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

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

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1 **Abstract**

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

20

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

23

## 24 **1. Introduction**

25 Predation is one of the most important interspecific interactions that shape communities  
26 (Paine, 1992). Predators have two kinds of effects on prey populations. First, by killing prey,  
27 predators affect the survival of prey individuals, and may ultimately affect prey population  
28 dynamics if the mortality is additive and not compensatory (i.e. predators kill individuals that  
29 are not weak or expected to die from another cause soon). This is referred to as the lethal  
30 effects or consumptive effects (this is the term we will use in this review - CE hereafter) of  
31 predators on their prey populations (Schmitz et al., 1997; Preisser et al., 2005; Creel and  
32 Christianson, 2008). Second, the mere presence of predators in the landscape represents a  
33 threat that leads prey to develop anti-predator responses, which often entail modifications of  
34 morphological, physiological or behavioural traits (Lima and Dill, 1990; Boonstra et al.,  
35 1998). These anti-predator responses should incur costs (food-mediated or stress-mediated),  
36 which may lead to a decrease in prey performance (growth, reproduction, survival), and  
37 ultimately affect prey population dynamics. This is referred to as the non-lethal effects or risk  
38 effects or non-consumptive effects (this is the term we will use in this review - NCE  
39 hereafter) of predators on their prey populations (Schmitz et al., 1997; Preisser et al., 2005;  
40 Creel and Christianson, 2008).

41 Historically, CE of predation were the most studied aspect of predation. NCE were not  
42 considered (Roughgarden and Feldman, 1975; Lima, 1998) or thought to have a negligible  
43 impact on prey population dynamics (Sih et al., 1985). However, studies on the trade-off  
44 between foraging and predation risk avoidance in invertebrates and small vertebrates revealed  
45 that anti-predator behavioural responses lead to a reduction in activity (Peacor and Werner,  
46 1997; Peacor, 2002) or a spatial/temporal avoidance of the predator associated with a shift to  
47 foraging areas/times where resource quality is lower (Abrams, 1984; McNamara and Houston,  
48 1987; Lima and Dill 1990; Peckarsky et al., 1993; Brown, 1999; Brown and Kotler, 2004;

49 Fraser et al., 2004). Besides, studies on stress in snowshoe hares (*Lepus americanus*) showed  
50 that exposure to high predation risk leads to chronic stress, which has an impact on variables  
51 such as the quantity of leucocytes and the body mass, and ultimately leads to smaller and  
52 lighter litter (Boonstra et al., 1998; Sheriff et al., 2009). These studies suggested that anti-  
53 predator behavioural responses carry costs for prey, and ultimately have consequences on  
54 population parameters such as survival and reproduction, which may affect prey population  
55 dynamics similarly to the CE of predation (Peckarsky et al., 1993; Nelson et al., 2004;  
56 Preisser et al., 2005). For instance, in the Lake Erie (USA-Canada), the NCE of an invasive  
57 species (*Bythotrephes logimanus*) on its prey populations (*Daphnia mendotae* and *Daphnia*  
58 *retrocurva*) was ten times greater than CE (Pangle et al., 2007). This importance of NCE was  
59 made clear in a meta-analysis mostly based on invertebrate predator-prey systems, which  
60 revealed that predators can have a greater effect on prey demography through NCE than  
61 through CE, with NCE that can reach 85% of the total predator effect (Preisser et al., 2005).

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

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

79

## 80 **2. Methods**

81 This literature review focused on large terrestrial mammalian carnivores (>15kg, Ripple et al.,  
82 2014) and their ungulate prey. We further included the coyote (*Canis latrans*, 7-18 kg, Way,  
83 2007) since it is the top predator of ungulates in several ecosystems. We conducted a  
84 literature search using the Web of Science Core Collection database (WoS hereafter). We  
85 searched all publications for the following key words: “antipredator strategy” (we also  
86 checked with the word “anti-predator” throughout), “antipredator behaviour (or behavior)”,  
87 “antipredator responses”, “risk of predation”, “predation risk”, “risk effect”, “non-lethal  
88 effect”, “non-consumptive effect”, “ecology of fear”, and “landscape of fear”. All of these  
89 keywords were combined (with the Boolean connector AND) with the three following  
90 keywords: “large mammal”, “large herbivore” and “ungulate”. We then performed a search  
91 with the keyword “predation risk” combined with the 29 species of large terrestrial carnivores  
92 (Appendix A(a)). Based on titles and abstracts, we excluded publications that were not  
93 empirical studies of NCE in a large carnivore-ungulate system. 266 publications were selected  
94 for a full and comprehensive reading. Studies that were either reviews or modelling works (n  
95 = 55) were excluded at this stage. We then excluded studies that quantified predation risk by  
96 using habitat data only (n=53), studies that focused on the CE of predators on juvenile prey (n  
97 = 9), and studies that looked at the effect of prey on their predator (n = 14). At the end of this

98 selection process, we retained 135 publications (see Appendix B for the summary of the  
99 selection process of the publications kept for this review, and see Appendix C for the list of  
100 publications).

101 Only a few studies existed between 1992 and 2004, and since then the number of  
102 publications has kept increasing (Fig. 1). This increase is due to the growing interest for NCE  
103 in the study of predator-prey interactions in large mammals but also to the improved  
104 technology (e.g. GPS technology, camera trapping) that makes these studies possible to  
105 conduct. During our literature search, we realized that most of the studies before the 1990s are  
106 not properly referenced electronically in WoS (missing keywords, abstract...). Thus, for this  
107 systematic review, we only considered studies from 1992 onwards. We are aware that a few  
108 pioneering studies took place before 1992, particularly with regard to vigilance behaviour, but  
109 we favoured maintaining a systematic approach based on the post-1992 WoS database over  
110 including pre-1992 studies that we were aware of, and therefore likely missing others. As our  
111 study shows, the study of NCE in large terrestrial mammals is relatively recent, and we  
112 believe including these few studies would not alter our conclusions.

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

116

### 117 **3. Where is our knowledge from?**

#### 118 ***3.1. Location of studies and species studied***

119 Before 2007 (n = 33 publications), almost all studies were carried out in North America (28  
120 publications), with a few studies in Southern and Eastern Africa (4 publications) (Fig. 2a).

