

Large carnivore impacts are context-dependent

Haswell, P.M.; Kusak, Josip; Hayward, M.W.

Food Webs

DOI:

[10.1016/j.fooweb.2016.02.005](https://doi.org/10.1016/j.fooweb.2016.02.005)

Published: 01/09/2017

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Haswell, P. M., Kusak, J., & Hayward, M. W. (2017). Large carnivore impacts are context-dependent. *Food Webs*, 12, 3-13. <https://doi.org/10.1016/j.fooweb.2016.02.005>

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1 Haswell PM, Kusak J, Hayward MW (2017) Large carnivore impacts are context-dependent. Food
2 Webs 12:3-13. doi: 10.1016/j.fooweb.2016.02.005

3
4 Article history:

5 Received 24 September 2015

6 Received in revised form 7 January 2016

7 Accepted 9 February 2016

8 Available online 6 March 2016

9

10 Large Carnivore impacts are context-dependent

11 Peter M. Haswell^{ab}, Josip Kusak^c, Matt W. Hayward^{adef}

12 ^aSchool of Biological Sciences, Bangor University, Bangor, Gwynedd, LL57 2UW, UK.

13 ^bUK Wolf Conservation Trust, Butlers Farm, Beenham, Berkshire, RG7 5NT

14 ^cDepartment of Biology, Veterinary Faculty, University of Zagreb, Heinzelova 55, 10000,
15 Zagreb, Croatia

16 ^dSchool of Environment Natural Resources and Geography, Bangor University, Bangor,
17 Gwynedd, LL57 2UW, UK.

18 ^eCentre for African Conservation Ecology, Nelson Mandela Metropolitan University, Port
19 Elizabeth, South Africa

20 ^fCentre for Wildlife Management, University of Pretoria, South Africa.

21 Corresponding author: Peter M. Haswell, p.m.haswell@bangor.ac.uk

22 **Keywords**

23 Landscape of fear; interspecific competition; apex predator; large carnivore; mesopredator
24 release hypothesis; predation risk.

25 **Abstract**

26 Interactions between large carnivores and other species may be responsible for impacts that
27 are disproportionately large relative to their density. Context-dependent interactions between
28 species are common but often poorly described. Caution must be expressed in seeing apex
29 predators as ecological saviours because ecosystem services may not universally apply,
30 particularly if inhibited by anthropogenic activity. This review examines how the impacts of
31 large carnivores are affected by four major contexts (species assemblage, environmental
32 productivity, landscape, predation risk) and the potential for human interference to affect
33 these contexts. Humans are the most dominant landscape and resource user on the planet and
34 our management intervention affects species composition, resource availability, demography,
35 behaviour and interspecific trophic dynamics. Humans can impact large carnivores in much
36 the same way these apex predators impact mesopredators and prey species - through density-
37 mediated (consumptive) and trait/behaviourally-mediated (non-consumptive) pathways.
38 Mesopredator and large herbivore suppression or release, intraguild competition and
39 predation pressure may all be affected by human context. The aim of restoring 'natural'
40 systems is somewhat problematic and not always pragmatic. Interspecific interactions are

41 influenced by context, and humans are often the dominant driver in forming context. If
42 management and conservation goals are to be achieved then it is pivotal to understand how
43 humans influence trophic interactions and how trophic interactions are affected by context.
44 Trade-offs and management interventions can only be implemented successfully if the
45 intricacies of food webs are properly understood.

46 **1. Introduction**

47 When understanding and managing trophic dynamics, what is deemed a natural or unnatural
48 interaction must first be considered (Rolston 2001). The aim of restoring ‘natural’ systems in
49 the modern era becomes somewhat problematic. Wildlife conservation is still possible in
50 human dominated landscapes but maintaining top-down ecological processes in such
51 landscapes is challenging (Chapron et al. 2014; Linnell et al. 2015; López-Bao et al. 2015).
52 The impacts of world-wide predator decline and the relative importance of direct and indirect
53 species interactions have been highlighted as fundamental ecological questions (Sutherland et
54 al. 2013). Yet caution has been expressed in seeing apex predators like the grey wolf
55 *Carnivora Canidae Canis lupus* as ecological saviours because ecosystem services may not
56 universally apply, particularly if inhibited by anthropogenic activity (Mech 2012).
57 Furthermore, there is only one intact terrestrial predator guild in the world (Africa), so all
58 other guilds may reflect the impacts of the Pleistocene megafauna extinctions and shifting
59 baselines to mesopredator-dominated systems (Fleming et al. 2012; Valkenburgh et al. 2015).
60 The question arises as to what the conservation benchmark or baseline is, was or should be
61 given a particular ecological context (Berger 2008; Hayward 2009; Hayward 2012).

