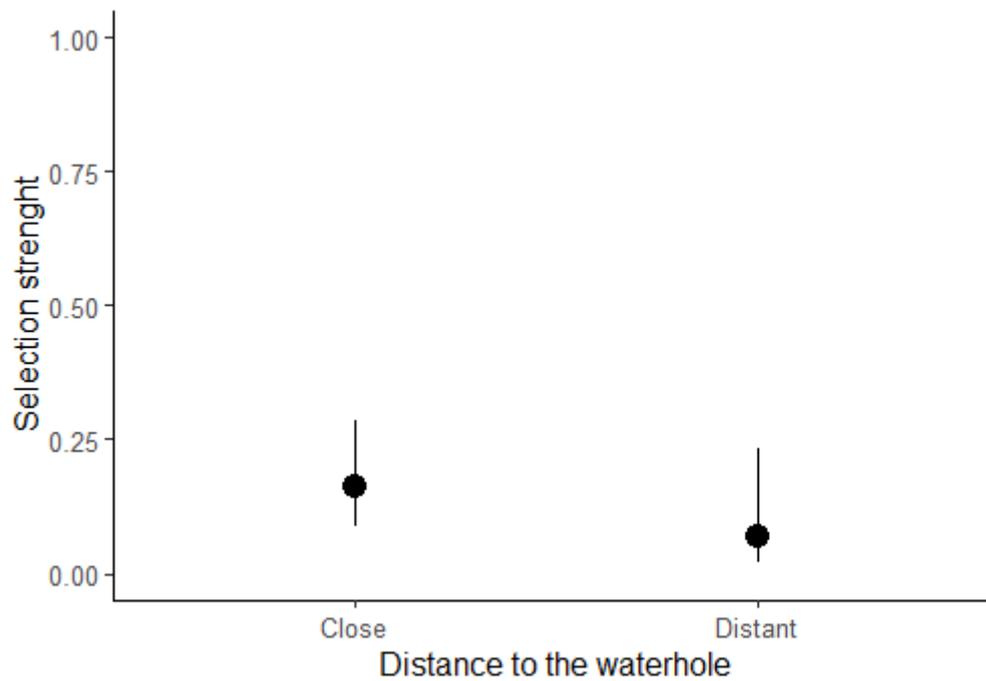
**Appendix C.**

Distributions of the time spent by zebras in the encounter area after an encounter with a lion, a hyaena and a control for zebras that did not initiate an “immediate flight” response after an encounter.



**Appendix D.**

Relative probability that an encounter between a zebra and a lion will occur (selection strength) according to the distance to water. The distance to water is represented by a discrete variable of two classes: 'Close' ( $\leq 1\text{km}$ ) and 'Distant' ( $> 1\text{km}$ ).



## Preamble

Initially, we had planned on conducting this experiment in a South-African reserve (Madikwe) from March to May 2020. The experimental protocol was conceived to study the immediate behavioural responses of both impalas (*Aepyceros melampus*) and zebras (*Equus quagga*) to predation risk simulated with playbacks from two predator species with contrasting hunting mode: the African lion (*Panthera leo*) and the spotted hyaena (*Crocuta crocuta*). Due to the coronavirus pandemic and the lockdown to which France was subjected to on March 16<sup>th</sup>, my South-African visa was cancelled, forcing me to interrupt the fieldwork for this experiment and fly back to France. Unfortunately, there was no possibility to go back to South Africa in order to implement the experiment during the whole of 2020. Therefore, we had to explore the possibility to relocate the experiment in France. This relocation of our fieldwork has obviously been associated with modification of the species used. The playback experiment was thus performed on roe deer (*Capreolus capreolus*) using playbacks from the Eurasian lynx (*Lynx lynx*) and the grey wolf (*Canis lupus*). After getting the required authorizations, we could implement the protocol by the end of August 2020. In order to expand and generalize our findings, we still aim to conduct the experiment, as initially planned, in the reserve of Madikwe during the year 2021. This would allow us working on two pairs of predators with contrasted hunting modes, with lions and lynxes as ambush predators, and wolves and hyaenas as cursorial predators, which appears as a great opportunity to test hypotheses on the role of the predator hunting mode in predator-prey interactions in large mammals.

# Chapter 3: When the sun goes down, which to fear the most? Sounds from the Eurasian lynx induce stronger antipredator responses than sounds from the grey wolf in roe deer

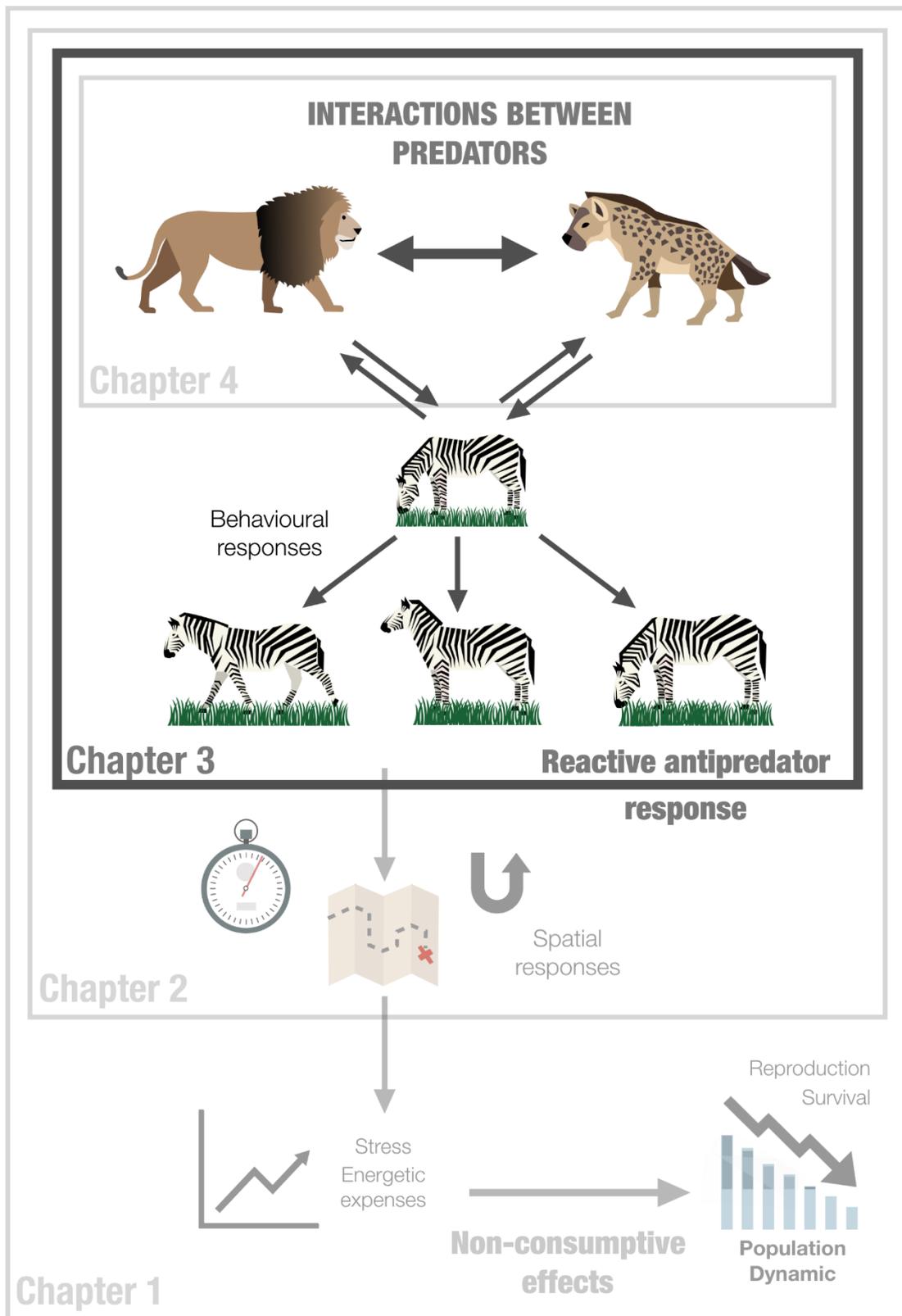


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**When the sun goes down, which to fear the most? Sounds from the Eurasian lynx induce stronger antipredator responses than sounds from the grey wolf in roe deer**

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**Abstract**

We implemented a playback experiment to test whether the predator hunting mode had an impact on the prey immediate behavioural response after a vocal stimulus of the presence of the predator. We predicted that the vocalization of an Eurasian lynx (*Lynx lynx*), which is an ambush predator, should induce a stronger behavioural response in roe deer (*Capreolus capreolus*), than that of the grey wolf (*Canis lupus*), a cursorial predator. At night, we simulated acute predation risk to prey with playbacks of both predators (and a control sound). We video-recorded and analysed the prey behavioural responses to the broadcasts. We found that roe deer abandoned more a site when a playback from lynx was broadcasted. They were more likely to be vigilant after a control, and more likely to run after a lynx playback. These results tend to support the hypothesis that ambush predators induce higher antipredator responses than cursorial ones.

## Introduction

Predation is one of the most important interspecific interactions that shape communities and one key challenge faced by prey lies in minimizing predation risk (Lima and Dill, 1990; Lima, 1998). Prey can manage predation risk by modifying their behaviour proactively, i.e. in response to an a priori assessment of the level of risk, or reactively, i.e. in response to an immediate threat. Examples of proactive antipredator responses include habitat selection depending on predation risk (Mao et al., 2005) and adjustment of vigilance in riskier habitats (Lima and Dill, 1990). The latter response often interacts with group size; indeed, as group size increases, collective vigilance and dilution of predation operate to reduce individual risk (Fitzgibbon, 1990; Hebblewhite & Pletscher, 2002). Examples of reactive antipredator responses include freezing (Croes et al., 2007; Takada et al., 2018), flying or fighting (Lingle & Pellis, 2002). Reactive antipredator responses have been far less studied than proactive antipredator responses in large carnivores-ungulates systems (Say-Sallaz et al., 2019). To assess an immediate predation risk, prey rely on direct cues, such as visual ones (Arteaga-Torres et al., 2020), or on indirect cues, such as olfactory cues (van der Meer et al., 2012; Bytheway, Carthey and Banks, 2013) or acoustic cues (Hettena et al., 2014). Although predators are usually quiet when they hunt, acoustic cues reliably predict their presence and thus an associated potential predation risk. Several studies indeed revealed that acoustic cues from predators trigger antipredator responses in prey (McComb et al., 2011; Suraci et al., 2016). Prey may be able to recognize their predator vocalization from birth even without having ecological experience of this predator (Hettena et al., 2014) or may learn discriminating predator sounds through direct interactions with the predator (Gil-da-Costa et al., 2003) but also by observing conspecifics (Barati & McDonald, 2017) or heterospecifics (Magrath et al., 2015; Meise et al., 2018). Literature reviews of playback experiments conducted to study predator acoustic recognition revealed that most prey species of birds and mammals respond to vocalizations of their

predators (Blumstein et al., 2008; Hettena et al. 2014). Although there are general acoustic characteristics to predatory sounds (Carthey & Blumstein, 2018), prey appear able to discriminate between different predator species (Manser, 2001).

Several factors affect the perception of fear in animals, including predator traits (Stankowich & Blumstein, 2005). In invertebrates, general rules about the role of the predator hunting mode have emerged, with sit-and-wait and sit-and-pursue predators causing stronger antipredator responses and non-consumptive effects than active predators (Preisser et al. 2007; Schmitz, 2008; Miller et al., 2014). In terrestrial large mammals, the hypothesis that ambush predators (i.e. predators that rely on concealment to hunt by surprise prey moving within a chasing distance; this is the case of most Felids, it is a strategy that resemble wait strategies for invertebrate species ) and cursorial predators (i.e. predators that can chase down their prey over long distances if needed, close to active predator in invertebrate species; this is the case of most Canids) may lead to antipredator responses that differ in nature and strength has thus emerged (Thaker et al., 2011; Creel et al., 2014; Makin et al., 2017). Only a few studies have assessed the effect of predator hunting mode on both the nature and strength of prey antipredator behaviours in large mammals. Therefore, there is a need to increase the number of studies considering different predator species characterised by contrasting hunting modes to be able to draw general conclusions.

In this sense, recent literature reviews on the non-consumptive effects of predation in large mammalian systems highlighted the lack of studies with several predator species to assess the role of predator traits in these effects (Montgomery et al., 2019; Say-Sallaz et al., 2019). Here, we studied the reactive antipredator response of a large mammalian prey species, the roe deer (*Capreolus capreolus*), to acoustic cues of the presence of two predator species characterised by contrasting hunting modes (the grey wolf (*Canis lupus*) -a cursorial predator- and the Eurasian lynx (*Lynx lynx*) -an ambush predator-). We performed a playback experiment

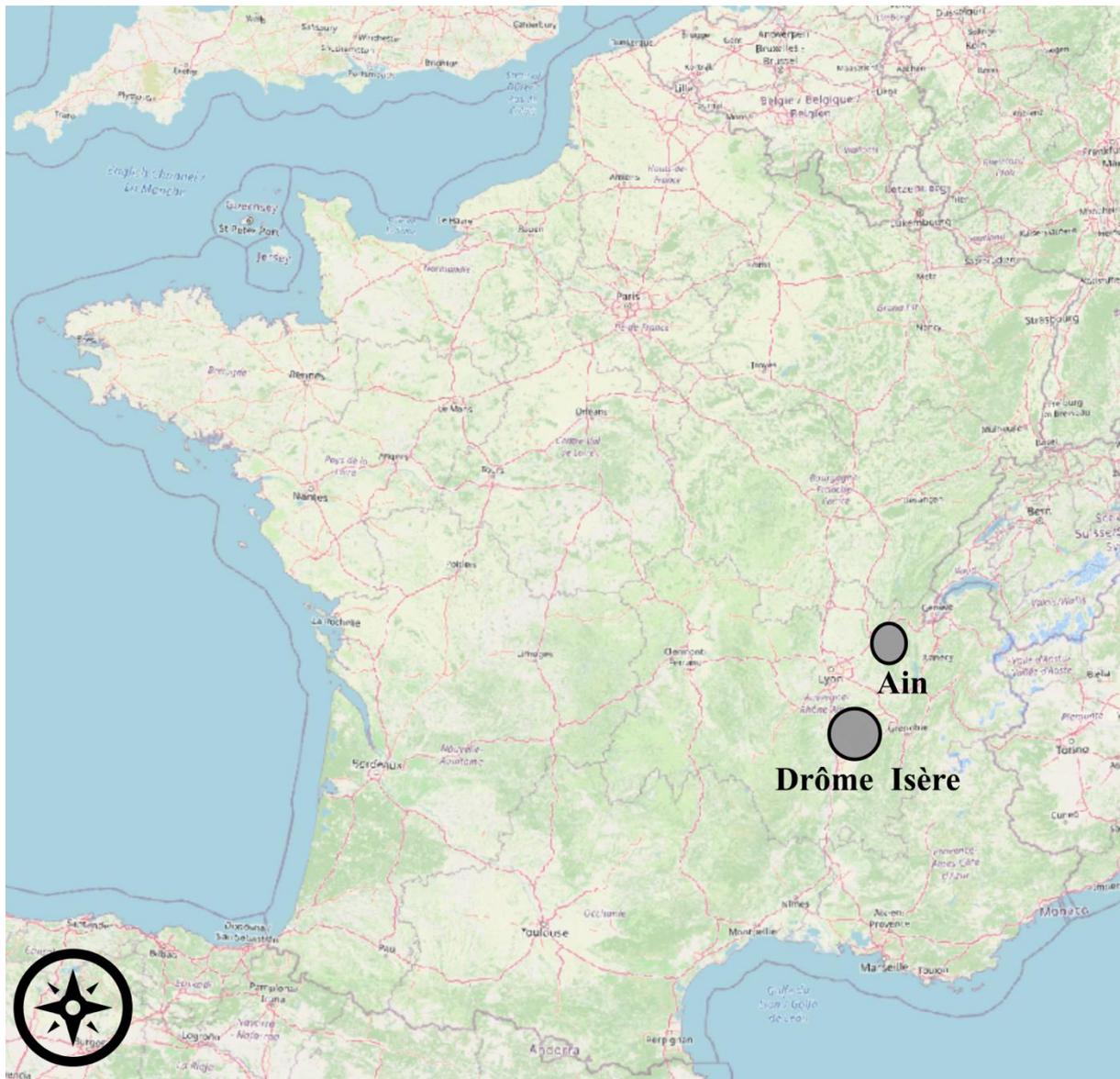
to test the hypothesis that ambush predators trigger stronger antipredator responses than cursorial predators in large mammals. Since lynx are ambush predators, we expected that roe deer would express stronger antipredator responses to the sound of a lynx than to the sound of a wolf in terms of type of response, duration of the response, and reaction time. We also expected roe deer to take more time to return to a baseline behaviour after the simulated presence of a lynx. The playback experiment was carried out at night, i.e. when predation risk is the highest, which contrasts with most studies done during the day or crepuscular times for convenience reasons.