121 This dominance of North American ecosystems led to a focus on the North American  
122 carnivores in the first NCE studies, with 20 studies on wolf (*Canis Lupus*), 6 on coyote (*Canis*



123 *latrans*), 3 on puma (*Puma concolor*), and 3 on grizzly bear (*Ursus arctos*; Appendix A(b)).  
124 Since 2008 (n = 102 publications), we note a diversification of the locations of the studies  
125 (Fig. 2b). Most studies still come from North America (48 publications). However, African  
126 ecosystems have been the focus of a growing number of studies (33 publications), a trend also  
127 noted for Europe (15 publications) where large predators have recolonized large parts of the  
128 landscape (Chapron et al., 2014). This resulted in a diversification of the predator species  
129 studied (Appendix A(b)) even though the most studied carnivore is still the wolf (48  
130 publications), followed by the African lion (*Panthera leo*; 28 publications) and the coyote (11  
131 publications). Overall, the Yellowstone National Park (n=19; 14% of the publications) is the  
132 ecosystem the most studied for NCE in large carnivore-ungulate systems. The total number of  
133 prey species studied was high (n=52). Studies on elk (*Cervus elaphus*) were dominant during  
134 the period 2005-2010, and studies on plains zebra (*Equus quagga*) increasingly contributed to  
135 NCE studies in the last years, but overall the literature was very heterogeneous in terms of the  
136 prey species studied (Appendix A(c)).

137

### 138 ***3.2. Assessment of predation risk in the study systems***

139 Our knowledge on NCE is clearly dominated by studies that considered one predator species  
140 only (79% of the publications; n = 107; Fig. 1a). However, only 10% of the studies (n = 13)  
141 were carried out in a system with one predator species (Fig. 1a). Predator communities are  
142 often composed of several predator species and predation risk faced by a prey can thus come  
143 from different predators. For the systems with two or more predator species (n=122), we  
144 calculated an index of predator community completeness as the number of large predators  
145 studied divided by the number of large predators present in the ecosystem (extracted from  
146 Ripple et al., 2014 – we could not extract this information for 17 studies). This index ranged  
147 from values very close to 0 (0 is excluded as it would mean that no predator species was

148 studied and hence this is out of the scope of this review) to 1 (meaning that the study  
149 considered the whole predator community). For the 105 studies for which we could calculate  
150 the index of predator community completeness, the average index value was 0.41 (SD = 0.25)  
151 and 61% (n = 64) of the studies had an index value lower than 0.5, highlighting that most  
152 studies focused on one or a couple of predator species in ecosystems with a richer predator  
153 community. However, 11% (n = 12) of the studies had an index value of 1, i.e. studied the  
154 whole predator community. The studies focusing on several predator species are becoming  
155 more common (Fig. 1a).

156

### 157 ***3.3. Level of anthropization of the study systems***

158 Only 15% of terrestrial lands and inland water are protected areas (World Database on  
159 Protected Areas). However, 62% of the 135 studies reviewed here were in protected areas.  
160 Basing our understanding of NCE from studies conducted in protected areas only would lead  
161 to biased predictions about the strength of NCE in contexts where human and their activities  
162 may interact with predator-prey interactions (Smith et al., 2015; review in Kuijper et al.,  
163 2016). Here, we used the human footprint index (from Sanderson et al., 2002, dataset from  
164 SEDAC, WCS and CIESIN) to evaluate the level of anthropization of the systems studied. In  
165 our dataset, 96 studies (out of the 135 selected for this review) reported GPS coordinates and  
166 we were able to collect the geographic position of an additional 37 studies (we encourage  
167 future studies to consistently report the GPS coordinates of the study systems). Studies were  
168 located in ecosystems with a human footprint index ranging from 0 (no human influence) to  
169 78 (high level of anthropization), but a majority (73%; n=99) was characterized by a low  
170 human footprint index (between 0 and 20). It is interesting to note however that there is a  
171 recent diversification in the human footprint values characterizing NCE studies with several  
172 studies in ecosystems with rather high human footprint indices in the past five years (Fig. 1b).

173

### 174 **3.4. Methodology used in NCE studies**

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

194

### 195 **4. What have we learnt?**

196 In this review, we decomposed the different components of NCE (Fig. 4; see also Creel,  
197 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).

223 Another well-studied aspect of anti-predator behaviour is how individuals modify their  
224 social dynamics when faced with increased predation risk (Fig. 4, 23 publications; e.g. Lima,  
225 1995; Roberts, 1996; Creel and Winnie, 2005; Creel et al. 2014). Most studies (n=18) found  
226 an increase of the group size due to predation risk. Indeed, larger groups are often associated  
227 with a reduced predation risk because of an improved detection of approaching predators  
228 thanks to collective detection (the “many eyes effect” (Powell, 1974)), and because of a  
229 “dilution effect” whereby the probability of an individual to be targeted by the predator  
230 decreases as group size increases (Bertram, 1978). However, a few studies found a negative  
231 correlation between predation risk and group size. This could arise because smaller groups are  
232 more difficult to detect for predators (Creel and Winnie, 2005), or because of interactions  
233 between vigilance and other anti-predator behaviours (Patin et al. 2019). The numbers of  
234 publications that looked at changes in group size as a proactive and reactive response are  
235 balanced.

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

244 The three other anti-predator responses are exclusively reactive responses: freezing,  
245 flying and fighting (Fig. 4). They are the anti-predator responses that have been the least  
246 studied (Fig. 4). However, the study of prey fighting when exposed to a predator is a growing

247 part of the literature (Mukherjee and Heithaus, 2013), especially because the dangerousness of  
248 prey influences prey preference by predators (Tallian et al., 2017).

249

#### 250 ***4.2. A focus on the studies that went beyond anti-predator behavioural responses***

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

261 Three studies on stress used experiments simulating predator's presence and  
262 concluded that prey stress level strongly increased as a response to an immediate predation  
263 risk (reactive response; Chabot et al., 1996; Christensen and Rundgren, 2008; Cooke et al.,  
264 2013). However, the three other studies measured fGCM (faecal Gluco-Corticoid Metabolite)  
265 in natural environments to investigate how prey stress levels vary with longer-term variations  
266 in predation risk (proactive response), and concluded that prey do not have higher baseline  
267 stress hormone level in risky areas (Creel et al., 2009; Périquet et al., 2017; Zbyryt et al.,  
268 2018).