62 Species at higher trophic levels are often lost more rapidly than those at lower trophic levels
63 (Dobson et al. 2006). Apex predator decline and trophic simplification is something of great
64 concern worldwide (Estes et al. 2011; Johnson 2010; Ripple et al. 2014). It is imperative to
65 understand the interactions and potential impacts of apex predators because their absence or
66 decline can have undesired effects (Berger et al. 2008; Jackson et al. 2001; Terborgh et al.
67 2001). The consequences of upper trophic level decline and the loss of ecosystem services
68 provided by large carnivores could lead to environmental degradation through the release of
69 top-down control upon herbivores (Beschta and Ripple 2012; Hebblewhite et al. 2005; Ripple
70 and Larsen 2000) and mesopredators (Newsome and Ripple 2014; Prugh et al. 2009; Ritchie
71 and Johnson 2009). If healthy populations of top predators can be maintained within
72 ecosystems, they should also contain healthy communities and populations of the many
73 species that perform a diversity of ecosystem services at lower trophic levels (Dobson et al.
74 2006).

75 As the most dominant landscape user and primary resource consumer on the planet (Paquet
76 and Darimont 2010), humans greatly modify the landscapes and communities that apex
77 predators interact with through a myriad of disturbance types (Blanc et al. 2006; Frid and Dill
78 2002; Sibbald et al. 2011). The positive (Kilgo et al. 1998; Kloppers et al. 2005; Leighton et
79 al. 2010) or negative (Hebblewhite et al. 2005; Jayakody et al. 2008; Pelletier 2006) nature of
80 this disturbance however depends entirely on management perspective (Reimoser 2003).
81 Humans can impact apex predators in much the same way as they impact smaller predators

82 and prey species, through density-mediated (consumptive) and trait/behaviourally-mediated
83 (non-consumptive) pathways (Ordiz et al. 2013). Impacts can be direct (Packer et al. 2009;
84 Virgos and Travaini 2005) or indirect through effects on other species or habitat (Rogala et
85 al. 2011; Sidorovich et al. 2003).

86 Context-dependent interactions between species are common but often poorly described
87 (Chamberlain et al. 2014). This review examines the contextual impacts of large carnivores
88 and the potential for human interference through effects on species assemblage,
89 environmental productivity, landscape and predation risk (Fig.1 and Table 1). If we are to
90 predict the consequences of predator management, it is critical to understand the dynamics of
91 interspecific relationships between organisms (Elmhagen et al. 2010; Prugh et al. 2009;
92 Ripple et al. 2014) and to determine if this context can be manipulated to achieve
93 management and ecosystem service goals (Kareiva et al. 2007).

94 A search of literature was conducted using Web of Science and Google Scholar with “OR”
95 and “AND” search operators and a mixture of key words (apex predator*, large carnivore*,
96 carnivore*, mesopredator release, mesopredator*, mesocarnivore*, large herbivore*,
97 herbivore suppression, grazing, browsing, predation pressure*, interspecific, interspecific
98 interaction*, interspecific killing, predation, intraguild predation, competition, competitor*,
99 trophic cascade*, predation risk*, ecosystem service*). Reference trails, recommended
100 papers or appropriate material already in the possession of the authors were also used to
101 inform this review.