## **Material and Methods**

### *Study sites*

This study was carried out from late August 2020 to early October 2020 in two French sites characterised by a high abundance of roe deer but contrasted in terms of presence of lynx and wolves. The first study site is situated in the department of Ain (site ‘Ain’ hereafter; Fig. 1). It is located in the Jura Mountains (average altitude: 800m) around the villages of Evosges (45°57’37.4”N, 5°29’49.4”E) and Hauteville-Lompnes (45°58’32.9”N, 5°35’56.9”E), and covers approximately 132 km<sup>2</sup>. The site is in the area of permanent occurrence of lynx but not of wolf (Chapron et al. 2014). The landscape is forged by past and present agricultural activities even though there are not intense, and there is an alternation between patches of forest and open fields used for crops and livestock. The area is characterised with a temperate climate. The second study site is situated at the border between the departments of Isère and Drôme (site ‘Drôme-Isère’ hereafter; Fig. 1). It is located at the foot of the Vercors Mountain range (altitude varies between 350m and 500m) and covers approximately 200 km around the villages le Grand-Serre (45°16’0.2”N, 5°6’18.5”E) and Montrigaud (45°13’6.9”N, 5°7’57.1”E). It is in the area of permanent occurrence of wolf but not of lynx (Chapron et al. 2014). The landscape

is similar to the first site with an alternation of patches of forests and fields for crops and livestock.



**Figure 1:** Map of France with the location (in grey) of the “Ain” study site and the “Drôme – Isère” study site.

### ***Sound track preparation***

In the two study sites, we used 3 playback treatments: sounds of wolf, sounds of lynx and roaring of red deer (*Cervus elaphus*) as control sounds. Red deer is common in the two study sites, its roaring activity is very common in September and October. Hence, we used such

a signal as a control signal, as it does not represent any predation value for roe deer and does not pose a threat for the roe deer. Three different recordings were used for each treatment in order to reduce pseudo-replication effect. Concerning the wolf, signals were recorded in South of France. Signals of Eurasian lynx were recorded in France. Red deer roaring are from the “Guide of European mammals’ sounds”.

Each of these natural signals was used to build a WAV soundtrack of 30 sec (frequency sampling 44100Hz) with the same signal length (12sec), i.e. the same stimulation of the tested animal. In addition, we adjusted the amplitude of the soundtrack to get the same value at 1m of the loudspeaker ( $90.3 \text{ dB (c)} \pm 1.67 \text{ dB}$ , mean  $\pm$  SD, Lutron SL-4001, C weighting, slow settings, re: 20 m Pa).

### ***Test procedure***

Tests were performed on calm nights with a low background noise level to ensure signal discrimination ( $45 \text{ dB (c)} \pm 3.86$ , mean  $\pm$  SD; Lutron SL-4001, C weighting, slow settings). We drove along roads throughout the study sites at night, from 21h00 (after sunset) to 3h00, to locate roe deer. Roe deer were always found in open areas (clearings or fields). As soon as we encountered a roe deer group, we stopped the car on average at  $95\text{m} \pm 40\text{m}$  (mean  $\pm$  SD) from the group and started filming a focal individual chosen randomly. We always chose an adult within the group, but the visibility was not good enough to discriminate between males and females. To do so, we used thermal vision binoculars adapted for night vision (Accolade LRF XQ38). After 30 seconds (to allow roe deer to settle down and return to their activity if disturbed by our arrival), we broadcasted one of the 9 soundtracks (3 per treatment: wolf, lynx or red deer) chosen randomly. We used an amplifier loudspeaker connected to a digital playback device (Bose revolve plus connected to a Sony NWA45). In the same night, we left a minimum of 250 m between two consecutive playback experiments to minimize the risk of filming a focal

roe deer that would have already heard the previous playback. Preliminary tests with loudspeaker showed that from 200m the sound decreased in audibility. Additionally, to avoid habituation, we waited at least 96hours before coming back to a zone to perform the experiment again. We managed to perform an equal number ( $n = 45$ ) of playbacks in the two sites, and for each treatment ( $n = 15$ ) (Table 1).

Table 1: Number of trials for each playback treatment played to roe deer in each study site.

<b>Sound</b>	<b>Ain</b>	<b>Drôme - Isère</b>	<b>Total</b>
<b>Lynx</b>	5	5	<b>30</b>
	5	5	
	5	5	
<b>Wolf</b>	5	5	<b>30</b>
	5	5	
	5	5	
<b>Red deer</b>	5	5	<b>30</b>
	5	5	
	5	5	
<b>Total</b>	<b>45</b>	<b>45</b>	<b>90</b>

We filmed the roe deer behaviour for 30 seconds before the playback and for 3 minutes after the playback sound started to be broadcasted. We analysed the videos using BORIS software (Friard & Gamba, 2016). We extracted for the whole playback sequence (before, during and after the playback sound) the time and occurrence of the different roe deer behaviours: (i) abandon, i.e. departure from the trial area; (ii) induced vigilance, i.e. the animal is standing up still with its ears facing forward - this behaviour is exclusive of any other behaviour (Blanchard & Fritz, 2007) -; (iii) routine vigilance, i.e. the individual is scanning the environment with its head up but can express another behaviour, such as chewing or moving (Blanchard & Fritz, 2007); (iv) running; (v) walking; (vi) bunching, i.e. animals that were spaced (and sometimes not even framed in the binoculars) get closer; (vii) foraging; (viii) ruminating, usually laying down and chewing; and (ix) other behaviours, such as standing up not being vigilant, grooming, urinating and resting. Abandon, induced vigilance, induced moving and grouping are classical antipredator responses with abandon being the strongest

response. For the rest of the analyses, we focused on one baseline behaviour, foraging, which was the most commonly observed, and three antipredator responses: abandon of the trial area, induced vigilance and running; which were the most common responses recorded.

### ***Environmental and biological variables***

In addition to behavioural data, time and geographic coordinates, we recorded contextual variables for each playback test such as the distance between us and the focal individual, the roe deer group size at the beginning of the trial (we defined a ten body length threshold to define a group), the presence of juveniles, the presence of individuals from other species, the distance between the focal individual and the closest cover (i.e. closest forest edge), the height of the grass (foot, shoulder or back height), light intensity (three classes based on our perception: low is when the night is very dark as well as the sky color, medium for when the luminosity allow to see more details and the sky color is lighter, and high when it is the full moon and the visibility is excellent), wind intensity (based on our perception: non for when there is now wind, low when there is a breeze and both leaves and branches in the vegetation are moving, medium when the breeze is turning into wind and the vegetation is moved a lot, high when the wind is stronger, the vegetation is moved a lot more and the sound of the wind is high as well), and if it was raining or not.

### ***Analyses***

All analyses were performed with R (R core team, 2021).

*1. Nature of the behavioural response* – For each antipredator response (abandon, induced vigilance, and running), we fitted a Generalized Mixed Model (GLMM) with a logit link function, a binomial distribution for the error term, and the nature of the playback sound (lynx,

wolf, red deer) as the explanatory variable. We used the package lme4 to estimate parameters and stats package to estimate confidence intervals (Bates et al., 2015).

2. *Duration of the behavioural response* – We assessed whether the nature of the auditory stimulus (lynx, wolf, red deer) affected the duration of behavioural response for induced vigilance and running. Additionally, we assessed whether the auditory stimulus affected the most common baseline behaviour, i.e. foraging. We used a 18s interval because the trials did not last exactly the same time ( $\pm 10$  sec) and calculated the proportion of time an individual spent doing a specific behaviour (induced vigilance, running, and foraging). We calculated these proportions before and after the stimulus started and calculated the difference between the two for each trial. Then, we fitted a linear mixed model and performed a pairwise comparison test. Finally, we assessed contrasts between the stimuli with the Tukey method using the lsmeans package (Lenth, 2016).

3. *Reaction time* - We assessed if the nature of the playback sound had an influence on the prey's reaction time before (i) expressing an antipredator response and (ii) returning to its baseline behaviour. We fitted GLMM with a log link function and a Poisson distribution for the error term using the lme4 package. The response variable is the time between the start of the playback and the moment the focal individual expressed an antipredator response or a baseline behaviour. The explanatory variable is the playback sound. We tested for overdispersion and zero inflation with the Dharma package. When zero inflation was detected, which was the case for the induced vigilance and foraging, we fitted a GLMM using maximum likelihood estimations via a Template Model Builder (glmmTMB package). If there was no zero inflation, we used the package lme4 to estimate parameters and stats package to estimate 95% confidence intervals.

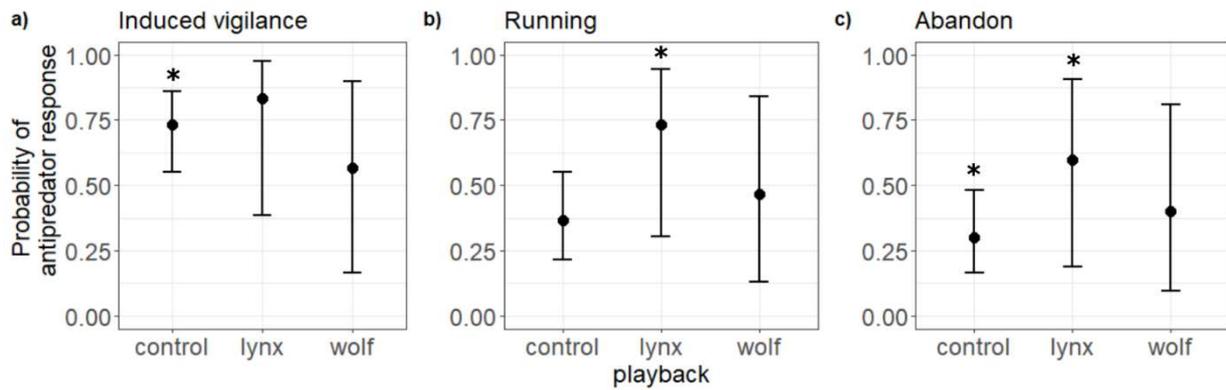
## Results

### 1. Nature of the behavioural answer

Roe deer expressed induced vigilance mainly after the control playback (Fig. 2 a,  $\beta=0.73$ , CI=0.55,0.86; Table 2). They mainly ran after a lynx playback (Fig. 2 b,  $\beta=0.73$ , CI=0.30,0.95; Table 2). Finally, roe deer were twice as likely to leave the trial area after a lynx playback than after a control playback (lynx playback, Fig. 2 c,  $\beta=0.60$ , CI=0.19,0.90; control playback  $\beta=0.30$ , CI=0.16,0.48; Table 2).

Table 2: Estimates of the three GLMM (Generalized Linear Mixed Models) that link the nature of the antipredator behavioural response (i.e. induced vigilance, running and abandon) to the nature of the playback sound roe deer has been exposed to.

	<i>Playback</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(&gt; z )</i>	<i>95% CI min</i>	<i>95% CI max</i>
<i>Induced vigilance</i>	<b>Control (intercept)</b>	<b>1.01</b>	<b>0.41</b>	<b>2.45</b>	<b>0.01</b>	<b>0.20</b>	<b>1.82</b>
	wolf	-0.74	0.55	-1.34	0.18	-1.83	0.34
	lynx	0.60	0.64	0.93	0.35	-0.66	1.85
<i>Running</i>	Control (intercept)	-0.55	0.38	-1.44	0.15	-1.29	0.20
	wolf	0.41	0.53	0.78	0.43	-0.62	1.45
	<b>lynx</b>	<b>1.56</b>	<b>0.56</b>	<b>2.78</b>	<b>0.01</b>	<b>0.46</b>	<b>2.66</b>
<i>Abandon</i>	<b>Control (intercept)</b>	<b>-0.85</b>	<b>0.40</b>	<b>-2.13</b>	<b>0.03</b>	<b>-1.63</b>	<b>-0.07</b>
	wolf	0.44	0.55	0.81	0.42	-0.63	1.51
	<b>lynx</b>	<b>1.25</b>	<b>0.55</b>	<b>2.30</b>	<b>0.02</b>	<b>0.18</b>	<b>2.32</b>



**Figure 2:** Probability of roe deer expressing a) induced vigilance, b) running and c) abandon (leaving of the trial area) according to the predator playback they have been exposed to. Vertical bars represent 95% confidence intervals and the star is for significant values.

### 2. Duration of the behavioural response

The nature of the playback sound did not affect the mean duration differences of both antipredator responses (running and induced vigilance) and the foraging behaviour (Table 3).

All the mean differences in behaviour duration oscillated around 0 (Appendix A).

Table 3: Estimates of the three contrasts comparisons of the mean difference in proportion of time spent in a behaviour before and after each playback sound (lynx, wolf, control).