269 Eleven publications attempted to assess the energetic costs of predation risk through  
270 prey foraging behaviour (Altendorf et al., 2001; White and Feller, 2001; Kluever et al., 2009;  
271 Creel et al., 2014), foraging patch quality (Harvey and Fortin, 2013), measures of prey body

272 condition (body fat: Middleton et al., 2013; chest size: Bourbeau-Lemieux et al., 2011), or  
273 faecal samples to evaluate diet quality (Hernández and Laundré, 2005; Christianson and  
274 Creel, 2008; Creel and Christianson, 2009; Christianson and Creel, 2010; Barnier et al.,  
275 2014). Most studies demonstrated correlations between the level of predation risk and the  
276 proxies used to assess energetic costs (Table 1). Of these 11 publications, four were  
277 associated with the study of habitat shift (Altendorf et al., 2001; White and Feller, 2001;  
278 Hernández and Laundré, 2005; Middleton et al., 2013) and two found an effect of habitat shift  
279 when predation risk was higher: reduction in diet quality (Hernández and Laundré, 2005) and  
280 reduction in browsing activity (White and Feller, 2001). Five publications on the energetic  
281 costs of predation risk were associated with the study of vigilance (Altendorf et al., 2001;  
282 White and Feller, 2001; Kluever et al., 2009; Middleton et al., 2013; Creel et al., 2014). Four  
283 of these studies found that an increase in prey vigilance level was linked to a decrease in the  
284 prey foraging rate (or higher giving-up densities) under high predation risk (Altendorf et al.,  
285 2001; White and Feller, 2001; Kluever et al., 2009; Creel et al., 2014). However, one study  
286 found no change in prey body condition associated to increased vigilance levels (Middleton et  
287 al., 2013). Finally, one study focused on the link between group size changes and energetic  
288 costs, but found no effect (Creel et al., 2014).

289         Only six publications looked at the effects of predation risk on prey individual  
290 performance: reproduction (4 publications that showed an effect; Table 1) or survival (2  
291 publications that showed an effect; Table 1). The effect of predation risk on prey reproduction  
292 was assessed through the pregnancy status of individuals harvested by people (Proffitt et al.,  
293 2014; Cherry et al., 2016), blood concentration of progesterone (Hayes et al., 2003) or  
294 concentration of progesterone from faecal samples (Creel et al., 2007). Two publications  
295 studied the effect of predation risk on survival (Bourbeau-Lemieux et al., 2011; Eacker et al.,  
296 2016). For the first time in large mammals, Bourbeau-Lemieux et al. (2011) showed that

297 during years of high puma predation, bighorn sheep *Ovis canadensis* lambs also suffered  
298 mortality through reduced growth (lambs would have been larger without predation and  
299 survival is a function of lamb body size), contributing a third of the total impact of predation  
300 on lamb survival (NCE: 8% decrease of survival; CE: 20%). Eacker et al. (2016) looked at the  
301 effect of predation risk by multiple carnivores on wapiti (*Cervus canadensis*) calf survival and  
302 showed that different predator species have contrasted effects and hat season matters.  
303 However, they could not disentangle the role of CE and NCE. No study investigated the  
304 consequences of NCE for prey population dynamics. Overall, the links between the different  
305 components of NCE have been seldom studied (Fig. 4).

306

## 307 **5. Discussion**

308

### 309 ***5.1. The importance of diversifying the systems studied***

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



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

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

347 Other important factors that can modulate the strength of NCE are the characteristics  
348 of the environment where predator-prey interactions occur (Brown and Kotler, 2004; Laundré  
349 et al., 2014). In a context of increasing overlap between human-dominated and carnivores'  
350 habitats (Chapron et al., 2014; Ripple et al., 2014), it is of particular importance to understand  
351 how people and their activities may interact with predator-prey interactions (see Kuijper et al.,  
352 2016 for a review of the mechanisms involved). For example, carnivores may increase their  
353 kill rate when they approach human settlements because of the fear of people (Smith et al.,  
354 2015), or prey may use human infrastructures as a shield against carnivores (Berger, 2007).  
355 Hence, human presence may influence the perceived predation risk by prey and hence affect  
356 the level of their anti-predator responses.

357

## 358 *5.2. The importance of considering the complexity of the systems studied*

359 By considering one prey and one predator only in often multi-prey multi-predator systems,  
360 interspecific interactions other than the predator-prey interaction studied are omitted.  
361 However, these interactions can modulate the NCE of predation on prey (Wootton, 2002; see  
362 also Montgomery et al., 2019). For example, in the Madison Valley (Montana, USA), it has  
363 been shown that elk shift to habitats that have more complex structure to reduce predation risk  
364 from wolves, but this significantly increases the predation risk from puma (Atwood et al.,  
365 2009). In that case, considering wolves only would minimize the overall NCE of predation  
366 suffered by elk. In natural ecosystems, it is difficult to study all large carnivore species but the  
367 development of GPS-technology, animal-borne video, and camera trapping in ecological  
368 studies provides increased possibilities to address this complexity (Prugh et al., 2019). This  
369 review has revealed a growing number of studies focusing on multiple predators when  
370 studying NCE. This effort needs to continue to understand how species interactions can  
371 modulate NCE. It is an important corner stone in future research of NCE to grasp the full

372 picture of NCE in natural ecosystems. The role of interactions between prey or of dilution  
373 effects in multi-prey systems, even though not addressed in this review, is important to  
374 consider when assessing the NCE of predation (Montgomery et al., 2019).

375

### 376 ***5.3. Anti-predator behavioural responses of prey: the tip of the iceberg***

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

383         It is easier to measure stress, energetic costs, reproduction and survival and to design  
384 experiments to disentangle the role of CE and NCE of predation in invertebrates or small  
385 vertebrates, which are short-lived species often easy to manipulate. In such systems, we have  
386 learnt a lot from experiments where predators were caged (e.g. Peacor, 2002) or the presence  
387 of the predator was simulated over critical periods for the reproduction and survival of prey  
388 (e.g. Zanette et al, 2011). In large mammalian systems, where species are long-lived and  
389 difficult to manipulate, this is more challenging. It is possible to carry out experiments where  
390 the presence of the predator is simulated (visual, olfactory or auditory cues). So far, this has  
391 been done over short periods to assess prey behavioural responses or stress responses.  
392 However, this will need to be done over much longer periods (if this is ethically possible) to  
393 assess the impact of predation risk on prey population dynamics. In any case, in natural  
394 ecosystems, it will be impossible to exclude the CE of predators that roam naturally in the  
395 landscape. The best way forward therefore lies in approaches similar to the one used by  
396 Bourbeau-Lemieux et al. (2011) who studied the impact of contrasting periods of puma