102 1.1 Predation risk

103 Predators consume prey but they also provide risk (Brown and Kotler 2007; Fortin et al.
104 2005). Harassment and the associated energetic losses of responding to predation risk can
105 carry costs to overall fitness (Creel 2011). Predation risk is a powerful motivator that can
106 affect behaviour and how an animal uses time and space as well as investment in other
107 antipredator strategies (Brown et al. 1999; Ripple and Beschta 2004; Willems and Hill 2009).
108 Predation risk and disturbance create trade-offs between avoiding risk or perceived risk and
109 other fitness enhancing activities (e.g. feeding and breeding), such that risk avoidance carries
110 energetic costs in the form of missed opportunities (Brown 1992; Brown et al. 1999; Eccard
111 and Liesenjohann 2014). Human disturbance may incur similar responses to risk in wildlife
112 (Erb et al. 2012; Frid and Dill 2002; Leighton et al. 2010).

113 Risk-induced interactions between predators and other organisms can have cascading effects
114 (Miller et al. 2012; Ripple et al. 2014; Ritchie and Johnson 2009). A forager’s response to its
115 landscape of fear (Laundré et al. 2014; Laundré et al. 2010) may alter the species
116 composition, behaviour, adaptive evolution or population dynamics of its prey and perhaps its
117 predators or competitors (Brown and Kotler 2007). Non-consumptive behavioural
118 interactions can be significant ecological drivers and should not be overlooked (Heithaus et
119 al. 2009; Peckarsky et al. 2008; Ritchie and Johnson 2009).

120 2. Interactions with mesopredators

121 Larger predators can sometimes limit the impacts, range and densities of smaller predators
122 (Henke and Bryant 1999; Levi and Wilmers 2012; Prugh et al. 2009). Soulé et al., (1988)
123 observed that, in the absence of larger more dominant predators, smaller predators and
124 omnivore populations explode: increasing abundance by up to ten times that before release.
125 The mesopredator release hypothesis predicts that a decrease in abundance of top-order
126 predators results in an increase in the abundance of mesopredators due to a reduction in intra-
127 guild predation and competitive suppression (Letnic and Dworjanyn 2011; Ritchie and
128 Johnson 2009). Suppression of mesopredators can result in density reductions or even
129 complete exclusion of these smaller predators from habitats or regions in both time and space
130 (Berger and Gese 2007; Linnell and Strand 2000; Newsome and Ripple 2014).

131 Interspecific competitive killing, intraguild predation and interspecific interference
132 competition are common in a whole range of mammalian carnivores (Lourenco et al. 2014),
133 particularly between species with elements of niche overlap and species of the same family
134 having not too dissimilar body mass (Linnell and Strand 2000; Palomares and Caro 1999;
135 Ritchie and Johnson 2009). Two main mechanisms offer explanation for mesopredator
136 suppression by apex predators, direct lethal encounters, and behavioural responses to risk
137 (Ritchie and Johnson 2009).

138 There is great debate about the strength of impacts large carnivores have upon mesopredators
139 (Allen et al. 2013; Letnic et al. 2011; Letnic et al. 2009b). There is some evidence that
140 predation threat and impacts of mesocarnivores upon native rodents, such as *Notomys fuscus*,
141 are lower in the presence of dingoes (Letnic et al. 2009a; Letnic and Dworjanyn 2011).
142 However, some express caution in assigning causality to short-term observations of
143 correlated, but unvalidated population indices which may falsely suggest mesopredator
144 release (Allen et al. 2013; Fleming et al. 2012; Hayward and Marlow 2014). While there is
145 little doubt in the value of stable ecosystems complete with top predators (Estes et al. 2011;
146 Ripple et al. 2014), untangling the web of ecological interactions and clearly identifying
147 ecosystem services from apex predators will require careful experimental design.

148 In an extensive review, Ritchie & Johnson (2009) discuss a number of trophic assemblages
149 where mesopredators are suppressed by larger predators and found only 2 studies identifying
150 scenarios where scent or vocal predator cues had little impact upon mesopredators (Gehrt and
151 Prange 2007; Prange and Gehrt 2007). Interactions between species may vary depending
152 upon context. Larger predators may competitively suppress smaller predators but also provide
153 scavenging opportunities (Khalil et al. 2014). Habitat complexity, resource availability and
154 the density or complexity of predator communities may affect the outcomes of interactions
155 between predators (Khalil et al. 2014; Ritchie and Johnson 2009). Mesopredator prey species
156 comprise a vast array of herbivores, detritivores, seed dispersers and seed predators (Catling
157 1988; Panzacchi et al. 2008; Russell and Storch 2004). Such species have variable
158 interactions with vegetation communities (Wang and Yang 2015; Yi and Wang 2015; Zamora
159 and Matias 2014). Any consequential cascades resulting from mesopredator release are also
160 likely to be context-dependent.