	<i>contrast</i>	<i>Estimate</i>	<i>SE</i>	<i>df</i>	<i>t.ratio</i>	<i>p.value</i>
<i>Running</i>	control - wolf	-0.02	0.04	87.00	-0.39	0.92
	control - lynx	-0.08	0.04	87.00	-1.89	0.15
	wolf - lynx	-0.06	0.04	87.00	-1.50	0.30
<i>Induced vigilance</i>	control - wolf	0.00	0.10	87.00	-0.01	1.00
	control - lynx	-0.07	0.10	87.00	-0.71	0.76
	wolf - lynx	-0.07	0.10	87.00	-0.70	0.76
<i>Foraging</i>	control - wolf	-0.06	0.12	33.98	-0.52	0.86
	control - lynx	0.17	0.11	32.90	1.52	0.29
	wolf - lynx	0.23	0.13	33.81	1.83	0.18

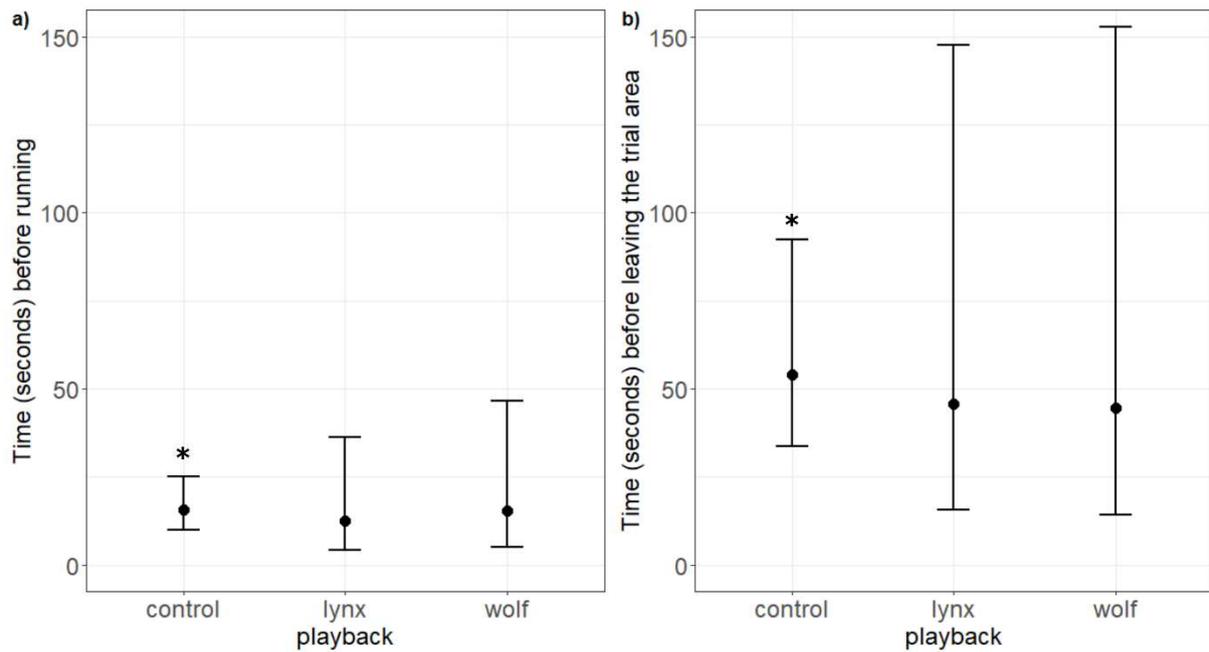
### 3. Reaction time

The nature of the playback sound did not affect the time an individual took before expressing induced vigilance (Table 4). However, roe deer waited longer to run after a playback if it was the control sound (Table 4; Fig. 3 a). They also waited longer to leave the trial area after the

control sound (Table 4; Fig. 3 b). The nature of the playback sound did not affect the time before roe deer returned to foraging activities (Table 4). The mean time individuals waited before returning to foraging is 52.7 ( $\pm$  57.1 SD) seconds.

Table 4: Estimates of the GLMM that link the time (in seconds) elapsed between the auditory stimulus and the initiation of the antipredator response (i.e. induced vigilance, running and abandon) by roe deer or the resuming to foraging activities to the nature of the playback sound roe deer have been exposed to.

	<i>Playback</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>Pr(&gt; z )</i>	<i>95% CI min</i>	<i>95% CI max</i>
<i>Induced vigilance</i>	Control (intercept)	-0.32	0.44	-0.74	0.46	-1.18	0.53
	wolf	-0.20	0.64	-0.31	0.76	-1.44	1.05
	lynx	0.25	0.59	0.42	0.68	-0.91	1.41
<i>Running</i>	<b>Control (intercept)</b>	<b>2.75</b>	<b>0.24</b>	<b>11.47</b>	<b>1.83e-30</b>	<b>2.28</b>	<b>3.22</b>
	wolf	-0.02	0.33	-0.06	0.95	-0.66	0.62
	lynx	-0.22	0.30	-0.74	0.46	-0.82	0.37
<i>Abandon</i>	<b>Control (intercept)</b>	<b>3.99</b>	<b>0.26</b>	<b>15.44</b>	<b>8.87e-54</b>	<b>3.51</b>	<b>4.52</b>
	wolf	-0.19	0.33	-0.58	0.57	-0.86	0.51
	lynx	-0.17	0.32	-0.54	0.59	-0.77	0.47
<i>Foraging</i>	Control (intercept)	1.50	0.98	1.53	0.13	-0.43	3.43
	wolf	0.31	1.56	0.20	0.84	-2.75	3.37
	lynx	-0.13	1.59	-0.08	0.93	-3.26	2.99



**Figure 3:** (a) Time (in seconds) before roe deer individuals start running according to the predator sound they have been exposed to and (b) Time (in seconds) before roe deer individuals leave the trial area according to the predator playback they have been exposed to. Vertical bars represent 95% confidence intervals and the star is for significant values.

## Discussion

This study revealed that (i) our presence was probably considered as a disturbance by roe deer, as they showed induced vigilance for similar duration before and after the broadcasting of the playback sound; (ii) in spite of our presence, roe deer responded to perceived predation risk induced by the playbacks of predator sounds in a different manner than after the control sound, with running and abandon being characteristic responses after a predator sound; and (iii) roe deer displayed the strongest antipredator response, i.e. abandoned the trial area, after the broadcasting of a lynx sound, supporting the hypothesis that ambush predators may induce stronger antipredator responses in prey.

First, the difference in the proportions of time spent being vigilant, running or foraging between before and after the playback were not significantly different from 0. This may arise

from either an absence of response to the auditory stimuli, or the presence of a disturbance before the stimuli. Because roe deer responded to the playback of predatory sound (see below), we believe this result means that a thirty-second period before the playback is probably too short for roe deer to accommodate to our presence. This is consistent with the fact that after a playback, roe deer took on average 52 seconds to resume to foraging. Our experiment started at the end of August and finished beginning of October. This period was chosen to maximize our chance of observing roe deer in open areas (as they preferentially use open areas during specific times of the year) but in periods when they are not intensively subjected to human hunting activities. The hunting season started in mid-September in the two study sites. Even though the first weeks of the hunting season are characterised by very low levels of off-takes, this may explain why animals were highly vigilant in response to our presence. Human disturbance can indeed have similar effect on animals than predation risk (Frid & Dill, 2002) and the effects of people on animal behaviour can outweigh the effects of predation risk induced by wild top predators (Clinchy et al., 2016). For roe deer specifically, it has been shown that they tend to select open landscapes at night and closed landscapes (habitat refuge for them) during the day in order to avoid human activities (Bonnot et al., 2012). Furthermore, roe deer have higher stress hormone levels when they are closer to human infrastructures (Carbillet et al., 2020). Hunting activity obviously accentuates animal behaviour to avoid humans. Roe deer are generally more vigilant during the hunting season (Benhaiem et al., 2008), and tend to select open habitats with high crops even less during the day even though these habitats often provide good resources (food and cover) for them (Bonnot et al., 2012). For future research, we would advise to wait for a longer period of time before starting the playback in order to let roe deer accommodate to human presence as much as possible and to also perform similar experiments in areas where they are not hunted.

Even though our presence was perceived as a disturbance, the experiment highlighted that roe deer responded to predation risk induced by playbacks of natural predators' sounds differently than to a non-predatory sound. Indeed, roe deer mainly ran and abandoned the area after a predatory sound, whereas they mainly invested in induced vigilance after a control playback. Abandon of the trial area is considered the most intense antipredator response. Our study showed that roe deer expressed the most intense antipredator behaviour after hearing a lynx or a wolf sound, whereas they invested in the least intense antipredator response (vigilance) after hearing the roaring of a red deer. Additionally, roe deer, when they displayed a "run" or "abandon" response, did it quicker after a predatory sound than after a control sound. In the case of the red deer sound, roe deer were vigilant most of the time right after playback and needed time to assess the risk of the perturbation to adjust their behaviour afterwards. It supports the FEAR hypothesis (Flush Early to Avoid the Rush, Blumstein, 2010) that states that when a threat is detected, prey will tend fly or flush and leave the area in order to avoid the risk posed by the threat. Studies on flight initiation distance on roe deer support this hypothesis (Bonnot et al., 2017).

Both lynx and wolf were absent from the French territory for nearly a century. Lynx went extinct in most of the country by the end of the 19<sup>th</sup> century (Kratochvil, 1968) and wolves went extinct in France by the beginning of the 20<sup>th</sup> century with the last wolf population seen in 1934 (Mech & Boitoni, 2004). Lynx were reintroduced in the 1970s in the Jura and Vosges Mountains (Breitenmoster et al., 2000) and wolves recolonized the French Alps and Vercors in the late 1990's-early 2000's (Louvrier et al., 2018). Nowadays, roe deer in the Ain are in the area of permanent occurrence of lynx but not of wolf (Chapron et al. 2014), and therefore exposed to regular predation by lynx but only anecdotally by wolf (a lone wolf individual was reported for the first time a few years ago and was apparently only passing through the area). Contrarily, in the Drôme and Isere, roe deer populations are in the area of permanent occurrence

of wolf but not of lynx (Chapron et al. 2014) and therefore exposed to regular predation by wolves but only anecdotally by lynx. However, roe deer from both study sites seemed to perceive both predator playbacks as predation risk. This is consistent with the literature, where it has been shown that prey are able to react to predator species even the ones that they have not been exposed to. For instance, a mule deer population in the Rocky Mountains (USA) recognized and reacted to wolf playbacks even though wolves had been extinct from that area since the beginning of the 20<sup>th</sup> century (Hettena, Munoz and Blumstein, 2014). Black-tailed deer introduced on an island with no wolf at the end of the 19<sup>th</sup> century and not exposed to wolves since then, still responded to wolf predation risk at the beginning of the 21<sup>st</sup> century (Chamaillé-Jammes et al., 2014).

Not only did roe deer respond to predation risk induced by predator playbacks differently from other playback sounds, they also expressed stronger behavioural antipredator responses to lynx playbacks than to wolf playbacks. The main result from this work is that roe deer were more likely to run and abandon the trial area after a lynx playback than after either a wolf or a red deer playback. Lynx being an ambush predator, its success to catch a prey relies on surprise and its capacity to go undetected before catching a prey (Kuijper et al., 2015). Further, ambush predators, such as lynx, do not run for long distances after their prey, which outcompete them in terms of speed over long distances. Being in an open landscape and leaving an area as soon as an ambush predator is detected seems to be an excellent strategy to reduce predation risk imposed by ambush predators, such as lynx. This would not be as efficient with wolves that are cursorial predators and do not rely on surprise effect to catch their prey. For other cursorial predators, it has been shown that they do have a better success in catching their prey when these ones flee when they detect the predator (Mills 1990). With roe deer being more likely to run and leave the trial area when exposed to lynx auditory cues, our results support the hypothesis that lynx predation risk induces stronger antipredator reactive responses than wolf

predation risk and are also consistent with the hypothesis that ambush predators induce stronger antipredator responses than cursorial ones.

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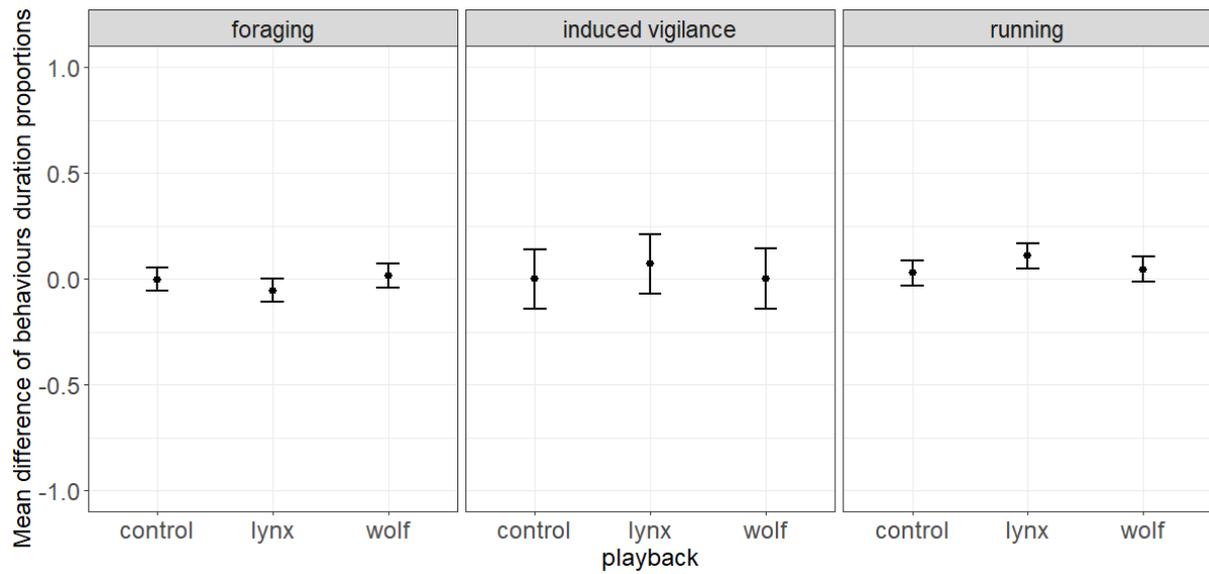
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## Appendices

### Appendix A

Mean differences of behaviours' proportion of duration before and after a playback, for the antipredator response induced vigilance and running and the baseline behaviour of foraging.

Vertical bars represent 95% confidence intervals.

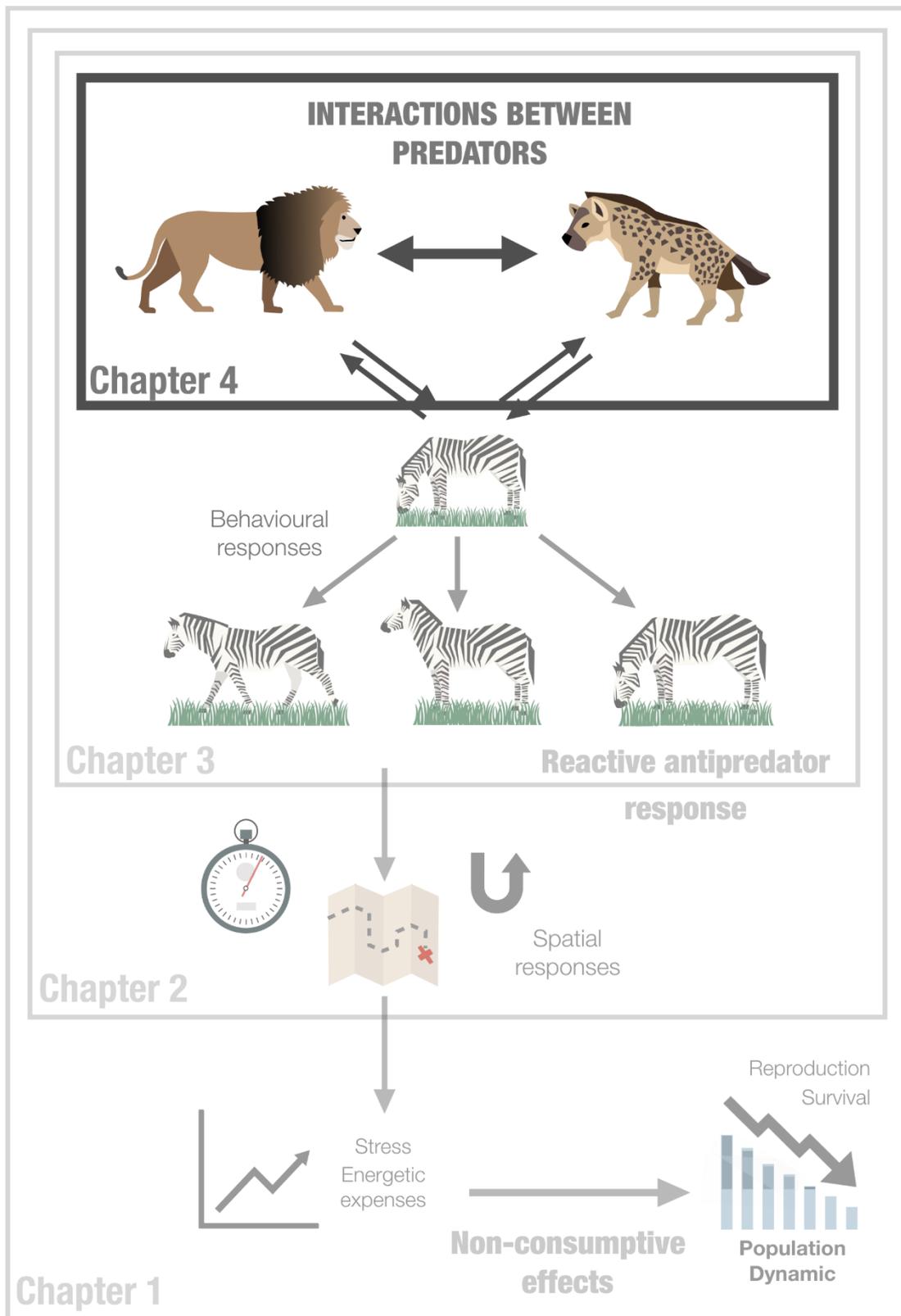


## Chapter 4: How do large carnivores coexist in savanna ecosystems? An analysis of their spatio-temporal dynamics



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**Status:** in preparation to be submitted to Oikos