397 predation on bighorn sheep body condition and survival over 27 years to disentangle the  
398 impacts of CE and NCE. The unique insights provided by this study rely on two important  
399 aspects: the long-term monitoring of the prey population and the handling of prey individual  
400 to measure individual performance proxies. Long-term studies are indeed crucial to assess the  
401 effect of predation on a prey population dynamics and the scarcity of such studies explains the  
402 knowledge gap on the effect of predation risk on prey reproduction and survival. Additionally,  
403 the capture of individual prey is needed to take biological samples and body measurements.  
404 People around the world harvest wild ungulate populations, and this could be considered as a  
405 useful source of information to evaluate the NCE of predators on prey population parameters.  
406 The studies that estimated energetic costs and stress due to predation risk made the implicit  
407 assumption that it would affect survival and reproduction of prey and that it would ultimately  
408 affect prey population dynamics. Even though this has been demonstrated in invertebrates  
409 (Peckarsky et al., 1993; Peacor and Werner, 2004), nearly nothing is known for large  
410 terrestrial mammals and this is a major challenge for future studies if we want to  
411 comprehensively understand NCE, from the behavioural responses of prey individuals to the  
412 modification of prey population dynamics. Behavioural anti-predator responses are just the tip  
413 of the NCE's iceberg.

414

## 415 **6. Implications for conservation**

416 Populations of large carnivores are characterized by major changes in their abundance and  
417 distribution worldwide with declines in many ecosystems (Ripple et al., 2014), recolonization  
418 of human-dominated habitats in Europe (Chapron et al., 2014), and reintroduction in many  
419 reserves (Hayward and Somers, 2009). These changes mean the loss or appearance of CE but  
420 also NCE of predators on ungulate populations, which will have cascading effects down the  
421 food chain and for the whole ecosystem functioning (Estes et al., 2011). While CE are well

422 understood and can be easily quantified, our review reveals that, in spite of the widespread  
423 evidence of anti-predator behavioural responses in ungulates, current knowledge prevents us  
424 for predicting the population-level consequences of NCE in large mammals (Fig. 4). Studies  
425 on invertebrates and small vertebrates demonstrated the underappreciated importance of NCE.  
426 For example, Zanette et al. (2011) demonstrated that predation risk (simulated with predators  
427 calls) reduced by 40% the number of offspring produced per year by songbirds. In large  
428 mammals, evidence of population-level consequences of NCE is extremely scarce. Bourbeau-  
429 Lémieux et al. (2011) were the first to demonstrate that NCE can account for a third of the  
430 total impact of predation on prey population survival. If NCE can have such an important  
431 impact, they need to be taken into account and anticipated in the management of large  
432 mammal populations (e.g. for the reintroduction of large carnivores; see also Allen et al.,  
433 2019 for animal welfare considerations). However, in natural environments, many factors  
434 may affect the strength of NCE (predator and prey attributes, landscape characteristics, and  
435 the complexity of large mammal communities) and NCE may be negligible under some  
436 circumstances (Fig. 1c; e.g. Middleton et al. 2013). Linking anti-predator behavioural  
437 responses to demography in different contexts is thus the key challenge ahead of us to fully  
438 understand the NCE of predators on their prey in large mammals. This information is crucial  
439 for a sound management and conservation of large mammals worldwide.

440

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722 *Behavioral Ecology* 29, 19–30. <https://doi.org/10.1093/beheco/arx142>  
723

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

Predator species	Prey species	Outcome	Reference
<b>Stress</b>			
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.
<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	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.
<b>Reproduction</b>			

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.
<b>Survival</b>			
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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728 **Figure legends**

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730 **Figure 1:** The number of publications per year according to **a)** whether the study was about  
731 one predator species or more (ecosystems with one predator only are represented with  
732 hatches), **b)** the human footprint index (index ranging from 0 to 100; from Sanderson et al.,  
733 2002), **c)** whether the study showed an effect of predation risk on the study NCE component.  
734 The total number of publications reviewed is 135. The length of the bars may differ as we  
735 could not extract the human footprint index for all study systems and as some studies tested  
736 several effects (all conclusions are reported in c).

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738 **Figure 2:** Number of publications per region **a)** between 1992 and 2007, **b)** between 2008 and  
739 2018. The countries where the studies took place are coloured according to the number of  
740 publications per continent. The colour legends are not homogenized between the two periods  
741 not to reflect just the overall increase in the number of studies. Note that this review focuses  
742 on carnivore-ungulate systems, which explains why there is no publication in Australia.

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

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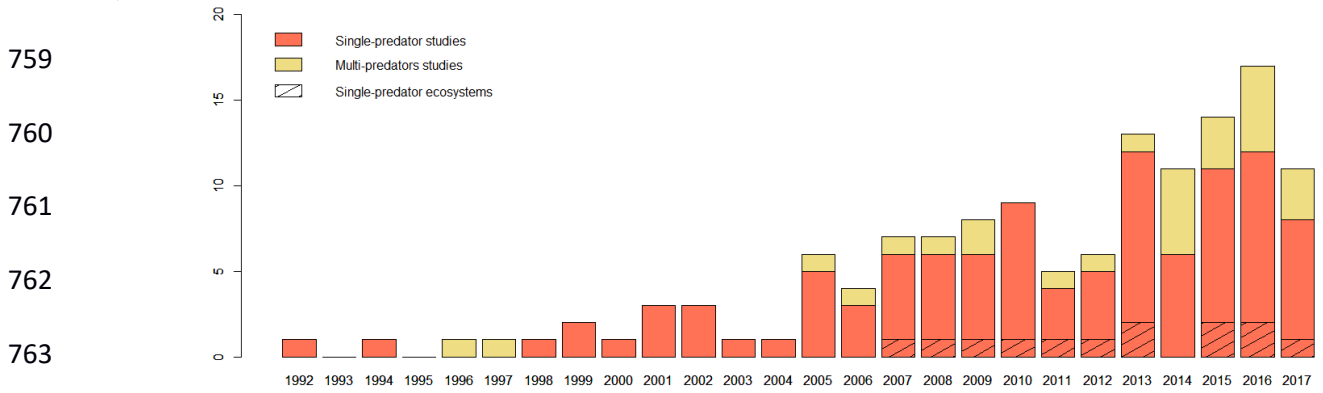
747 **Figure 4:** **a)** Conceptual diagram of NCE components and the links between the different  
748 components. **b)** Representation of our empirical knowledge. Rectangle size and link width are  
749 proportional to the number of studies that focused on the different NCE components and on  
750 the links between the different components. Brown colour represent the proportion of studies  
751 that found a proactive effect of predation risk, orange colour represents the proportion of  
752 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.