161 **2.1 Contexts affecting mesopredator interactions**

162 2.1.1 Species assemblage

163 Vulnerability and interactions between predators may be influenced by niche overlap and
164 relatedness (Berger and Gese 2007; Gehrt and Prange 2007; Ritchie and Johnson 2009), but
165 also by species specific factors such as defence or grouping behaviour (Cooper 1991;
166 Palomares and Caro 1999; Prange and Gehrt 2007). Mesopredators, such as the bobcat
167 *Carnivora Felidae Lynx rufus* (5-15kg), can coexist with larger predators of similar size but
168 different families, like the coyote *Carnivora Canidae Canis latrans* (8-20kg), even when a
169 smaller mesopredator the grey fox *Carnivora Canidae Urocyon cinereoargenteus* (3-5kg) did
170 not (Fedriani et al. 2000).

171 In many North American trophic systems lacking larger carnivores, coyotes can interact
172 competitively and suppress mesocarnivores (Henke and Bryant 1999; Kamler et al. 2003;
173 Linnell and Strand 2000). The extent of this suppression may be somewhat dependent on the
174 presence of other predators. Red fox *Carnivora Canidae Vulpes vulpes* for example pose
175 more of a threat to kit fox *Carnivora Canidae Vulpes macrotis* populations because they can
176 access dens (Cypher et al. 2001; Ralls and White 1995). Coyotes could have an additive
177 negative impact (through predation) or benefit kit foxes through interference competition and
178 suppression of red foxes (Cypher et al. 2001).

179 In the presence of a larger canid, coyotes were suppressed by wolves and red foxes became
180 more abundant (Levi and Wilmers 2012). North American wolves impact coyote distribution,
181 abundance (33% lower in wolf abundant sites) and dispersal survival rates (Berger and Gese
182 2007; Newsome and Ripple 2014). In the presence of a feline apex predator however, coyotes
183 were only killed by mountain lions *Carnivora Felidae Puma concolor* defending or usurping
184 food caches during winter when diets overlapped significantly more (Koehler and Hornocker
185 1991). The overall impacts of predator communities and the outcomes of mesopredator
186 suppression might depend directly on the number, density and composition of predator
187 dominance levels (Chakarov and Krueger 2010).

188 At its most extreme scale, human influence can result in mesopredator range expansion and
189 population growth, through the removal of apex predators (Kamler et al. 2003; Ripple et al.
190 2013; Selås and Vik 2006) or competing mesopredators (Courchamp et al. 1999; Rayner et al.
191 2007; Trewby et al. 2008). In some circumstances, release can result in the increase of a prey
192 source shared by apex and mesopredators (Henke and Bryant 1999). Decline in prey species
193 of mesopredators is however more common (Elmhagen et al. 2010; Sargeant et al. 1984;
194 Sovada et al. 1995). Caution must be expressed when interfering with ecological interactions
195 as mesopredator release can carry economic and social costs (Prugh et al. 2009).

196 The introduction of alien predators may also alter trophic dynamics, complicating intraguild
197 competition and affecting food webs (Crooks and Soulé 1999; Krauze-Gryz et al. 2012;
198 Rayner et al. 2007). Wolf-dog interactions in particular stand out as an anthropogenic
199 introduction to species assemblage with variable context-dependent outcomes (Lescureux and
200 Linnell 2014). Levels of co-existence between native and alien species may be dependent on
201 niche flexibility, landscape and resource abundance (Bonesi et al. 2004; Bonesi and

202 Macdonald 2004; Brzezinski et al. 2008). The maintenance and recovery of native or
203 naturalised predators may in some contexts help to mitigate the impacts of invasive
204 mesopredators (Glen et al. 2007; McDonald et al. 2007; Ritchie et al. 2012). Introduced
205 predators, although posing their own threat to native prey species may also suppress the
206 impacts of smaller alien predators in certain contexts (Hanna and Cardillo 2014). Predator
207 eradication can have unforeseen consequences even with conservation in mind. Invasive
208 species removal may have undesired effects through mesopredator release, rather than
209 alleviating predation pressure upon native species as intended (Rayner et al. 2007).