## **How do large carnivores coexist in savanna ecosystems? An analysis of their spatio-temporal dynamics**

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**Abstract:**

Coexistence of sympatric large carnivore species is common in many ecosystems worldwide. On the one hand, the potential for competitive interactions, ranging from kleptoparasitism to intraguild predation, is high, so carnivore species are expected to avoid each other. On the other hand, positive interactions such as scavenging opportunities, also exist and may explain the attraction of some carnivores to others. In this study, we assessed the patterns of spatio-temporal co-occurrence at different scales of the three sympatric and most common large carnivores of African savannas: the spotted hyaena (*Crocuta crocuta*), the African lion (*Panthera leo*) and the leopard (*Panthera pardus*). We used data from an extended camera-trapping survey (14316 camera trap days; 1669 detection pictures of the study large carnivores) covering the ~ 15 000 km<sup>2</sup> of Hwange National Park, Zimbabwe, which is one of the largest African protected area and a key ecosystem of the world's largest trans-frontier conservation area (Kavango-Zambezi). We assessed the overlap in pattern of diel activities, the general spatial overlap and finer scale spatio-temporal co-occurrence patterns between the three species. All three species have an important overlap in their diel activity pattern as expected. Lions and leopards do not co-occur spatially very often (in one fourth of the camera trap stations). Time-to-event analyses suggest that carnivores tend to use areas previously used by another carnivore species closely in time (in the 2 hours following the use of the area by the other species) but also during the consecutive nights, which led us to lay the “follower hypothesis” and the “delayed exploration hypothesis” respectively. We discussed the potential underlying interspecific interactions that take place between species such as kleptoparasitism, scavenging opportunities, interference competition and indirect interactions through prey catchability for instance.

## Introduction

Coexistence of competing species arises from diet, spatial or temporal partitioning (MacArthur & Pianka, 1966), which allows a decrease in competition intensity (Schoener, 1974). Resource-based niche differentiation reduces exploitation competition and allows coexistence in a variety of taxa from amphibians (Schiesari et al., 2009) to mammalian carnivores (Bonesi, Chanin and Macdonald, 2004; Mitchell & Banks, 2005; Vanak & Gompper, 2009). For species foraging on the same resource item, partitioning can occur at a very fine scale, with two insect species feeding on different parts of a same plant for instance (Kaplan & Denno, 2007). Spatial partitioning happens when species consuming the same resources (and possibly having the same diel activity pattern) use different areas of the landscape or different habitats in order to decrease interference competition (Ziv et al., 1993; LeFlore et al., 2019). Temporal partitioning occurs when species using the same resources (and possibly living in the same area) are active at different times, hence reducing interference competition (Kotler et al., 1993; Valeix et al. 2007; Rasphone, Kamler and Macdonald, 2020). However, species may not totally avoid (in space or time) competing species, as this may prevent them from accessing valuable resources such that complete avoidance would result in substantial foraging costs. Spatio-temporal avoidance can thus occur at fine scales. For instance, species may adjust their activity within the day to avoid a high predation risk (Smith et al., 2019) or a high risk of encounter with a larger competitor in the predator guild (Dröge et al., 2016; Vanak et al., 2013). Sometimes this can happen at even finer scales (hour or less) and these reactive adjustments to avoid negative interspecific interactions are likely to be less costly than long-term avoidance and hence more common (Broekhuis et al., 2013; Swanson et al., 2016).

Carnivore species are a good model to study niche partitioning, as they potentially can exploit very similar niches (Caro & Stoner, 2003). Competitive interactions between these species can be very intense, ranging from kleptoparasitism (Gorman et al. 1998; Scantlebury et

al. 2014; Balme et al. 2017) to intraguild predation that is very common among predator species (Palomares & Caro, 1999; Donadio & Buskirk, 2006). However, interactions among carnivores can also be positive, illustrating cases of intraguild facilitation. Positive intraguild interactions have been clearly overlooked in ecological studies, but recently gained increased recognition in community ecology (Bruno, Stachowicz & Bertness, 2003; Prugh & Sivy, 2020). The most documented positive interactions in carnivores are scavenging opportunities, whereby one carnivore leaves a carcass after killing it and feeding on it, which provides carrion for other, often smaller species (Wilmers et al., 2003; Sivy et al., 2017a). Other subtler and indirect forms of positive interactions can also occur. This is the case when a prey, by avoiding areas where the risk of predation by one predator is important, becomes more vulnerable to another predator. For example, caribous (*Rangifer tarandus*) that avoid wolf (*Canis lupus*) predation risk become more exposed to black bear (*Ursus americanus*) predation risk in Canada (Leblond et al., 2016). Facilitation mechanisms can also be an explanation of species coexistence. Patterns of avoidance/attraction between coexisting carnivore species are thus likely to emerge from a balance between spatio-temporal partitioning and facilitation. There is a need to integrate negative and positive interactions in our understanding of the functioning of communities of sympatric carnivores (Prugh & Sivy, 2020). Further, the relative importance of the different interactions linking two species can be affected by environmental conditions and change temporally (Périquet et al., 2021). Scale is important to consider when looking at these coexistence mechanisms, as illustrated by the fatal attraction hypothesis (Sivy et al., 2017b). In this hypothesis, the presence of carcasses provided by large carnivores attracts mesocarnivores at a local scale, suggesting facilitation, whereas the probability of interference competition and aggressive interactions, up to intraguild predation, increases near the carcasses, which may ultimately lead to species suppression at the landscape scale (Sivy et al., 2017b). Temporal scale also can play a role and has to be considered (Cusack et al., 2017; Rafiq et al., 2020). In

predation-prey interactions studies, spatial and temporal niche axes are thought to interact, with prey being more vigilant in places that are riskier (assessed on large spatial scale) only at riskier times, i.e. when predation risk is higher on the short term (Dröge et al., 2017). Considering both axes at different scales is highly recommended when studying interspecific interactions (Prugh et al., 2019).

Camera trap data are increasingly being used to characterise the patterns of spatio-temporal activities in sympatric species to ultimately infer or discuss underlying interspecific interactions (Burton et al., 2015). Here, we use camera trap data covering one of the largest protected area in Africa, Hwange National Park, Zimbabwe, to assess the spatio-temporal co-occurrence patterns of the three most common large carnivores of African savannas: the African lion (*Panthera leo*), the spotted hyaena (*Crocuta crocuta*) and the leopard (*Panthera pardus*). We first study the diel activity patterns of these species. Diel activity patterns are informative but often large carnivores are nocturnal and will thus show little partitioning in activity patterns (Cozzi et al. 2012). We thus further investigate the general spatial co-occurrence patterns, as diel activity patterns disregard the spatial axis of the co-occurrence patterns. Finally, as interactions are likely to occur at local scales (e.g. Broekhuis et al. 2013), we assess whether the spatio-temporal activity patterns at fine scales can unveil these large carnivore interactions that allow them to coexist. Although these interactions start to be well documented (for hyaenas and lions: Périquet et al., 2014; for hyaenas and leopards: Balme, Hunter and Slotow, 2007; Balme et al. 2017; for lions and leopards: du Preez et al. 2015), the degree to which they avoid each other, attract each other or use the landscape independently is less clear (but see Swanson et al. 2016; Miller et al. 2018; Havmøller et al., 2020; Rafiq et al. 2020). In this study, we test the hypothesis that the three carnivore species use the same areas in the landscape, i.e. the prey-rich areas, and have overlapping diel activity patterns (following Cozzi et al., 2012), but are not independent from each other at fine spatio-temporal scales. To gain insights into the fine-scale

spatio-temporal dynamics between species, we calculate attraction-avoidance ratios (Parsons et al., 2016, Niedballa et al., 2019) and the time difference between two individuals from different species detected at each camera trap station within 72 hours (Swanson et al., 2016). We then determine whether species are attracted by each other or try to avoid each other by comparing observed patterns to patterns obtained through a randomisation method. At these fine scales, we expect (1) lion activity patterns to be independent from the two other carnivores, because lion is the larger and most often the dominant carnivore; (2) hyaenas to be attracted to both lions and leopards because of scavenging or kleptoparasitism opportunities (hyaena-lion interactions are highly diverse and complex (Périquet et al. 2014) and seem to even change depending on the conditions (Périquet et al., 2015, 2021), so we made a simplistic hypothesis on purpose and will discuss the complexity of these interactions in the discussion); (3) and leopards, which is the less competitive species (Caro & Stoner, 2003), to avoid both other species in order to minimize interference competition and kleptoparasitism.

## **Material and method**

### *Study area*

The study area is Hwange National Park, an unfenced protected area of approximately 15000 km<sup>2</sup> in western Zimbabwe (19°00'S, 26°30'E). It is part of a large and open protected area embedded in the world's largest trans-frontier conservation area (Kavango-Zambeza [KAZA]). It is a dystrophic semi-arid savanna. The vegetation comprises mainly bushlands and woodlands, with small patches of grasslands (Arraut et al., 2018). The main woody plant species are *Baikiaea plurijuga*, *Colophospermum mopane*, *Terminilia sericea*, *Acacia* spp. and *Combretum* spp. (Roger, 1993). Most of the rain falls between November and April (mean annual rainfall = 600mm; CV = 30%). Water is available to wildlife through natural waterholes

that dry up as the dry season progresses and through some waterholes that are pumped throughout the dry season.

### *Camera traps surveys*

Two hundred and three camera trap stations were set up throughout the park, distributed in six zones: Dzibanini, Guvalala, Jozibanini, Ngamo, Robins and Shakwanki (Fig. 1). There were a mean of 34 ( $\pm 7$  SD) camera trap stations per zone (from 27 to 45, Table 1) and camera traps were set up for a mean of 67 ( $\pm 34$  SD) days (Table 1). Camera trap stations are composed of two camera traps (Cuddeback models 1125, 1149 and C1, Non-typical, WI, USA; Panthera V4, Panthera, NY, USA; Stealthcam G42NG, Grand Prairie, TX, USA) that were positioned on each side of a trail or a road, as it is the best set-up for large carnivore identification (du Preez et al., 2014). During each survey, camera traps were checked regularly for batteries and memory cards. Pictures of lions, hyaenas and leopards were collected at the end of each survey. We discarded records from individuals that were within a period of 60 minutes after another individual of the same species at the same camera trap in order to ensure temporal independence between records (as in Niedballa et al., 2019; Meek et al., 2014; Sollman et al., 2013).

Table 1: Number of camera trap stations, information on when they were set up, and number of detections for each zone of the study area.

<i>Zones</i>	<i>Number of camera trap stations</i>	<i>Duration of the survey in days</i>	<i>Months</i>	<i>Year</i>	<i>Number of detections</i>
Dzibanini	29	59	September - October	2017	175
Guvalala	45	134	May - July	2014-2015	351
Jozibanini	27	63	September - November	2017	241
Ngamo	29	56	September - November	2014	241
Robins	38	45	September - November	2013	392
Shakwanki	35	44	August - September	2013	269



**Figure 1:** Map of Hwange National Park with crosses indicating the camera trap stations in the six zones.

## *Analyses*

### *1. Spatial patterns overlap*

To assess overlap in space use at the landscape scale, we calculated the percentage of times two species are detected at a same camera trap station with no limit of time and no order of species apparition. We calculated that percentage for each pair of species: hyaenas-lions, hyaenas-leopards, and lions-leopards. We then randomised the data set by permuting the identifications 1000 times, in order to calculate confidence intervals and assess if the percentages calculated with the observed data fall within these confidence intervals.

### *2. Random records*

In order to compare the observed patterns to distribution patterns obtained under the null hypothesis of independence between the species, we generated random records (used by Karanth et al. 2017; Cusack et al. 2017; Niedballa et al. 2019). Hereafter, we will use the terms species A and species B with A being the first species detected at the camera trap station and B the second one. For this randomisation method, which considers asymmetric interactions, we simulated the random records of species B while conserving the actual records of species A. To do so, we first generated random times for the records of species B while accounting for the diel activity pattern of this species, we then generated random dates within the period of activity of the camera traps in the zone. We then assigned these random times and dates to the actual records of the species B. For each study pair (lion-hyaena, hyaena-lion, lion-leopard, leopard-lion, hyaena-leopard, leopard-lion), we generated a thousand distribution patterns with this randomisation method.

#### *2.1 Activity patterns overlap*

To evaluate how similar are the diel activity patterns of the three species, we estimated the overlap between the temporal activity patterns of species for each pair of species (lion-hyaena,

leopard-hyaena, lion-leopard) using the coefficient of overlap for activity  $\Delta$  (Ridout & Linkie 2009) calculated by the `overlapEst` function from the package `overlap` in R (Meredith & Ridout, 2016).  $\Delta$  corresponds to the area under the probability density functions of the estimated diel activity density curves for each species ( $f(t)$  and  $g(t)$ ):

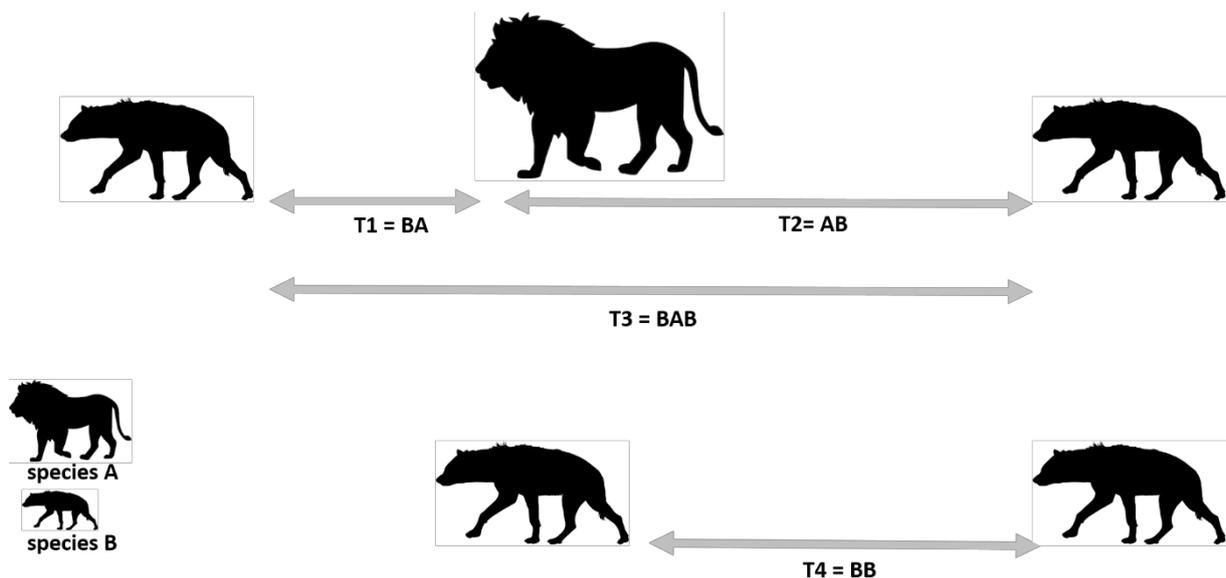
$$\hat{\Delta} = \int_0^1 \min\{\hat{f}(t), \hat{g}(t)\} dt \quad (1)$$

We calculated confidence intervals from the random records' distributions.