756 **Figure 1**

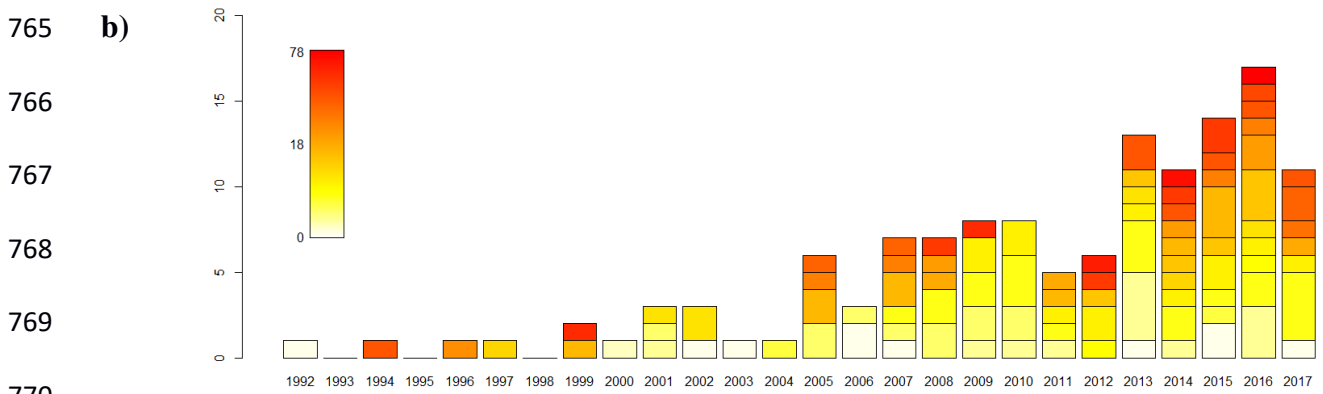
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758 **a)**