210 2.1.2 Environmental productivity

211 Apex predators can affect food availability to smaller predators through the provision of
212 carrion (Wilmers and Getz 2005), exploitative competition (Selås and Vik 2006),
213 kleptoparasitism (Gorman et al. 1998), landscapes of fear (Kuijper et al. 2013; Laundré et al.
214 2010), and possibly through indirect impacts on habitat structure and provisioning of refuge
215 for mesopredator prey (Letnic and Dworjanyn 2011). Bottom-up factors however influence
216 population densities of herbivores and consequently their predators (East 1984; Hayward et
217 al. 2007).

218 The strength of top-down mesopredator control and consequently the strength of cascades
219 from large carnivores can be determined by ecosystem productivity (Elmhagen et al. 2010;
220 Elmhagen and Rushton 2007; Hollings et al. 2014). In contexts where bottom up effects are
221 strongly influential the mesopredator release response to apex predator control may be
222 limited. Coyote predation upon kit foxes can account for 75-90% of mortality (Eliason and
223 Berry 1994; Linnell and Strand 2000; Ralls and White 1995). Such predation may be most
224 significant when food availability is low or when kit fox populations are small (Cypher et al.
225 2001). During a coyote control programme where kit fox release did not occur as expected,
226 food availability (lagomorph abundance) was observed to be the primary factor driving
227 population dynamics of both species (Cypher and Scrivner 1992).

228 Humans can influence the type and severity of interspecific competition amongst carnivores
229 by artificially boosting food availability, and consequently mesopredator populations
230 (Bateman and Fleming 2012; Crooks and Soulé 1999; Linnell and Strand 2000). Maintaining
231 mesopredators far above their carrying capacity with nutritional subsidies may particularly
232 unbalance natural regulation if accompanied by habitat fragmentation (Crooks and Soulé
233 1999; Dickman 2008). Large carnivores can also adapt to capitalize on anthropogenic food
234 sources (Ciucci et al. 1997; Kusak et al. 2005; Newsome et al. 2014). However, humans often
235 inhibit large carnivore use of space and time (Whittington et al. 2005). Both direct and
236 indirect human influence on prey numbers, accessibility and hunting opportunities may cause
237 prey switching and impact activity patterns with consequences for competitive interactions
238 and the resultant impacts of large carnivores (Allen and Leung 2012; Theuerkauf et al. 2003).

239 2.1.3 Landscape

240 The interplay between predation risk and habitat features can shape foraging decisions and
241 habitat use (Camacho 2014). Predation risk is not homogenous across landscapes or species;

242 habitat features can interact with escape tactics to shape interspecific interactions (Wirsing et
243 al. 2010). Predation risk is not always driven by predator density alone and mesopredator
244 landscape use can sometimes be more dominantly driven by habitat features (Heithaus et al.
245 2009).

246 In many cases humans have drastically reduced available habitat for native fauna (Paquet and
247 Darimont 2010). The impacts large carnivores have on other species and ecosystems may be
248 relative to their interactions with anthropogenic landscapes. Human landscape modification
249 may alter species interactions and occupancy by benefitting those species more adaptable to
250 anthropogenic disturbance (Cove et al. 2012; Erb et al. 2012; Ruiz-Capillas et al. 2013).
251 Urban predators can provide ecosystem services as well as conflicts but human conflict often
252 dominates management decisions (Dodge and Kashian 2013).