## 2.2 Attraction-avoidance ratios

To assess patterns of attraction/avoidance, we calculated time intervals between the record of a first species A and the record of a second species B, first in that order (AB, T2 in Fig. 2) then in the reverse order, i.e. between B and A (BA, T1 in Fig. 2). We also calculated the time interval between the record of the secondary species B, the record of the primary species A and a second record of the secondary species B (BAB, T3 in Fig. 2). We finally calculated the time interval between consecutive records of the same species B (BB, T4 in Fig. 2). We calculated the median for each of these time intervals and calculated the two following attraction-avoidance ratios: AB/BA and BAB/BB (Parsons et al., 2016; Niedballa et al., 2019). The first ratio compares the time intervals between a primary species and a secondary species to the reserve situation (AB/BA). High values of this ratio could arise from either avoidance of species A by species B or by attraction of species A to species B. The second ratio compares the time intervals between records of secondary species with or without the passage of a primary species in between (BAB/BB). Values above 1 indicate avoidance of species A by species B. We calculated ratios by zone because there were not enough records by station. Then we used random records to generate random distributions of the ratios and calculate confidence intervals

for the ratios. To provide insights into the time scale of the patterns of attraction-avoidance detected, we further assessed whether the simple time interval AB calculated from the observed data fell in the confidence interval calculated from the random distributions.



**Figure 2:** Different times (T1, T2, T3, and T4) calculated (in hours) between two species (A and B; illustrated here by lions and hyenas respectively) detected at the same camera trap station and used to calculate the attraction-avoidance ratios as in Parsons et al. (2016).

### 2.3 Time-to-event analysis

We only used data from the night detections of the three species as it is when they are the most active, and likely to be foraging. There were not enough data on the lion-leopard pair to allow performing this analysis for that pair. We calculated how many times an individual from species B was detected after an individual from species A at a same camera trap station, within different time intervals (2 hours, 4 hours, 6 hours, 8 hours, 10 hours, 12 hours, 24 hours meaning the night after, 48 hours meaning two nights after, and >72 hours meaning three nights after and more). We did it for each pair of species considering both orders, i.e. asymmetric interactions (hyaena - lion, lion - hyaena, hyaena - leopard, leopard - hyaena), and for every study zone. We summed the values obtained from each zone, for each time interval. From the

randomised data set, we calculated the median values of the 1000 simulations with the same procedure as above. To assess the intensity of association between species A and B, we calculated ratios (observed/expected), a value  $>1$  indicates attraction between species and a value  $<1$  indicates avoidance between the two species. We performed a chi2 test to compare ratios from observed data sets and from simulated data sets at each time interval. Chi square values  $>3.84$  are considered significant.

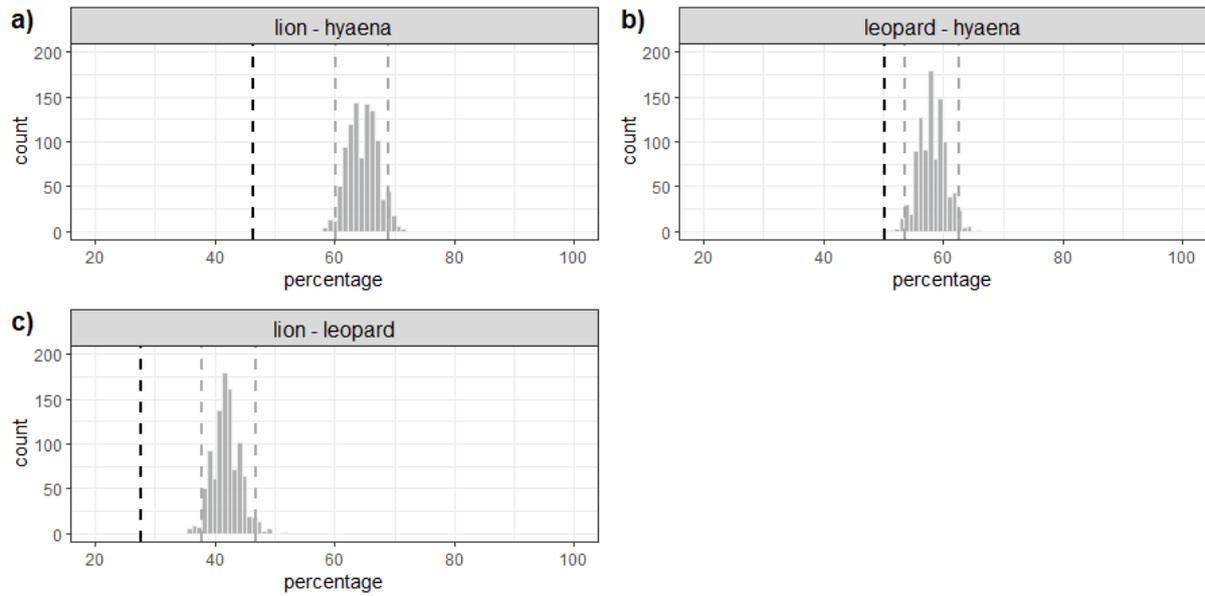
All analyses were performed with R (R core team, 2021).

## Results

We implemented 14 316 camera trap days for the whole survey and collected 1 669 detection pictures of the three large carnivore studied (see Table 1 and Appendix A for details by zone and by species). Overall, hyaenas were the most detected with 68.6% of the detections, compared to lions (17.7%) and leopards (13.7%) (Appendix A). Hyaenas were detected at 93.1% of the stations, lions at 55.2% and leopards at 50.3%.

### *1. Spatial patterns overlap*

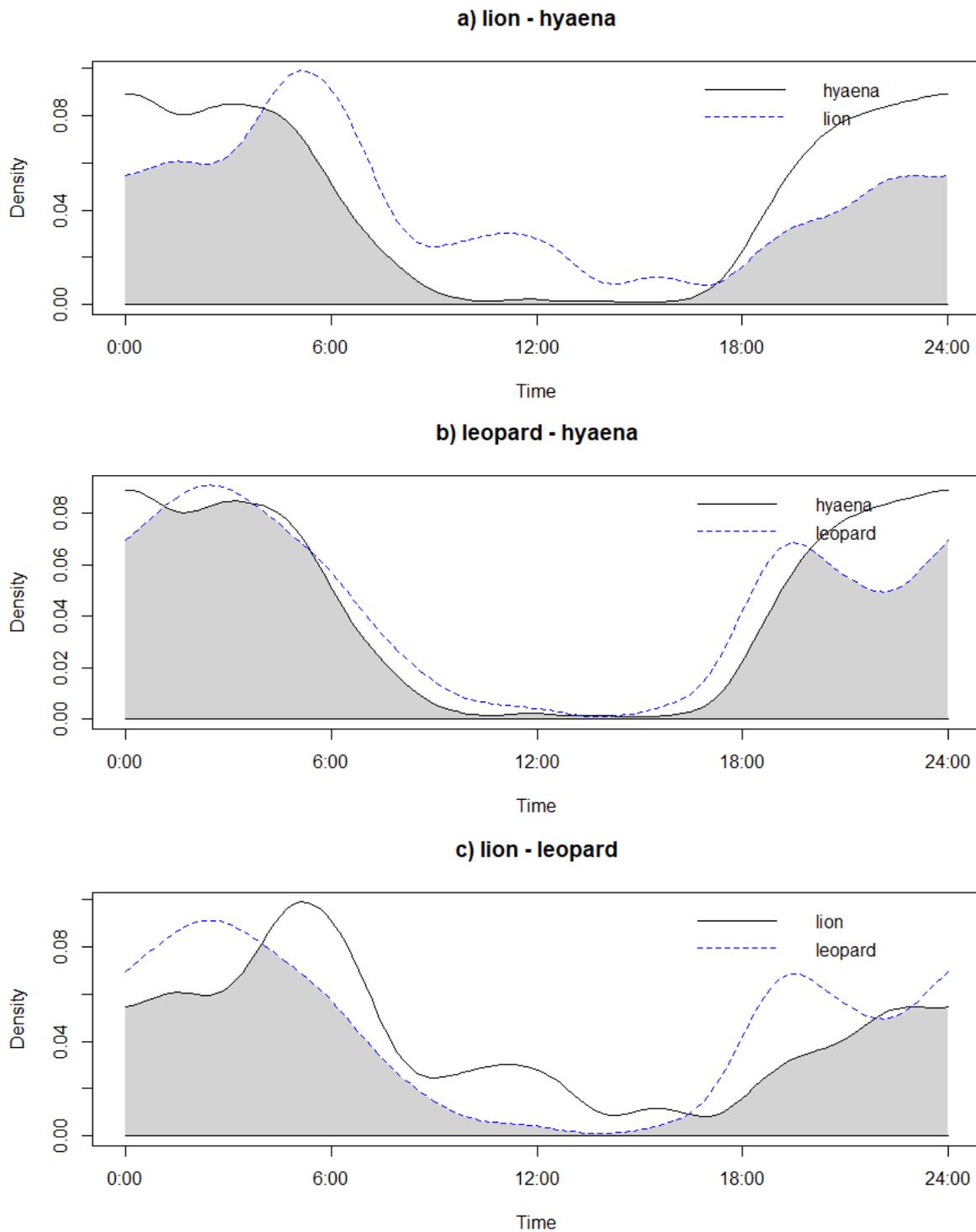
Lions and hyaenas were detected at the same camera trap station in 46.31% of the stations (Fig. 3 a), leopards and hyaenas in 50.25% of the stations (Fig. 3 b), and lions and leopards in 27.59% of the stations (Fig. 3 c). For all pairs of species, these percentages fall outside of confidence intervals (Fig. 3) meaning that these species' space uses overlap less than expected by chance.



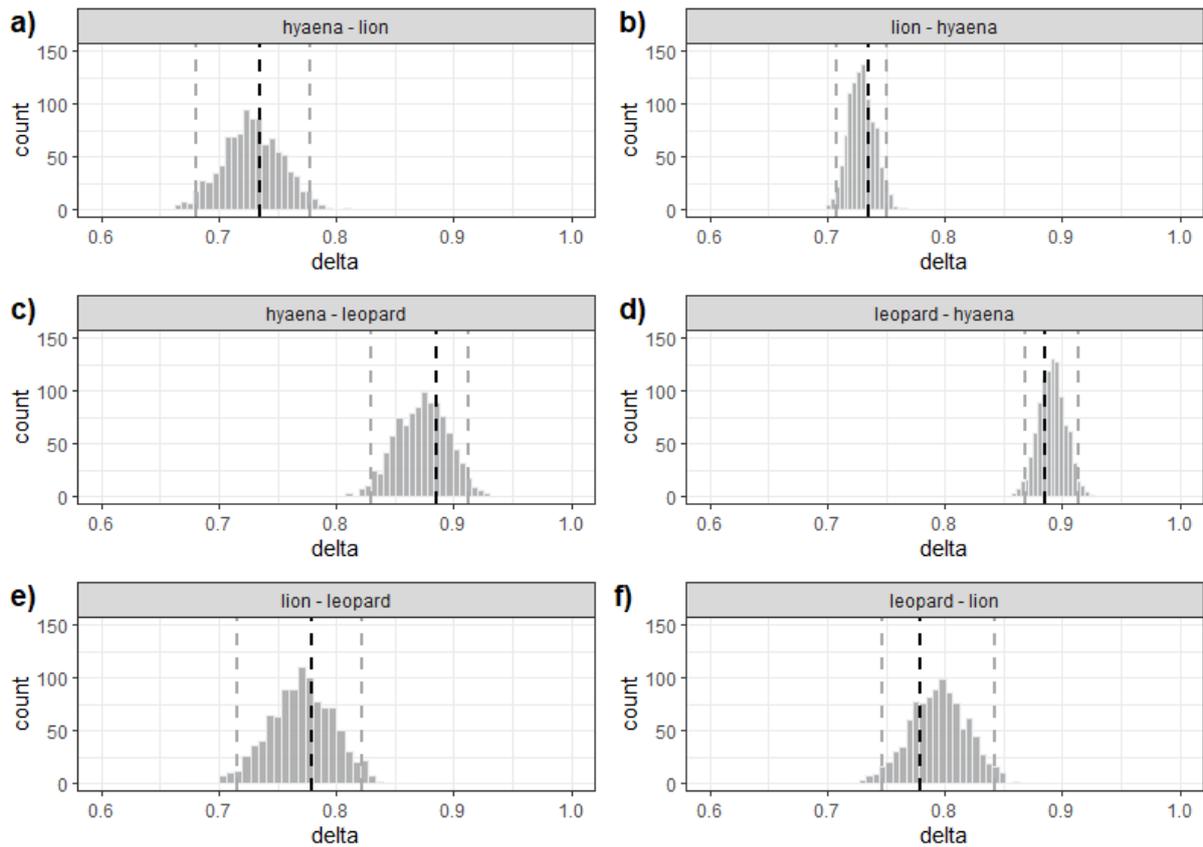
**Figure 3:** Space use overlap between lions, hyaenas and leopards in Hwange National Park. The vertical dotted black line represents the percentage of times two species are detected at the same camera trap station for a) hyaenas and lions, b) hyaenas and leopards, and c) lions and leopards. The distribution randomly generated with permutations is indicated in grey with vertical grey dotted lines representing the confidence interval (95%).

## 2. Activity pattern overlap

Overlaps between the diel activity patterns of the three carnivore species were high: 0.74 for lions and hyaenas (Fig. 4 a), 0.89 for leopards and hyaenas (Fig. 4 b) and 0.78 for lions and leopards (Fig. 4 c). For all species pairs, the observed  $\Delta$  is within the confidence interval of the distributions generated using the random records (Fig. 5).



**Figure 4:** Patterns of diel activity of the three species with their overlap (grey area) between a) hyaenas and lions, b) hyaenas and leopards and c) lions and leopards.

