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

Elise Say-Sallaz^{1*}, Simon Chamaillé-Jammes^{2,3,4}, Hervé Fritz^{1,4,5}, Marion Valeix^{1,4,6}

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

² CEFÉ, CNRS, Univ. Montpellier, Univ. Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

³ Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa

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

⁵ Sustainability Research Unit, Nelson Mandela Metropolitan University, George Campus, Madiba Drive, 6531 George, South Africa

⁶ Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Oxford OX13 5QL, United Kingdom

* corresponding author: elise.saysallaz@gmail.com

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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.

Keywords: *anti-predator responses, lethal effects, predator-prey interactions, risk effects, ungulates.*

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 were 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 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 (>15kg, 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 key words: “antipredator strategy” (we also checked with the word “anti-predator” 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 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 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.

198

199 ***4.1. Behavioural responses of prey to predation risk***

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

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

216 The second most studied anti-predator response is the increase of prey vigilance level
217 (Fig. 4, 38 publications; e.g. FitzGibbon, 1994; Laundré et al., 2001; Creel, et al. 2014).
218 Indeed, vigilant prey have a better chance to detect an approaching predator before it launches
219 an attack, which will often lead the predator to abort the hunt. This response has been mainly
220 investigated as a reactive mechanism (25 publications), even though proactive vigilance in
221 response to a priori knowledge of long-term variations in risk exists too (11 publications; Fig.
222 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 Figure 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 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 hat 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 (Fig. 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

Figure 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 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-Lémieux 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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723

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

Predator species	Prey species	Outcome	Reference
Stress			
Wolf Puma Coyote	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.
Wolf Lion	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.
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), 12388–93.
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 Eurasian Lynx	Roe deer Red 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>Behavioral Ecology</i> , 29(1), 19–30.
Energetic costs			
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	Hernández, L., Laundré, J. W. (2005). Foraging in the ‘landscape of fear’ and its implications for

	Bison	significantly lower in areas where wolves were present than in areas without wolves.	habitat use and diet quality of elk <i>Cervus elaphus</i> and bison <i>Bison bison</i> . <i>Wildlife Biology</i> , 11(3), 215–220.
Wolf	Elk	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>Behavioral 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 Mountain Lion	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.	Kluever, B. M., Howery, 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.
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., Chamaillé-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), 20140446–20140446.
Lion Spotted hyaena	Zebra Wildebeest Gazelle Impala Giraffe	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>Behavioral Ecology</i> , 25(4), 773–784.
Reproduction			

Wolf Grizzly bear	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.
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	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.

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Figure legends

Figure 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).

Figure 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.

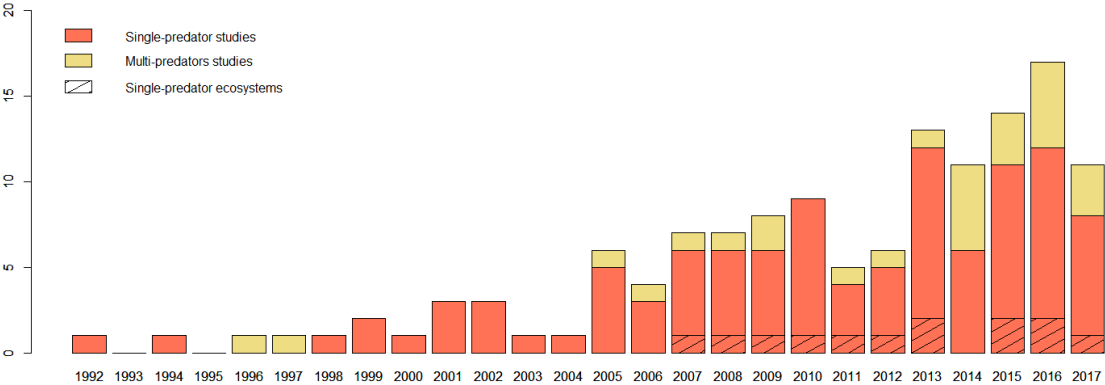
Figure 3: Proportion of the different types of data used to assess predation risk and the prey response to predation risk depending on the NCE component studied (n=135 publications).