253 Human presence does not always necessitate extreme avoidance by large carnivores
254 (Theuerkauf et al. 2007) and not all human landscapes will inhibit ecological interactions
255 between predators (Berry et al. 1992; Standley et al. 1992). Landscape modification and the
256 management of larger predators in fenced reserves for example can also have conservation
257 benefits for mesopredators (Van Dyk and Slotow 2003). In other contexts, human landscape
258 use may have negligible impact on mesopredator occupancy (Schuette et al. 2013) or
259 negative effects through elevated populations of domestic competitors (Krauze-Gryz et al.
260 2012).

261 2.1.4 Predation risk

262 As well as direct killing, large carnivores impact habitat use and foraging effort of smaller
263 mesopredators (Palomares and Caro 1999; Ritchie and Johnson 2009; Thurber et al. 1992).
264 Interference competition between carnivores through harassment (Berger and Gese 2007;
265 Linnell and Strand 2000; Mukherjee et al. 2009), prey competition (Cypher et al. 2001) and
266 kleptoparasitism (Cooper 1991; Gorman et al. 1998) can generate avoidance of larger
267 carnivores through spatio-temporal partitioning (Crooks and Soulé 1999; Durant 2000;
268 Hayward and Slotow 2009).

269 Rarity and inconsistency of agonistic interactions and/or behavioural avoidance of encounters
270 may permit co-existence between some predators (Durant 2000; Fedriani et al. 2000).
271 Distribution of predators over large spatial scales can however be driven by competitive
272 interactions (Elmhagen et al. 2010; Newsome and Ripple 2014). Mesopredators sometimes
273 use peripheries of larger predator territories (Berger and Gese 2007; Miller et al. 2012;
274 Thurber et al. 1992), presumably reducing encounter rates and increasing fitness. Fearful
275 interactions between predators may permit the co-existence of multiple prey species, with
276 certain species existing where dominant predators limit the spatio-temporal presence of
277 subordinate predators (Berger et al. 2008; Miller et al. 2012).

278 As a consequence of interspecific aggression between carnivores (Berger and Gese 2007;
279 Palomares and Caro 1999; Thurber et al. 1992), foraging decisions by mesopredators are also
280 influenced by risk from their own predators (Mukherjee et al. 2009; Ritchie and Johnson
281 2009; Roemer et al. 2009). The extent to which mesopredators are impacted by larger

282 predators and the degree to which they have to adjust their foraging efforts, activity patterns,
283 vigilance and risk taking is likely to vary depending on predator assemblage, habitat and food
284 availability (Ritchie and Johnson 2009).

285 Humans can also influence interspecific interactions (Crooks and Soulé 1999). Additional
286 anthropogenic landscapes of fear (Frid and Dill 2002) could further limit foraging
287 opportunities for mesopredators. Alternatively anthropogenic interference with larger
288 predators (Erb et al. 2012; George and Crooks 2006; Theuerkauf et al. 2003) could
289 potentially reduce suppression.

290 **3. Interactions with large herbivores**

291 Large carnivores can be important mortality drivers of ungulate populations (Jędrzejewski et
292 al. 2002; Melis et al. 2009), maintaining herd health through the removal of unhealthy
293 individuals (Kusak et al. 2012). Although not universal, density-driven terrestrial cascades
294 are common (Schmitz et al. 2000). On Isle Royale, USA for example, wolves have been
295 found to regulate moose *Cetartiodactyla Cervidae Alces alces* population dynamics and in
296 doing so dampen the effects of climactic change upon herbivore and scavenger communities
297 (Wilmers et al. 2006).

298 Both herbivore density and behaviour can be altered by the presence and actions of predators
299 (Beckerman et al. 1997; Montgomery et al. 2013). In many circumstances the role of
300 “landscapes of fear” (Laundré et al. 2010), predation risk and the avoidance of predators are
301 also believed to be closely linked to how ungulates use time and space (Brown et al. 1999;
302 Harmsen et al. 2011; Kronfeld-Schor and Dayan 2003) as well as how they forage (Altendorf
303 et al. 2001; Kotler et al. 1994; Laundré et al. 2001). There is an increasing amount of
304 literature investigating the impacts that ungulate foraging patterns may have upon ecosystems
305 and vegetation community structure (Gill 2000; Reimoser et al. 1999; Tschöpe et al. 2011).
306 Large carnivores may hold influence over patterns of ungulate grazing pressure and its
307 consequent impacts (Creel et al. 2005; Estes et al. 2011; Ripple and Beschta 2004).