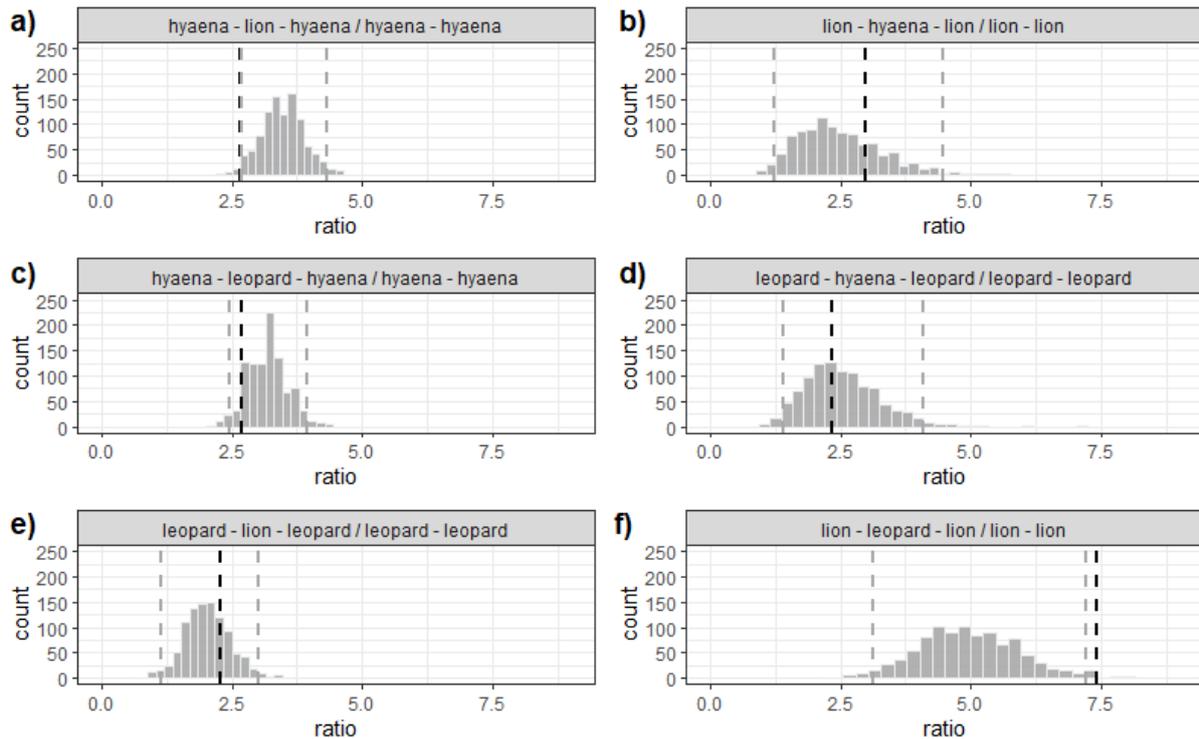


**Figure 5:** Distributions of the  $\Delta$  values obtained with the random records for the pairs of species: a) hyaenas and lions, b) hyaenas and leopards and c) lions and leopards. The black line represents the  $\Delta$  value obtained with the observed data and the grey lines represent confidence intervals at 95%.

### 3. Attraction-avoidance ratios

Regarding AB/BA ratios, all the observed values were within confidence intervals (Appendices B, C, D). Regarding the BAB/BB ratios, the observed value of the ratio is outside of the confidence interval and at the left of the random distribution when focusing on the effect of lions on hyaenas (Fig. 6 a), suggesting that hyaenas tend to use areas previously used by lions. The observed value of the ratio also falls outside the confidence interval but this time on the right of the random distribution when focusing on the effect of leopards on lions (Fig. 6 f), indicating that lions were detected after a longer period if a leopard had been detected before. For the AB time intervals, observed values for all species pairs were in the lower end of the random distributions' tail, suggesting that the three carnivore species tend to use preferentially

areas previously used by another carnivore species (Appendices B, C, D). This seems to be particularly true for hyaenas using areas previously used by lions (Appendix B(b)), leopards using areas previously used by hyaenas (Appendix C(d)), and lions using areas previously used by leopards (Appendix D(d)). It is important to note the order of magnitude of the values observed (more than 40 hours).

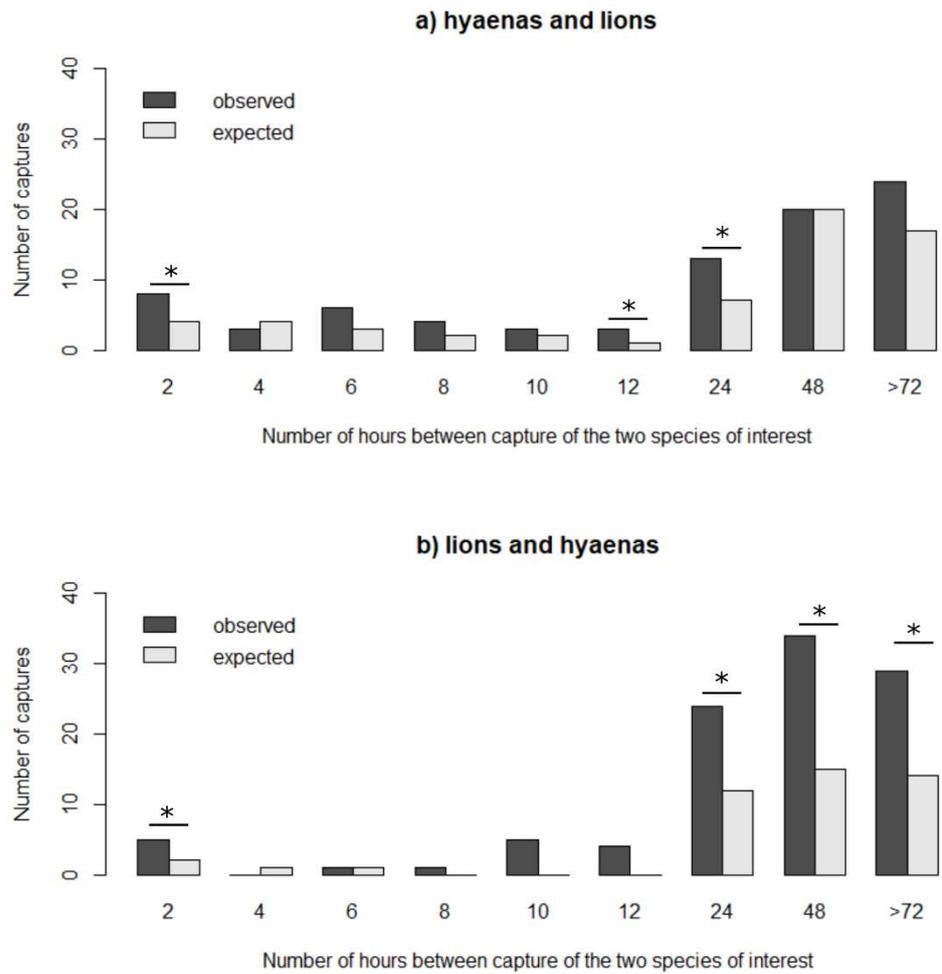


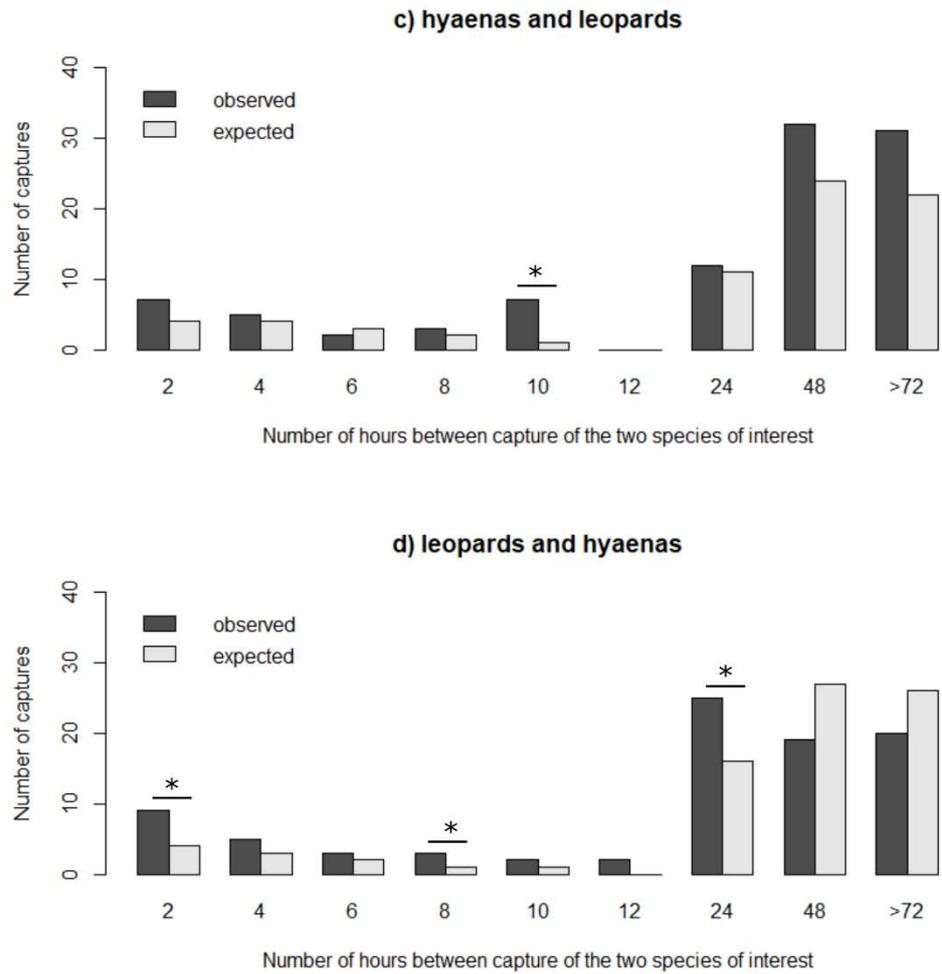
**Figure 6:** Attraction-avoidance ratio (BAB/BB) values (black dotted line) versus the distribution of the simulated values with the random records method (grey lines with 0.95 confidence interval indicated by the vertical dotted grey lines), for each combination of species with a) effect of lions on hyaenas, b) effect of hyaenas on lions, c) effect of leopards on hyaenas, d) effect of hyaenas on leopards, e) effect of lions on leopards and f) effect of leopards on lions.

#### 4. Time-to-event analysis

For the pair hyaena – lion, lion had been significantly more detected 2 hours, 12 hours and 24 hours after a hyaena detection (Fig 7 a; Table 2). For the pair lion – hyaena, hyaena has been significantly more detected 2 hours, 24 hours, 48 hours and 72 hours after a lion detection (Fig

7 b; Table 2). For the pair hyaena – leopard, leopard had been significantly more detected 10 hours after a hyaena detection (Fig 7 c; Table 2). For the pair leopard – hyaena, hyaena has been significantly more detected 2 hours, 8 hours and 24 hours after a leopard detection (Fig 7 d; Table 2).





**Figure 7:** Number of times two species were detected at the same station according to different time intervals between the two detections for the observed data and the random records data a) for detection of lions after detection of hyaenas, b) for detection of hyaenas after detection of lions, c) for detection of leopards after detection of hyaenas, d) for detection of hyaenas after detection of leopards. Significant values given with the chi-square test are indicated with a star (see details in Table 2).

Table 2: Distribution of the observed values (O) and the expected values generated with the random records (E), the ratio (O/E) and chi-square ( $\chi^2=(O-E)^2/E$ ) values for each pair of species at every time interval. Ratios greater than 1 indicate positive association between the two species and ratios inferior to 1 indicate negative association between the two species. Significant chi-square values are superior to 3.84 and are indicated in bold.

	<i>time (hours)</i>	<i>O</i>	<i>E</i>	<i>O/E</i>	$\chi^2$
<i>lion - hyaena</i>	<b>2hrs</b>	<b>5</b>	<b>2</b>	<b>2.50</b>	<b>4.50</b>
	4hrs	0	1	0.00	1.00
	6hrs	1	1	1.00	0.00
	8hrs	1	0	0.00	0.00
	10hrs	5	0	0.00	0.00
	12hrs	4	0	0.00	0.00
	<b>24hrs</b>	<b>24</b>	<b>12</b>	<b>2.00</b>	<b>12.00</b>
	<b>48hrs</b>	<b>34</b>	<b>15</b>	<b>2.27</b>	<b>24.07</b>
	<b>72hrs</b>	<b>29</b>	<b>14</b>	<b>2.07</b>	<b>16.07</b>
<i>hyaena - lion</i>	<b>2hrs</b>	<b>8</b>	<b>4</b>	<b>2.00</b>	<b>4.00</b>
	4hrs	3	4	0.75	0.25
	6hrs	6	3	2.00	3.00
	8hrs	4	2	2.00	2.00
	10hrs	3	2	1.50	0.50
	<b>12hrs</b>	<b>3</b>	<b>1</b>	<b>3.00</b>	<b>4.00</b>
	<b>24hrs</b>	<b>13</b>	<b>7</b>	<b>1.86</b>	<b>5.14</b>
	48hrs	20	20	1.00	0.00
	72hrs	24	17	1.41	2.88
<i>hyaena - leopard</i>	2hrs	7	4	1.75	2.25
	4hrs	5	4	1.25	0.25
	6hrs	2	3	0.67	0.33
	8hrs	3	2	1.50	0.50
	<b>10hrs</b>	<b>7</b>	<b>1</b>	<b>7.00</b>	<b>36.00</b>
	12hrs	0	0	1.00	0.00
	24hrs	12	11	1.09	0.09
	48hrs	32	24	1.33	2.67
	72hrs	31	22	1.41	3.68
<i>leopard - hyaena</i>	<b>2hrs</b>	<b>9</b>	<b>4</b>	<b>2.25</b>	<b>6.25</b>
	4hrs	5	3	1.67	1.33
	6hrs	3	2	1.50	0.50
	<b>8hrs</b>	<b>3</b>	<b>1</b>	<b>3.00</b>	<b>4.00</b>
	10hrs	2	1	2.00	1.00
	12hrs	2	0	0.00	0.00
	<b>24hrs</b>	<b>25</b>	<b>16</b>	<b>1.56</b>	<b>5.06</b>
	48hrs	19	27	0.70	2.37
	72hrs	20	26	0.77	1.38

## Discussion

As expected, lions, leopards and hyaenas have high overlaps in their activity patterns, corroborating existing knowledge on their ecology (Cozzi et al., 2012). All three species are nocturnal; with lions having some activity during the day compared to the two other species. These high diel overlaps imply that there are other mechanisms at play allowing for coexistence. Lions and leopards were the least detected at the same camera trap station. Two non-exclusive mechanisms may explain this space-use partitioning. One explanation is that the two species select different habitats. In Hwange, lions select areas close to waterholes (Davidson et al., 2012) where prey are the most abundant. These areas, often associated with open grasslands, are where lions mostly hunt (Valeix et al., 2009a, 2010), ambushing prey in the vegetation surrounding these open areas (Davidson et al., 2012). Leopards, on the other hand, are woodland predators that select their hunting grounds in term of vegetation density associated with a low visibility and a higher catchability (Balme, Hunter & Slotow, 2007). The other explanation is that there is spatial partitioning to a certain extent allowing leopards to minimize the risk of encounter with the dominant and larger predator. Both lions and hyaenas are known to kill leopards but lions pose a far greater threat to the safety of leopards than hyaenas (Balme et al., 2013). An important proportion of the known mortalities in leopards are due to intraguild predation (Prugh & Sivy, 2020). Additionally, avoidance of kleptoparasitism is a driving force of leopard ecology, and leopards immediately abandon a kill when a lion arrives at the kill site (Balme et al., 2017). The small spatial overlap between lions and leopards can thus result from competitive exclusion. A study across 10 reserves in South Africa did not detect that interference competition affects the spatial habitat selection of the leopard (Miller et al., 2018). Another study came to a similar conclusion but also underlined the potential for competitive interactions between lions and leopards (Bashant et al., 2020).

Leopards was the least detected species by camera traps. However, camera traps were located on trails and roads, and leopard is a cryptic species highly impacted by human activities (Ngoprasert, Lynam and Gale, 2007; Van Cleave et al., 2018). Roads are likely to be used by humans (tourists, managers, researchers) and trails are visited for maintenance reasons for this protocol but also are known to be used intensively by the larger carnivores, which may explain a lower detectability of leopards. Using GPS collars is thus definitely an important complementary approach to camera trapping to better understand leopard ecology and its interaction with other predator species.