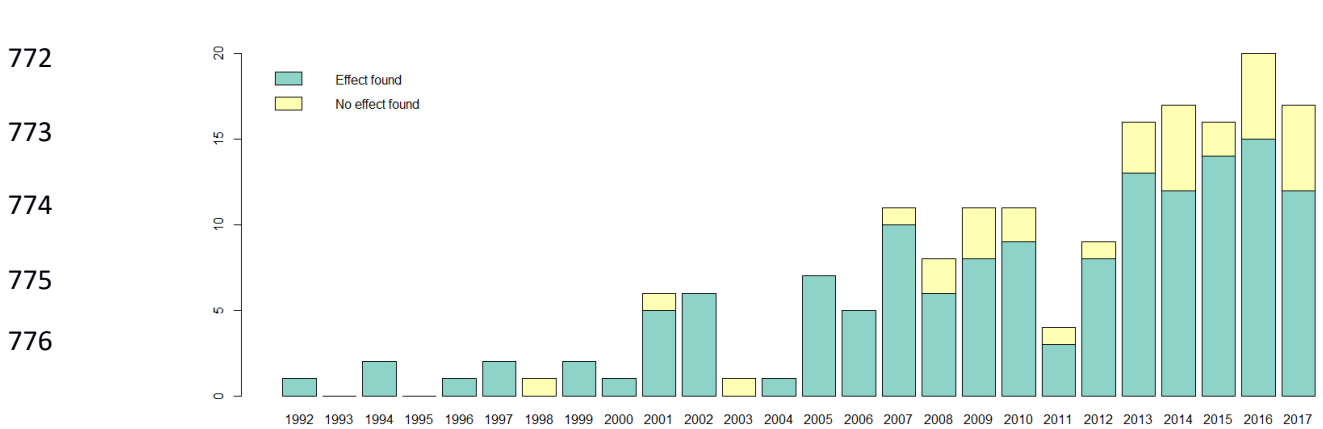


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765 **b)**



771 **c)**



777 **Figure 2**

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779 **a)**

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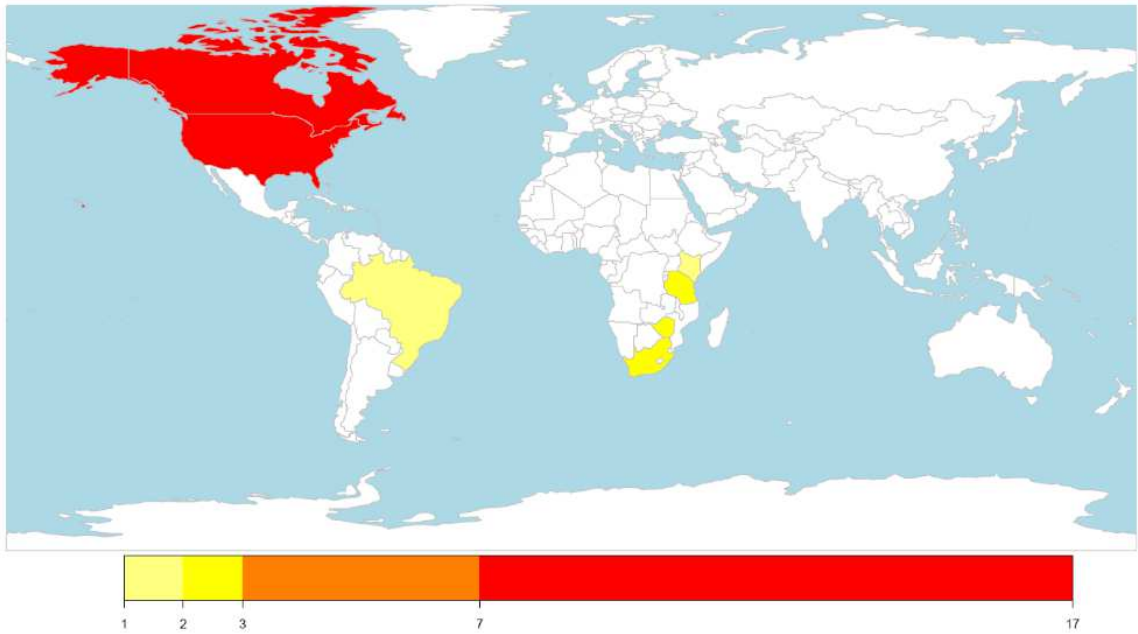
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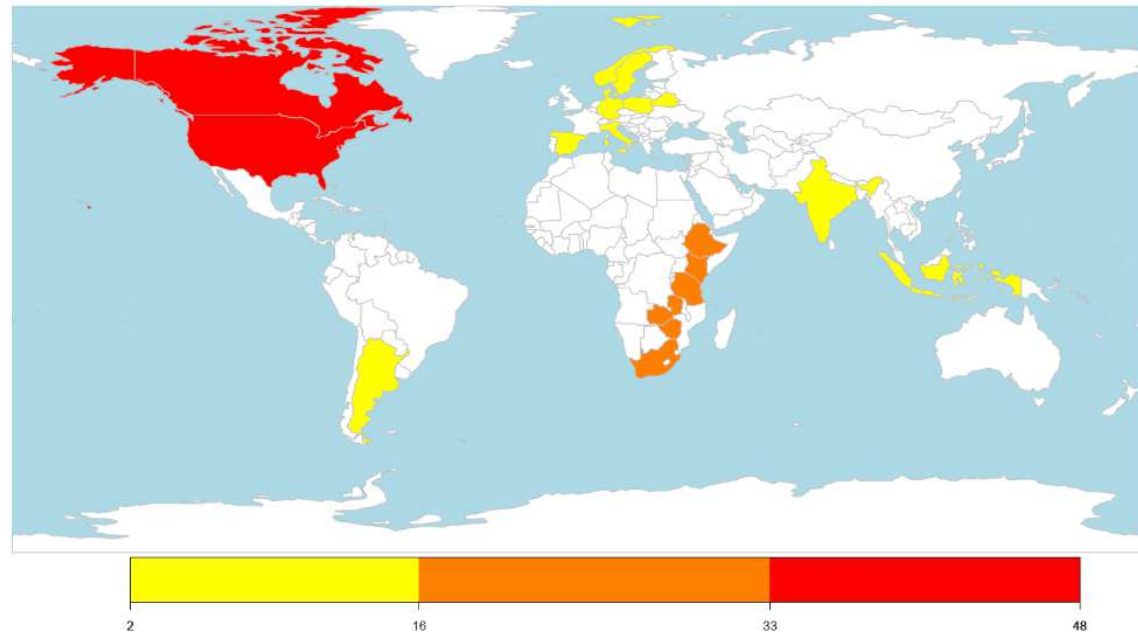
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**b)**





800 **Figure 3:**

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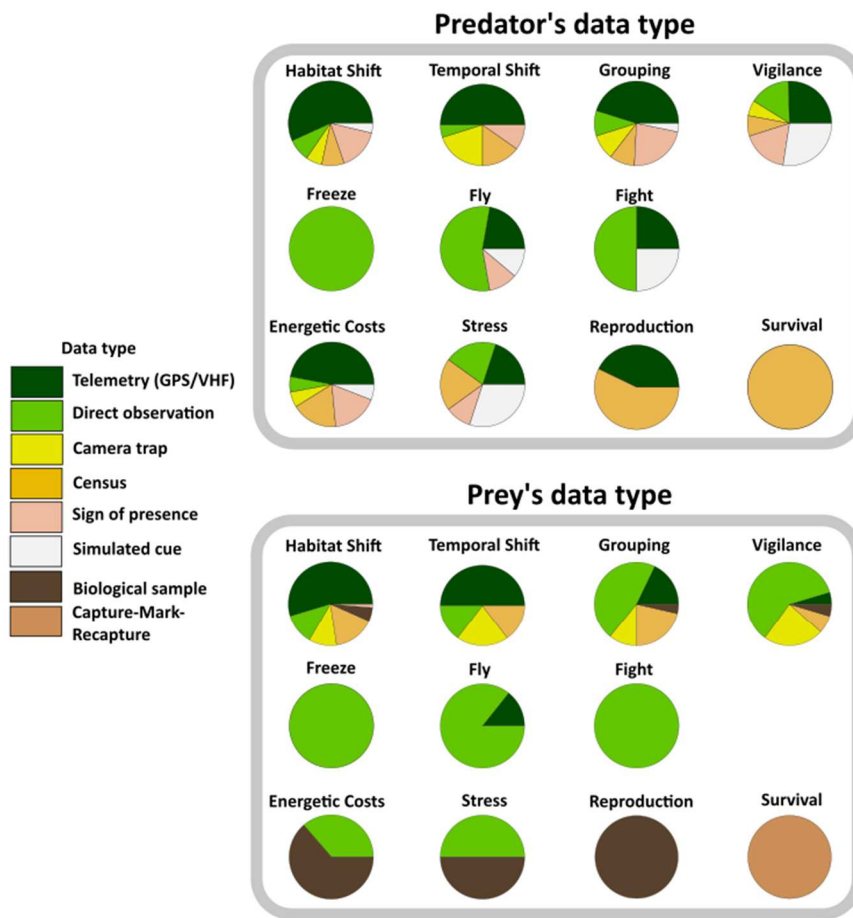
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816 **Figure 4:**