308 There is a great deal of flexibility in how large carnivores such as wolves use time and space
309 (Kusak and Haswell 2013). The causal factors behind activity patterns are highly variable
310 (Ballard et al. 1997; Kolenosky and Johnston 1967; Theuerkauf 2009). Anthropogenic
311 influences are often strong drivers (Ciucci et al. 1997; Kusak et al. 2005; Theuerkauf et al.
312 2003). How large carnivores interact with herbivores is likely to be dependent on this context.
313 Foraging and space-time use patterns of herbivores and the role of behaviourally-mediated
314 carnivore impacts may ultimately dictate potential ecosystem services that could benefit local
315 communities (Hebblewhite et al. 2005; Ripple et al. 2014). However trophic cascades from
316 large carnivores are not guaranteed in every ecological context (Ford et al. 2015).

317 **3.1 Context’s affecting interactions with large herbivores**

318 3.1.1 Species assemblage

319 In Europe, the limiting effects of lynx *Carnivora Felidae Lynx lynx* and wolf upon roe deer
320 *Cetartiodactyla Cervidae Capreolus capreolus* density were stronger when both species were

321 present than by one species alone (Melis et al. 2009). Where one species was present alone
322 (most commonly the wolf) mean roe deer density was 917 per 100km² but only 167 in the
323 presence of both predators (Melis et al. 2009). This suggests that predators can have additive
324 effects on shared prey and that generally lynx are a more dominant predator of roe deer in
325 Europe. The composition of large carnivores in a given scenario is clearly consequential to
326 the effects upon herbivore communities.

327 In south-eastern Norway, roe deer fawns were consumed by red foxes (8.6% spring-summer
328 diet, (Panzacchi et al. 2008). Red foxes had a highly varied diet so fawns were not considered
329 important to the population dynamics of red foxes, implying that there was unlikely to be any
330 stabilising feedback mechanism between the species (Panzacchi et al. 2008). Where
331 mesopredators are released from apex predator suppression, mesopredators could have more
332 pronounced impacts on herbivore recruitment (Berger et al. 2008). This may offer some
333 compensation for a lack of adult ungulate predation by large carnivores. However, even if
334 density-driven effects could be compensated by mesopredators, smaller carnivores are
335 unlikely to replace the behavioural dynamics between larger carnivores and adult ungulates.

336 Harvesting of larger trophy individuals or the removal of larger predators in general due to
337 human conflicts could have catastrophic effects (Packer et al. 2009). Larger wolves >39kg
338 (usually older and/or male animals) have been observed to have higher attack and kill rates in
339 Yellowstone National Park where improvements in handling success are not counteracted by
340 a reduction in pursuit ability (MacNulty et al. 2009). The association between increased body
341 weight and prey size in carnivores could be driven by size-related energetic costs (Carbone et
342 al. 1999; Carbone et al. 2007) and size-related predator performance (MacNulty et al. 2009).
343 Local conditions may affect composition and characteristics (gender, size or age) of predator
344 social groups (Van Orsdol et al. 1985). Food loss rates from kleptoparasites like ravens are
345 relative to wolf pack size and can consequently further affect kill rates (Hayes et al. 2000;
346 Kaczensky et al. 2005). Temporal success, preferences and social structure can influence
347 predation rates and consumption of different prey species (Jędrzejewski et al. 2002). Social
348 dynamics and population demography could also influence the direction or strength of
349 cascades due to predation patterns.

350 Interspecific relationships may also have a variable temporal context that is not constant
351 (Koehler and Hornocker 1991). Herbivores can have seasonal habitat preferences and dietary
352 requirements (Degmečić et al. 2011). Large carnivores can also exhibit seasonal or context
353 driven dietary shifts (Garrott et al. 2007; Latham et al. 2013; Odden et al. 2006) and habitat
354 use (Alexander et al. 2006). Population structure, body condition, parasite load, climate,
355 predator density and predation risk may all interact to drive herbivore landscape use
356 (Montgomery et al. 2013).