At finer scales, we found two interesting patterns:

- (i) hyaenas tend to use areas previously visited by lions or leopards very closely in time (in the 2 hours following the use of the area by the other species), suggesting that hyaenas may “follow” the other two predators. Lions also show this behaviour following the detection of a hyaena (not tested after a leopard). We will refer to this hypothesis as the “follower hypothesis”.
- (ii) hyaenas tend to use areas previously visited by lions or leopards the night(s) consecutive to the detection of the other predator, suggesting that they wait for some time before going where a lion or a leopard went. Lions also show this behaviour following the detection of a hyaena (not tested after a leopard, as unfortunately not enough data at this scale for this pair of species). We will refer to this hypothesis as the “delayed exploration hypothesis”.

Regarding the “follower hypothesis”, a probable underlying mechanism is that a carnivore species may “follow” another one to benefit from foraging opportunities, whether it is through kleptoparasitism (the stealing of a prey recently caught by the other predator) or scavenging (to use of a carcass killed and left by the first predator). Such interactions are common between lions and hyaenas (Périquet et al., 2014). Hyaenas loose more kills to lions than the opposite (Périquet et al., 2014). The outcome of aggressive interactions at a kill

depends on the group size of both species and the presence of males in the lion group (Cooper, 1991). If there is a male lion, hyaenas are more likely to lose the interaction, while if there are only female lions, the species with the larger group size (ideally a factor 4 for hyaenas to lions) is more likely to win (Périquet et al., 2014). This offers good directions for future research, with sex and group size important variables to consider to have a better insight on the interactions between the two species. Scavenging is very frequent in both species, and hyaenas can acquire significant amounts of food from lions' leftovers under some circumstances (Périquet et al., 2014, 2015). Similarly, hyaenas tend to "follow" leopards, which makes perfect sense in a context of strong kleptoparasitism, as leopards are known to mainly lose their kills to hyaenas (Balme, Hunter and Slotow, 2007; Balme et al., 2017). Kleptoparasitism from hyaenas is demonstrated to even have an impact on female leopard reproductive success (Balme et al., 2013), and hiding their kills in trees is probably an adaptation of leopards to reduce kleptoparasitism from hyaenas (Balme et al., 2017). Sociality and predator group size play a role in predator interaction. While lions are a highly social species and mostly hunt within a group and live in pride, leopard is a solitary species. It seems then easier for hyaena to steal kills from a solitary leopard than to a pride of lions especially if there is a male (Périquet et al., 2015), an indeed hyaenas are responsible for the majority of leopards lost kills (Balme, Slotow and Hunter, 2009) explaining the pattern of hyaena following leopards. Lions, on the other hand, are a real threat to leopards' survival than hyaenas (Balme et al., 2013; Balme et al., 2017).

Regarding the "delayed exploration hypothesis", one possible underlying mechanism is, again, the access to a scavenging opportunity. Hyaenas can come back regularly to a carcass to wait for access to it for up to one week after they detected the carcass (Périquet et al., 2021). This is obviously mainly the case for very large carcasses. However, we cannot rule out more subtle indirect effects of one predator on another predator (Sih et al., 1998). For example, in

multi-predator systems, prey may exhibit conflicting anti-predator responses such that the response to one predator increases the risk of predation by another predator, illustrating a case of predator facilitation (Kotler et al., 1992; Leblond et al. 2016). Whereas hyaenas are cursorial predators that are mostly efficient in open habitats, lions and leopards are ambush predators, which rely on dense vegetation to launch successfully their attack by surprise (Sunquist & Sunquist, 2002). African herbivores tend to use open habitats when lions are nearby (Valeix et al., 2009b, Courbin et al., 2016). Such reactive response of herbivores to the presence of an ambush predator can last 24h (Courbin et al., 2016) and hyaenas could benefit from this habitat selection as prey end up in open habitats where hyaenas are the most successful. Although there is no published evidence that herbivore use more wooded habitats when hyaenas are in the vicinity, this could be an effective anti-predator response to a cursorial predator, in which case it would benefit ambush predators. Such a mechanism could explain why lions tend to use areas previously used by hyaenas and avoid areas previously used by leopards. Indeed, lions and leopards are ambush predators, and being in the same area for a hunt with another predator with the same hunting mode may reduce the chances of a hunt being successful, as if prey detect one of the predator it will become uncatchable for the other one as well.

Altogether, our results suggest that positive interactions may be important drivers of the fine-scale spatio-temporal dynamics of large carnivores. Our work calls for further research to explore the “follower hypothesis” and the “delayed exploration hypothesis”.

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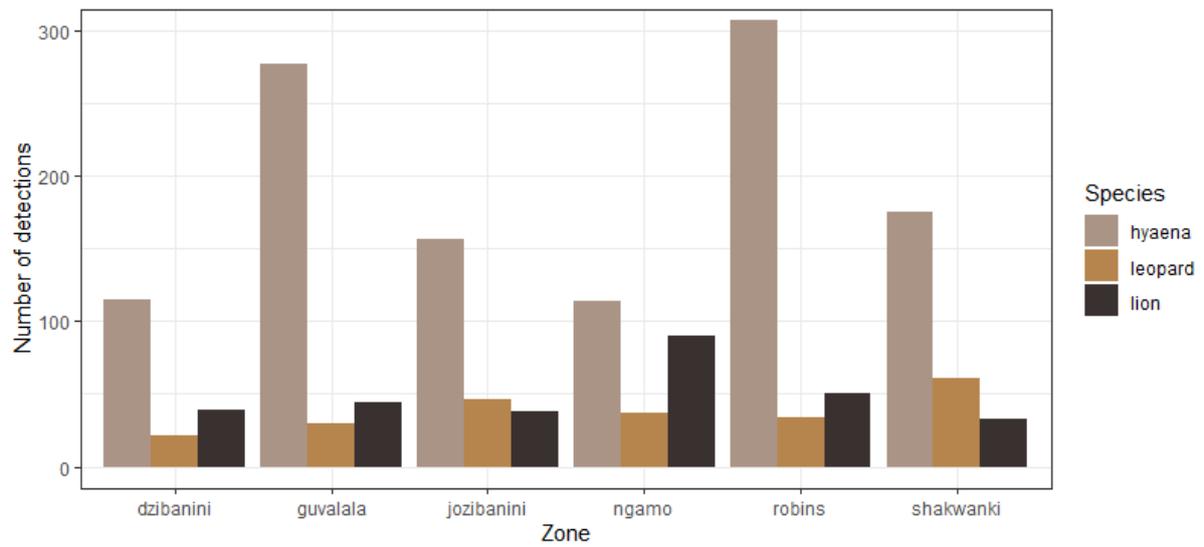
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*Appendices*

**Appendix A**

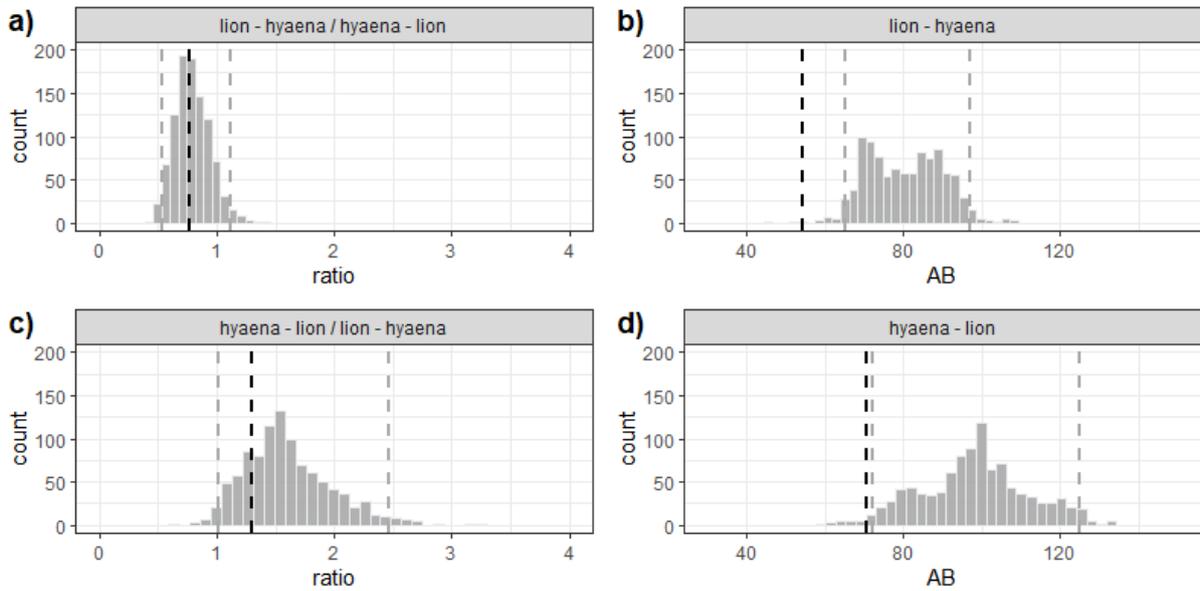
Number of detections (records) per species per zone.



<i>Zone</i>	<i>Hyaena</i>	<i>Leopard</i>	<i>Lion</i>
<i>Dzibanini</i>	115	21	39
<i>Guvalala</i>	277	30	44
<i>Jozibanini</i>	157	46	38
<i>Ngamo</i>	114	37	90
<i>Robins</i>	307	34	51
<i>Shakwanki</i>	175	61	33

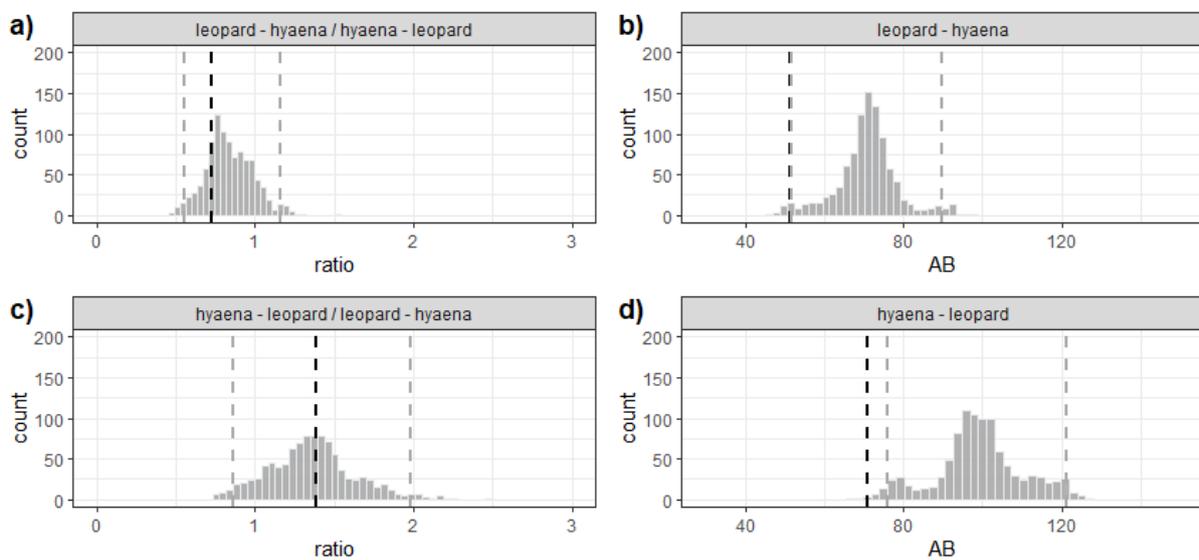
**Appendix B**

Vertical black lines are the values of the ratios AB/BA a) for lion and hyaenas c) for hyaenas and lions, and AB et BA median time between the detections of b) lions and hyaenas d) hyaenas and lions, distributions are from data generated with the random method records grey vertical lines are the confidence intervals at 95%.



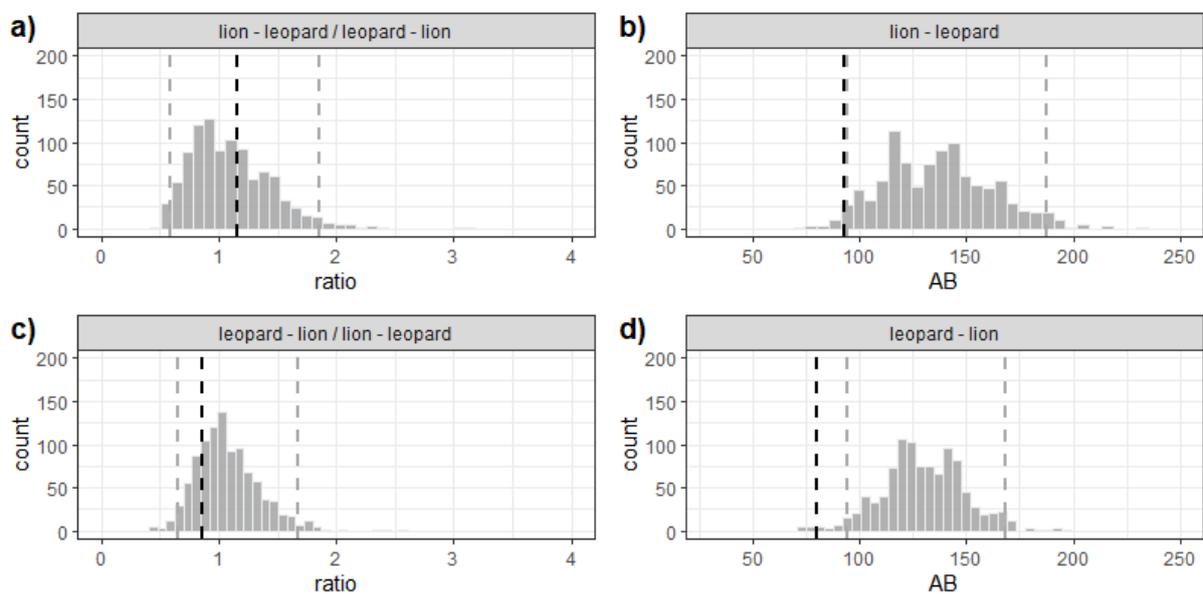
## Appendix C

Vertical black lines are the values of the ratios AB/BA a) for leopards and hyaenas c) for hyaenas and leopards, and AB et BA median time between the detections of b) leopards and hyaenas d) hyaenas and leopards, distributions are from data generated with the random method records grey vertical lines are the confidence intervals at 95%.



## Appendix D

Vertical black lines are the values of the ratios  $AB/BA$  a) for lions and leopards c) for leopards and lions, and  $AB$  et  $BA$  median time between the detections of b) lions and leopards d) leopards and lions, distributions are from data generated with the random method records grey vertical lines are the confidence intervals at 95%.



## Discussion



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“Community ecology is a mess, with so much contingency  
that useful generalisations are hard to find.”

John H. Lawton, 1999

## **Community ecology within large terrestrial mammalian species**

### *The complexity of ecosystems leads to uneven knowledge in ecology: the case of large terrestrial mammalian species*

Universal laws and theories are rare in ecology. By definition, ecology is the study of how “organisms interact with one another (no species, anywhere in nature, lives in splendid isolation) and with their environment.” (Lawton, 1999). However, the complexity of the living world is an obstacle to generalisation. Indeed, when it comes to studying multiple species living in interaction, as it the case for community ecology, many levels (from one individual to the entire species via populations) interplay with different spatiotemporal scales according to the species studied. Indeed, microorganisms live the in vicinity of a rhizosphere (Schmidt et al., 2007), while some mammalian marine species cover hundreds of kilometres in oceans (Robbins et al., 2011) and some bird species migrate between different continents (Hake, Kjellén and Alerstan, 2011). There are disparities in terms of time scales as well, because of the differences of species lifetimes, which can vary from a few days with microorganisms (Schmidt et al., 2007) to years with large mammalian species (Pacifici et al., 2013). Historically, community ecology relied mostly on field observations. Nowadays, it relies on a variety of methods to understand and infer interspecific interactions, such as mathematical modelling (Northfield et al., 2017), experimentation (Schmitz, 2008) or satellite tracking of animals for instance (Wilmers et al., 2015). In the study of predator-prey interactions, most of the times, hypotheses are generated with theoretical modelling and tested with experimentation that creates empirical data. This leads to a very uneven knowledge because it relies on the capacity to experiment and create empirical data. This has been highlighted with the first chapter of the thesis: compared to what is known on the Non-Consumptive Effects (NCE) of predation in invertebrates, there is still a lot to understand for large terrestrial mammals. The study of NCE encompasses the study of how prey react to predation risk and the consequences of this on prey population

dynamics. While it is achievable with invertebrate species, which can be manipulated and for which generation times are short (Anderwartha & Burggren, 2012), this is much more challenging when it comes to large mammals, as most of these species have generation times of several years (Pacifici et al., 2013).