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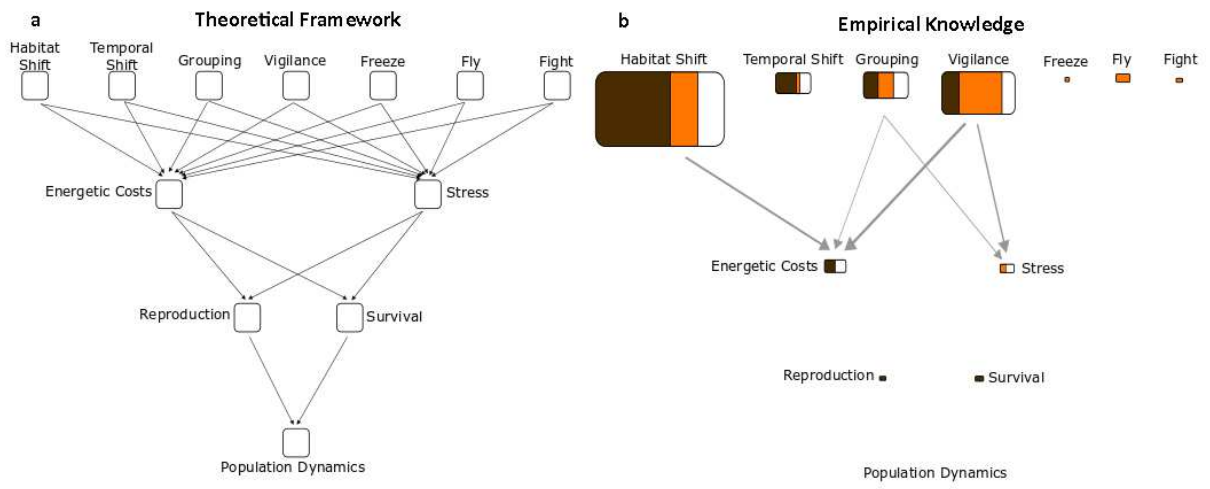
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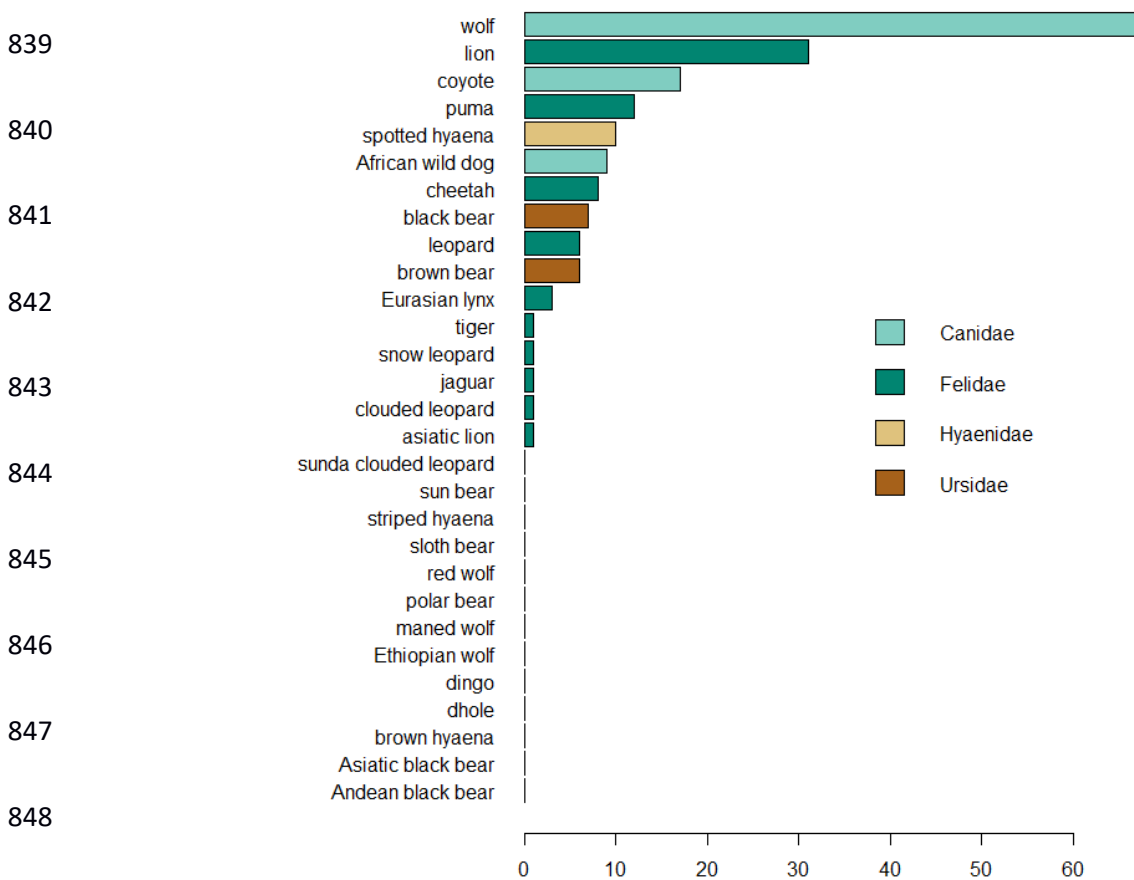
828 **APPENDICES**

829 **Appendix A: a)** Number of publications per large carnivore species (body weight > 15kg as  
 830 defined in Ripple et al., 2014), and according to the taxonomic group. The graph shows that  
 831 NCE studies focused on a small proportion of large predator species. **b)** Number of  
 832 publications per year according to the predator species studied (the “other species” category  
 833 refers to the carnivore species listed in (a) and not detailed in (b)). **c)** Number of publications  
 834 per year according to the prey species studied. The length of the bars in (b) and (c) is  
 835 sometimes different from that of the corresponding bars in figure 1 because of the multi-  
 836 predator or multi-prey species studies.