Figure 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

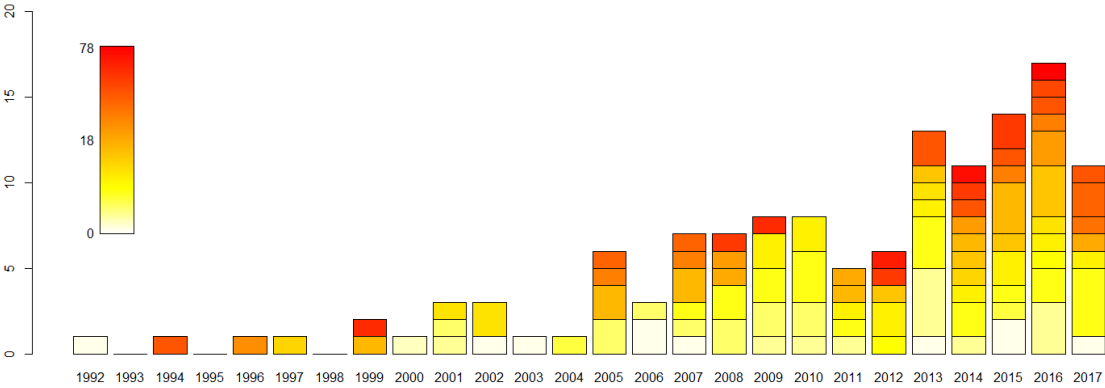
753 proportion of studies that investigated the component and found no effect. Anti-predator
754 behavioural responses can be induced by stress but in this figure, we simplified and focused
755 on stress as a consequence of anti-predator responses.

Figure 1

a)



b)



c)

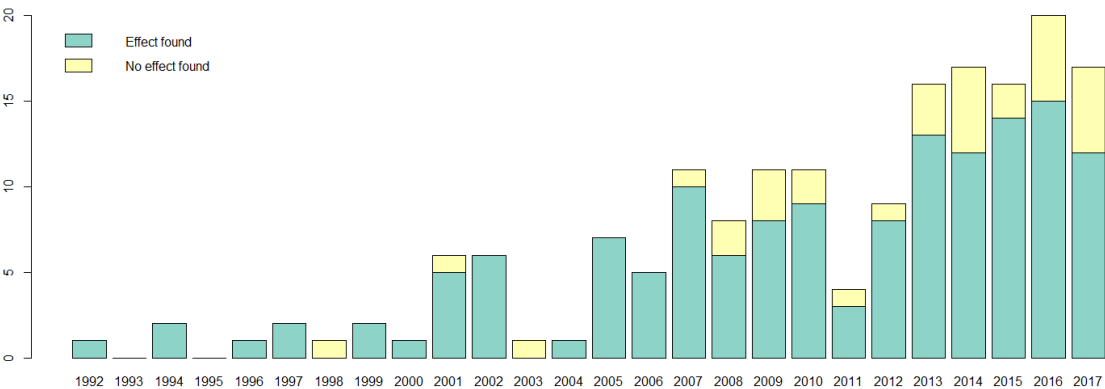
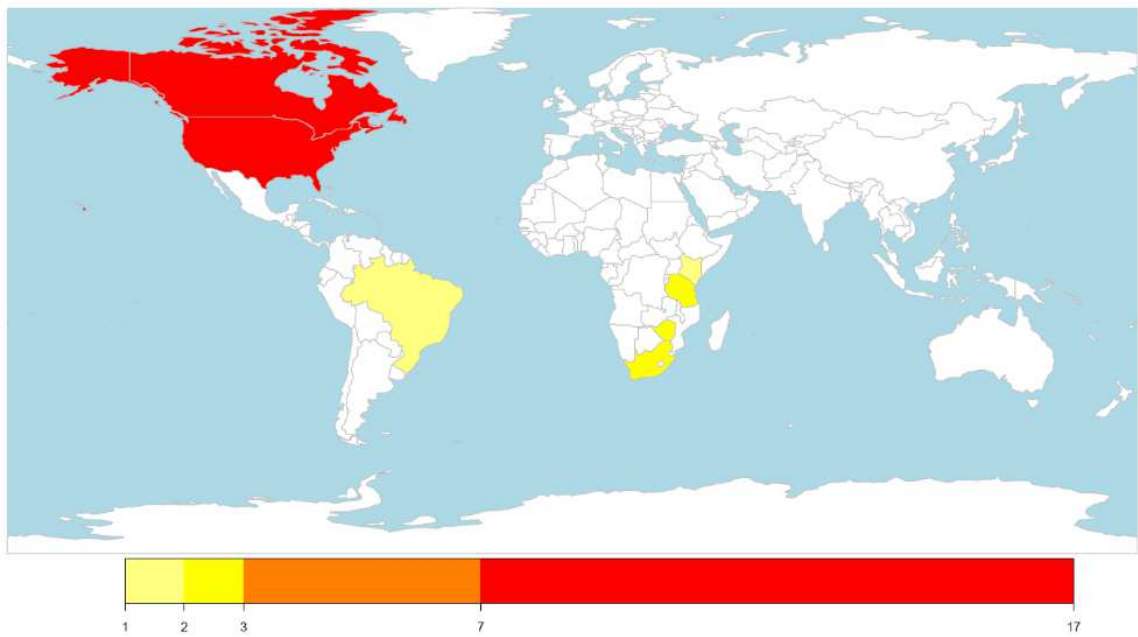