*The technical progress is aiming to reduce knowledge gap between species*

Technical improvements made over the last decades helped a lot in acquiring empirical data in an efficient way. It comes mostly from progresses with telemetry and GPS technology, camera trapping that allow monitoring for continuous periods large areas, and the development of adequate recording device (audio or video). The first step in the study of NCE is the understanding of prey proactive and reactive behavioural responses to predation risk. In this thesis, I used both an experimental approach in natural ecosystems (chapter 3) and the study of telemetry data (chapter 2) to assess reactive responses of prey to large carnivores. While the study of the behavioural response to an auditory stimulus of the presence of predator focused on the immediate antipredator response (chapter 3), the study of telemetry data allowed having an insight on a longer time scale for the spatial reactive response. Over the last two decades, huge progresses have been made on animal-borne sensors (from VHF to GPS collars with accelerometers), with the development of batteries that can last longer while being lighter and the sampling intensity that increased (up to every few minutes) without affecting the longevity of the collar (Brown et al., 2012). Progresses on developing sophisticated animal borne-sensors allow for a better and more accurate inference on prey behaviour (Wilmers et al., 2015). Thanks to these progresses, in the second chapter I benefited from data from GPS collars that were simultaneously deployed on two predator species (spotted hyaena and lion) and on one prey species (plain zebra). Ultimately, having these types of device on both prey and predator simultaneously provided us with unique insights into encounters between prey and their predators, the prey response to an acute predation risk, the outcome of the encounters, and this

on a longer spatiotemporal scale than observations could allow. Then, for the third chapter, I did a behavioural experiment that required observation. Most of the times, studies of predator-prey interactions that required observations were performed during the day or at crepuscular times, but most large carnivore species are active and hunting at night (chapter 4 for African predators, Schmidt, 1999 for the Eurasian lynx). Thanks to night vision binoculars, in the third chapter, I could record prey reaction to a simulated predation risk with predator playbacks at night, which is a more relevant time to simulate predation risk. This is now possible to construct camera traps with integrated speakers to do that type of experiment (Suraci et al., 2017). Even though camera traps do not allow monitoring areas as large as I did in chapter 3, using such equipment would allow replicating the experiment in many different ecosystems (Suraci et al., 2017), hence allowing for comparisons and generalisation.

Camera traps are now massively popular in ecology. Between 2008 and 2013, at least 266 publications used camera traps in ecology (Burton et al., 2015). Camera trap data are useful for the study of predator-prey interactions (e.g. Smith et al., 2020; Swanson et al., 2016; Wikenros et al., 2015), or predator-predator interactions (e.g. chapter 4, Niedballa et al., 2019), as they can provide a variety of information from abundance, to behaviour, presence-absence and activity patterns (Burton et al., 2015). In the fourth chapter, I used data from a camera trap set up that was deployed over the entire park of Hwange (Zimbabwe), allowing us to investigate coexistence mechanisms between three sympatric apex predators: the lion, the spotted hyaena, and the leopard. Leopard is a very elusive felid difficult to observe (Balme et al., 2009). That is why camera traps is one of the best way to monitor this species (Brassine & Parker, 2015). However, camera-trap surveys generate massive quantities of data that are not always straightforward to process. Some solutions lie in citizen science, as illustrated by the snapshot safari project, using an online dedicated platform where everyone can help identify camera trap pictures (Pardo et al., 2021). Otherwise, deep learning for identification of species or even

individuals has helped develop fast and reliable methods to process camera trap data (Schneider et al., 2018).

As highlighted in the first chapter, the second step in the study of NCE focuses on food-mediated and stress-mediated costs of the behavioural adjustments of prey to the risk of predation, as they may have consequences on prey life history traits (Sheriff et al., 2009) and ultimately on prey population dynamics. This final step is very often achieved through capture-mark-recapture (CMR) protocols, as they aim to collect data at the individual scale, such as body mass or reproduction status, which serves as proxies of individuals' fitness to then assess survival, reproduction and growth rate in populations and model prey population dynamics (Lebreton, Pradel and Clobert, 1993; Pradel, 1996). This requires years of population monitoring. Most studies using CMR protocols are using data from population monitored on the long term such as the Soay sheep (Soay islet, Scotland) population (Coulson et al., 2001). This monitoring started in 1985. Monitoring large carnivores on the long term and capturing them every year can get quite complicated, as these species are at the heart of several debates. Depending on their conservation status, it is sometimes not possible to use invasive protocols on them. This is where the use of camera traps can become an interesting alternative, as it allows cutting costs and it is a non-invasive method. Camera trap data are now even used with CMR protocols as it is now possible to recognize individuals with photos (Schneider et al., 2018), and recent developments of photogrammetry now provides the possibility to assess proxy of individual fitness (body mass, reproductive status age) without capturing the individuals (Smith, Bongi and Ciuti, 2021).

Chapters 2, 3 and 4 illustrates the use of different technologies, whose progresses open new avenues of research and make it easier to acquire reliable and robust empirical data to test and even generate hypotheses on predator-prey interactions in natural complex ecosystems.

## **Predator attributes and their role in predator-prey interactions**

Predator-prey interactions are affected by the environment where interactions occur (Laundré et al., 2014), prey attributes, such as prey body size or diet (Creel, 2011), and predator attributes (Preisser, Orrock and Scmitz, 2007). As highlighted in the first chapter, when it comes to understand the impact of NCE in large mammals, the importance of prey attributes and environment characteristics start to be well understood, but less is known on the importance of predator attributes. This is why chapters 2, 3 and 4 took into account predator species with different hunting modes to understand if and how it can modulate not only prey antipredator responses but also interactions between predators.

### *Predator attributes modulate risk effects in prey*

A strong body of knowledge on the role of predator attributes comes from other taxa, such as invertebrate species. One important hypothesis is about the predator hunting mode: predators with a sit-and-wait and sit-and-pursue hunting mode induce higher NCE on prey population than active predators. The underlying mechanism would be that cues left by predators with a sit strategy are associated with a high probability of the predator still being in the area, whereas this probability is very low with active predators as they cover large distances to catch prey (Preisser, Orrock and Scmitz, 2007). This theory is yet to be tested in large terrestrial mammals. Ambush predators in large mammals use a strategy that is close to that of sit predators in invertebrates, and being a cursorial predator in large mammals is equivalent to being an active predator in invertebrates. In order to have a first insight into testing that hypothesis, we tested in chapters 2 and 3 the hypothesis that ambush predators induce stronger antipredator responses (i.e. the first component of NCE) than cursorial predators. Results from both chapters support this hypothesis. More studies are clearly needed to confirm that it is the hunting mode that is responsible of the differences detected and not other predator attributes,

such as the predator body size or a combined effect of both attributes. Founding similar results in the two chapters that used different sets of predator species, with the ambush predator inducing a stronger antipredator response than the cursorial predator, gives some credit to the initial hypothesis. Guidelines for future research would be to compare antipredator responses to different pairs of ambush/cursorial predators in different ecosystems, as we did and at the same spatiotemporal scale. Indeed, it would allow being able to test more directly the hypothesis that ambush predators induce higher antipredator responses than cursorial ones. This is why I plan to replicate the experimental protocol of the third chapter in a savanna ecosystem with playbacks of lions and hyaenas to study zebras' response to stimuli from different predators.

Overall, in both chapters 2 and 3, prey responded differently according to the predator they were exposed to. As prey availability is an important factor in predator habitat use (Santos et al., 2019; Karanth et al., 2017) according to the space race between prey and predator (Sih, 2005), these differential responses might contribute to explain space use by large carnivores.

#### *Predator attributes modulate predator-predator interactions*

As mentioned in chapter 1 and discussed in chapter 4, indirect interactions through prey are likely to occur between carnivore species, especially when prey respond differently to different predators. The last chapter explored the spatio-temporal dynamics of co-occurrence between three large carnivore species: two ambush predators (leopards and lions) and one cursorial predator (spotted hyaenas). Based on this work, we formulated two hypotheses: the “follower hypothesis” whereby predators tend to follow closely (in the 2 hours) another predator for potential kleptoparasitism or scavenging opportunities, and the “delayed exploration hypothesis” whereby one predator species is detected the nights after the detection of another predator species. For the latter hypothesis, one possible underlying mechanism is an exploration for scavenging opportunities (especially for very large carcasses) but we cannot rule out a scenario of indirect facilitation via increased prey vulnerability to explain the tendency of lions

to follow hyaenas in the 12 hours and 24 hours. Chapter 2 revealed that hyaenas induced weaker anti-predator spatial response than lions, with zebras tending to stay in an encounter area after an encounter with a hyaena. Altogether, the results from chapters 2 and 4 suggest that (i) either zebras invest in other anti-predator responses, such as increased vigilance, which may lead to a short behavioural depression of prey, explaining why lions do not follow hyaenas between 4 hours and 12 hours after a hyaena detection but only later once zebras resume to their baseline behaviour, possibly with a lower level of vigilance as hyaenas have gone, (ii) zebras invest in other anti-predator responses, such as the relocation into bushed areas where hyaenas are less successful hunters, which may make them more vulnerable to ambush predators, such as lions, in the period following the detection of the hyaena, illustrating a case of indirect facilitation between the two predators. Similarly, hyaenas visited a site after a period of at least 24hours before following lions. Indirect facilitation could also occur in this way as 24h is the time during which zebras are impacted by a lion encounter (Courbin et al., 2016) and hence stay in open areas where hyaenas are more likely to do successful hunts. Previous works already demonstrated that while trying to reduce predation risk from one predator species, a prey species can become more vulnerable to another predator species (Kotler et al., 1992; Leblond et al. 2016). Furthermore, we know from previous work that lions tend to leave in the 48hours after a successful kill (Valeix et al., 2011), waiting that amount of time is maybe a way for hyaenas to avoid interference interactions with lions while still having prey more catchable.

To reach a comprehensive understanding of these indirect interactions between predators, future research will need to consider the full set of anti-predator responses (vigilance, space use, habitat use, grouping) and study the duration of these anti-predator responses in parallel with the monitoring of space use by the predators.

## **Large carnivore in the Anthropocene: the importance of drawing general conclusions**

General conclusions can lead to formulate hypotheses and maybe theories that will have a predictive power. This is useful considering the massive biodiversity decline due to anthropogenic activities through climate change (Dirzo et al., 2014; Pimm et al., 2014). Furthermore, a review based on 600 studies highlighted that environmental changes can affect any type of interspecific interaction, e.g. mutualism, competition and even pathogen infections (Tylianakis et al., 2008). Because of the importance of large mammals in their ecosystem, being able to predict how environmental changes will affect predator-prey interactions, and ultimately the functioning of communities and ecosystems, is of paramount importance.

### *A changing environment leads to a modification of interactions*

Large carnivores are species that deeply affect ecosystems through top down effects such as trophic cascades. Any change they are facing can profoundly affect the ecosystems they are in (Estes et al., 2011). First, prey availability (either prey abundance or prey vulnerability) is affected by climatic conditions (Morin et al., 2021), as well as by anthropogenic activities (Ripple et al., 2015), and is directly influencing predator habitat selection, and hence predator temporal and spatial overlaps (Karanth et al., 2017). Changes in prey availability will thus ultimately affect interactions between large carnivores. If prey availability reduces significantly, there is a high probability that the ecosystems will not have the sufficient carrying capacity for many carnivore species. It is the case in Kasungu National Park, Malawi, where densities of spotted hyaenas and leopards are low supposedly due to reduced prey availability because of poaching (Davis et al., 2021). In addition, the relative importance of different interactions may change depending on environmental conditions (Périquet et al., 2021). Understanding the context of predator-prey and predator-predator interactions is therefore

crucial for a better conservation and management of large carnivore species. Habitat loss and fragmentation are some of the main threats faced by large mammals (Ripple et al., 2014), as they have large home ranges (Haskell et al., 2002) and can cover long distances to consume resources (Holt, 1996). Habitat loss reduces population sizes and ultimately causes local extinction (Hagen, 2012). Because large carnivores have important home ranges, habitat fragmentation is likely to reduce the encounter rate with prey and other predators and this induces a diminution of the interactions between large mammalian predator and prey (Hagen, 2012).

*The importance of considering human activities when studying predator-prey interactions*

Chapter 1 highlighted that while only 15% of terrestrial lands are protected, 62% of the studies used for the review on NCE were done in protected areas. Consequently, human activities and infrastructures cannot be ruled out of the equation to grasp the full picture of predator-prey and predator-predator interactions (Kuijper et al. 2016). First, humans by just being present or through their infrastructure seem to affect predator space use. Coyotes for instance avoid areas with a high intensity of human infrastructures (Moll et al., 2018). Lynx travel faster around human infrastructures and because their preferred prey are in these areas they tend to be active in these areas at night when human activities are low (Gehr et al., 2017). Second, large carnivores and humans in some cases share the same prey. It is the case with roe deer in Europe. An extensive study across the entire continent showed that human non-lethal and lethal activities influenced the most roe deer diel activity pattern (Bonnot et al., 2019). Roe deer are nocturnal to avoid human disturbance, which is emphasized with the hunting season (Bonnot et al., 2019). Hence, not considering humans when studying the interaction between lynx and roe deer could lead to biased conclusions. Finally, Human is considered as a “superpredator” as it kills animals at a rate that has not been reached by any other predator (Darimont et al., 2015). Its impact on large carnivores can have similarities with the impacts of

predation risk by large carnivores on prey, and thus, as a cascading effect, impact predator-prey interactions and ultimately the whole food web (Smith et al., 2017).

*Toward a peaceful coexistence?*

Coexistence between large carnivores and humans is one of the most important challenge for conservation nowadays. Although large carnivores are considered as flagship species and can be fascinating for the general public (Dickman et al., 2011), they are also perceived as frightening, especially for the people living along them. They are a threat to livestock (Morehouse et al., 2011; Valeix et al., 2012; Miller et al., 2015) and can be to humans as well (Penteriani et al., 2017; Dhanwatey et al., 2013). As a result, they have been victims of heavy human persecution for decades that led in Europe, USA and Canada, to a large reduction of large predator geographic range (Ripple et al., 2014). Therefore, this led to the dramatic increase of deer populations; the roe deer is the most abundant ungulate on the European continent (Burbaité & Csanyi, 2010). Deer too are involved in human-wildlife conflicts as they can cause damage to crop culture (Gross et al., 2019), transmit disease to livestock (Gordon, 2009), or threaten human lives through vehicle collision (Seiler, 2004). The aim is to manage enough space for carnivores to continue to exist and not only in protected areas, as landscapes will continue to be human-dominated (Lopez-Bao, Bruskotter and Chapron, 2017). As only 15% of the terrestrial lands and inland water on the planet are protected areas, finding adapted cohabitation measures is the most important challenge that we are facing because protecting large predators is protecting entire ecosystems.

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# Appendix