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838 **a)**

**Number of publications per species**



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851 **b)**

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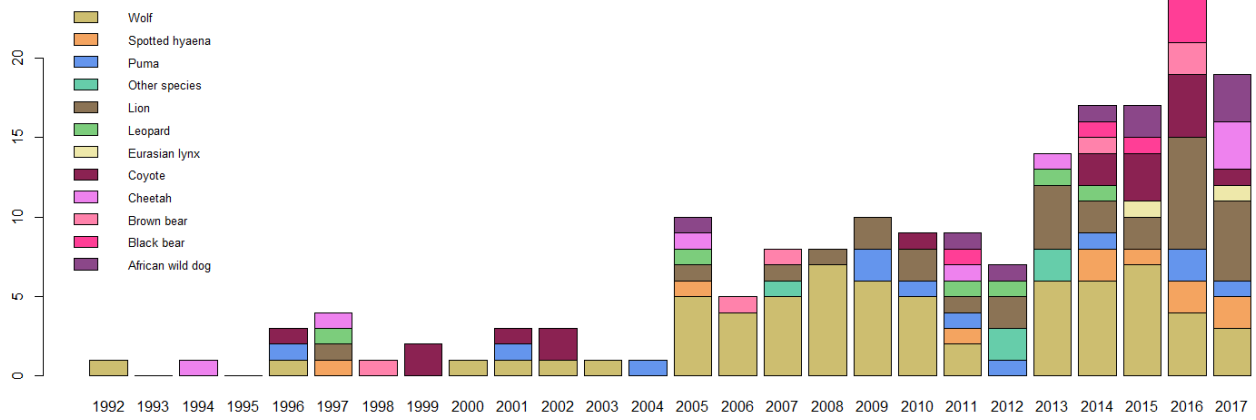
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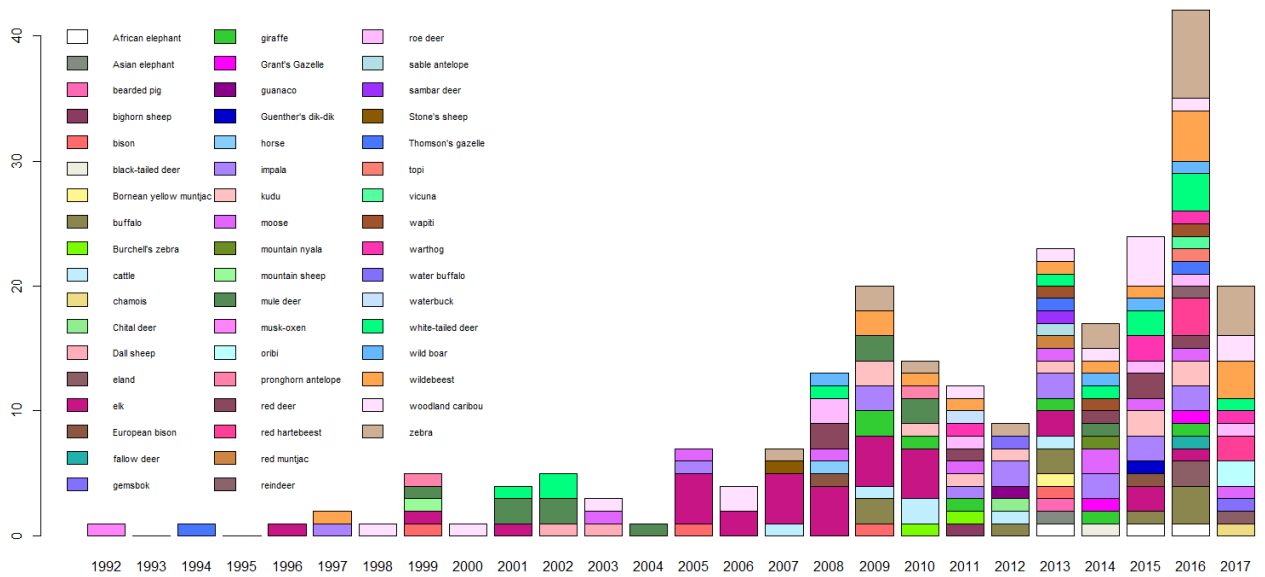
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870 **Appendix B:** Schema of the literature reviewing process. The research process was done with  
871 Web of Science Core Collection database, and was stopped the 12<sup>th</sup> of April 2018.

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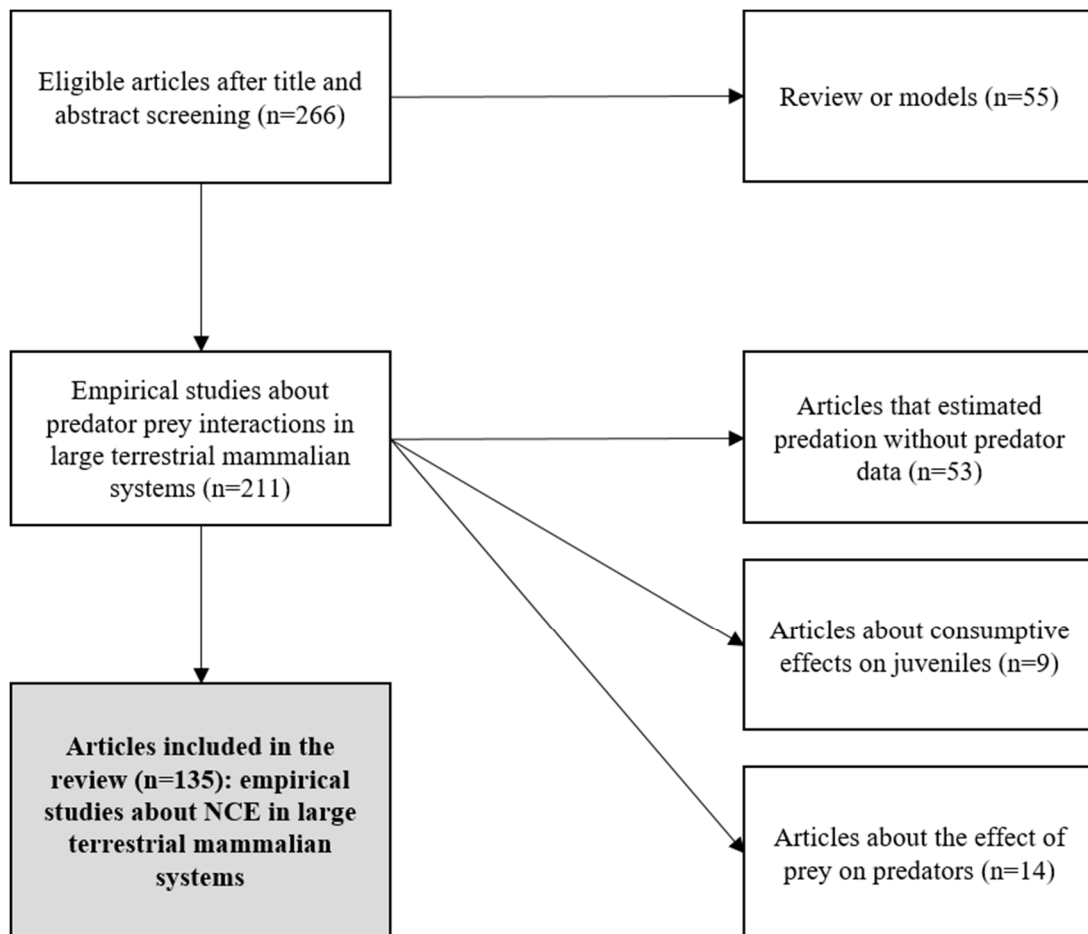
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891 **Appendix C: Data sources**

- 892 Altendorf, K.B., Laundré, J.W., Pez, C.A.L., Lez, G., Brown, J.S., 2001. Assessing effects of  
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