Figure 2

a)



b)

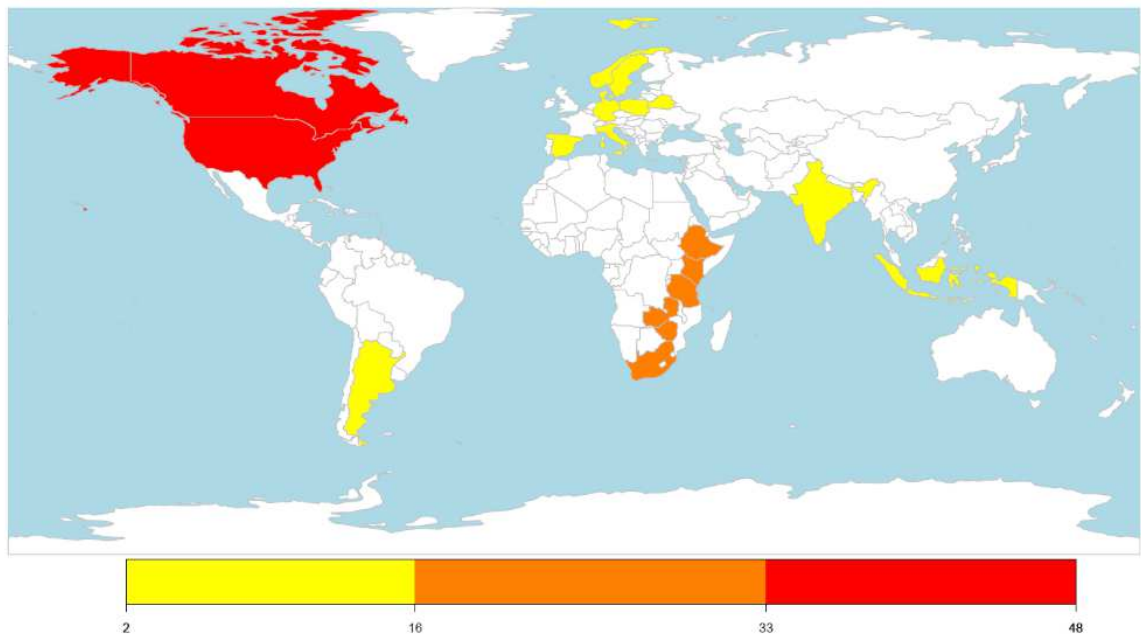


Figure 3:

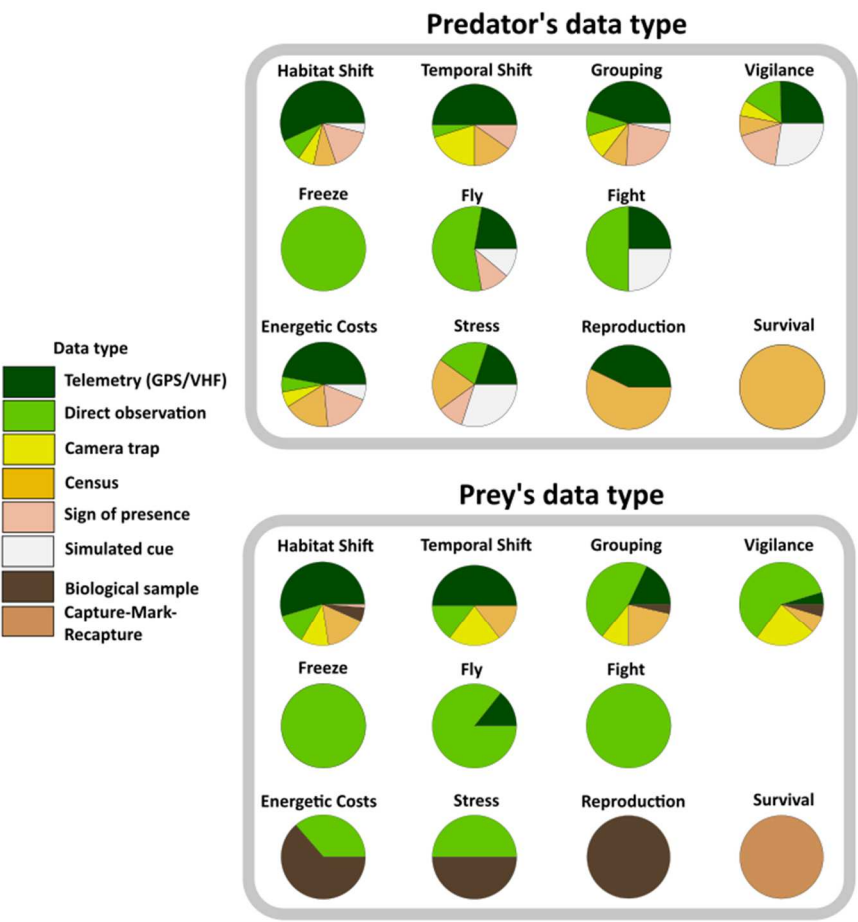
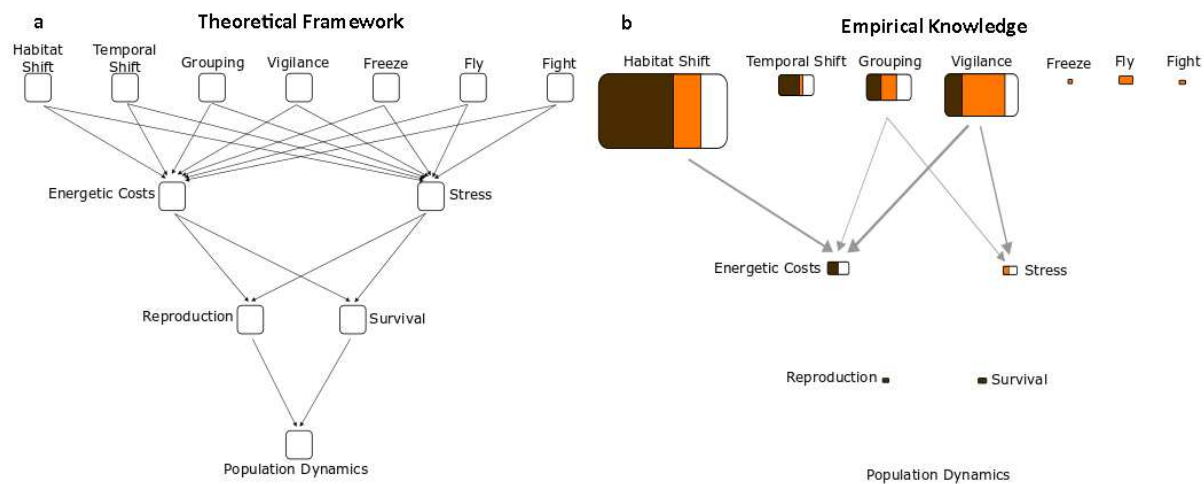


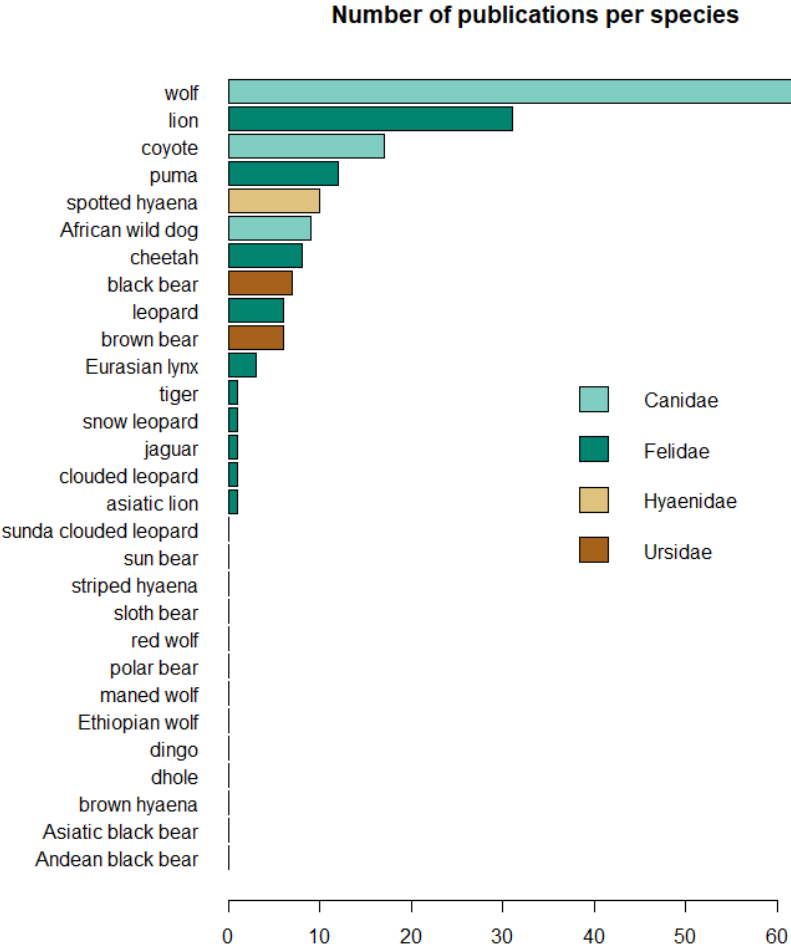
Figure 4:



APPENDICES

Appendix A: a) Number of publications per large carnivore species (body weight > 15kg 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 figure 1 because of the multi-predator or multi-prey species studies.

a)



851 **b)**

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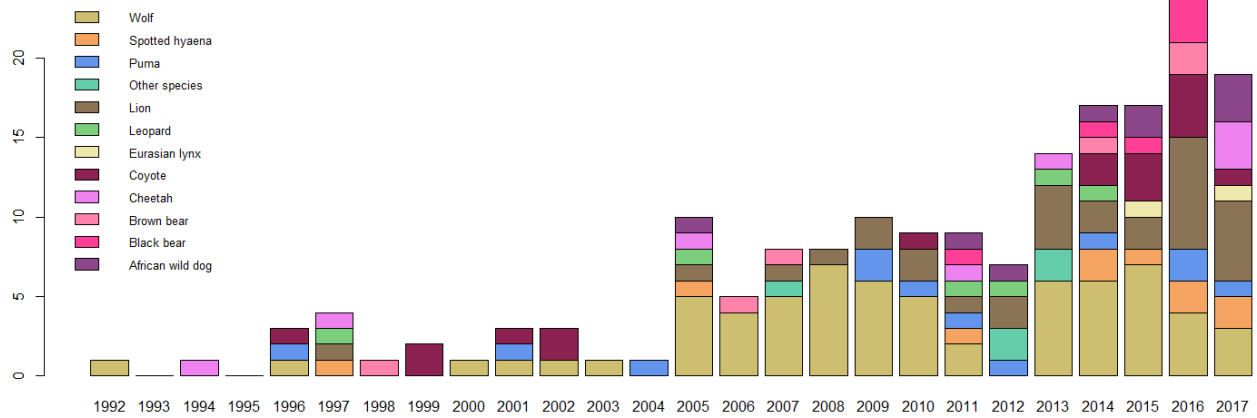
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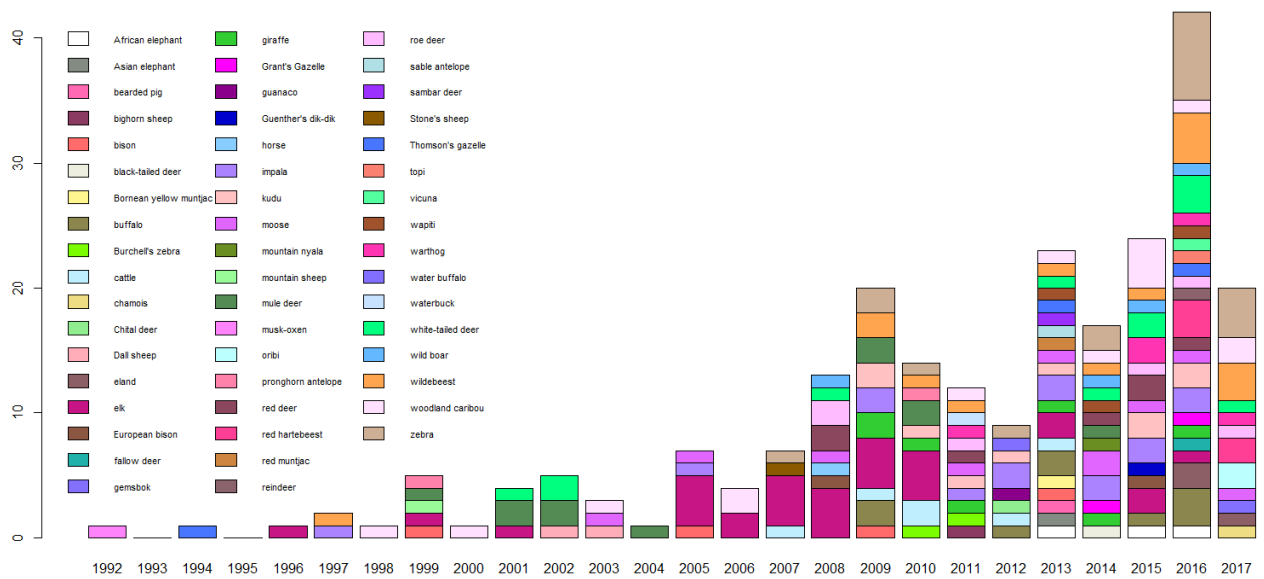
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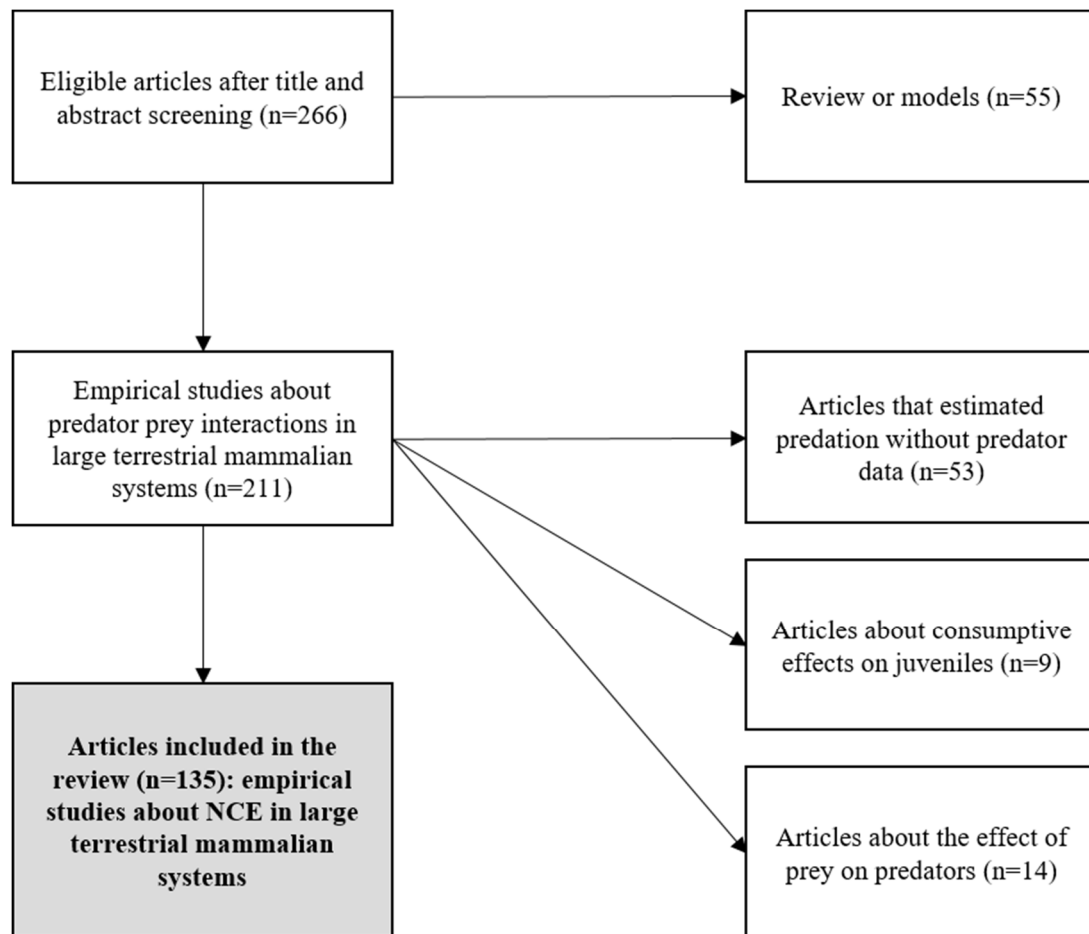
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Appendix B: Schema of the literature reviewing process. The research process was done with Web of Science Core Collection database, and was stopped the 12th of April 2018.



Appendix C: Data sources

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