357 Herbivore response to risk may in itself be subject to competitive partitioning between
358 herbivores, particularly around key habitat sites such as water sources (Hayward and
359 Hayward 2012). Resource competition between herbivores may alter landscape use patterns
360 (Dolman and Waber 2008; Hibert et al. 2010). While displacement is context specific and

361 likely to be dependent on levels of niche overlap (Iranzo et al. 2013), the potential for
362 domestic herbivores to outcompete wild herbivores is probably high (Latham 1999).

363 Wild and domestic herbivores forage and interact with vegetation communities in different
364 ways, with domestic stock often causing greater degradation (Fuller 2001; Hester and Baillie
365 1998; Hill et al. 1991). Domestic livestock often aggregate more, and their limited ranging
366 behaviour is exacerbated through herding and human directed foraging at convenient
367 locations (Albon et al. 2007). This type of herbivory will likely result in limited impacts from
368 large carnivores upon domestic grazing/browsing pressure, with consequences being
369 predominantly human driven. When livestock are free-ranging their response to predation
370 risk is still different to that of wild herbivores, as well as being somewhat attenuated (Muhly
371 et al. 2010).

372 The introduction of competitive alien herbivores (e.g. domestic stock) can also lead to
373 apparent competition and increased predation of native species by predators (Dolman and
374 Waber 2008). Poor husbandry practices and high livestock predation rates could potentially
375 either exacerbate or reduce large carnivore impacts on native species depending on context.
376 Furthermore, livestock guarding dogs that accompany livestock interact with predators
377 (Lescureux and Linnell 2014). Livestock guarding dogs, along with human presence may add
378 to landscapes of fear for large carnivores but may also serve to maintain interactions between
379 predators and native prey.

380 The traditional role of humans as part of the predator guild in communities is often
381 overlooked. Aboriginal hunters were important apex predators in Australia following their
382 arrival and the extinction of the megafauna (Fleming et al. 2012). In the absence of its human
383 hunting partners, the dingo may not truly fulfil the role of an apex predator and its modern
384 ecological function may differ given vast anthropogenic habitat modification (Fleming et al.
385 2012). In a similar fashion, our understanding of how indigenous North American's impacted
386 the landscape is still developing (Lightfoot et al. 2013). The sustainability of such impacts are
387 debateable, but it is clear that the removal of human regimes from wilderness designations in
388 the USA will not replicate the ecological conditions present since its colonisation by
389 European settlers (Kay 1994).

390 The role of humans in the modern food web and the very different nature of our interactions
391 and impacts is something worth considering. Modern hunting practices and regulations vary
392 dramatically across the globe and the impacts will no doubt vary too. The attractive re-
393 wilding concept of re-establishing self-sustaining ecosystems with minimal human disruption
394 may help to maintain large carnivore-herbivore interactions, but requires careful
395 consideration of desired outcomes (Brown et al. 2011). Such management intervention may
396 not always be pragmatic or necessarily a true reflection of the historic *status quo*. An
397 understanding of how humans influence trophic dynamics could help to better predict and
398 steer landscape management to desired outcomes.

399 3.1.2 Ecosystem productivity

400 Resource driven landscape use (Owen-Smith 2014) and bottom-up effects of environmental
401 productivity are often a major driving force influencing large herbivore distribution and
402 abundance (Coe et al. 1976; East 1984; Karanth et al. 2004). For example, roe deer
403 abundance in Europe was positively correlated with environmental productivity (Melis et al.
404 2009). The impacts of large predators were however weak in productive environments and
405 regions with mild climate but noticeably greater in regions with harsher winters and lower
406 productivity (Melis et al. 2009). Climatic features such as temperature or snow depth can also
407 interact with local complexities, impacting the strength of predation pressure and trophic
408 cascades (Post et al. 1999; Sanford 1999). The strength of impacts from large carnivores may
409 be dependent on productivity and climatic context.

410 A forager in a low energy state has less to lose from predation and a higher marginal value of
411 energy to be gained so is more likely to forage in riskier habitats, change their forage
412 selection decisions and reduce food patches to a greater extent (Brown and Kotler 2007;
413 Brown et al. 1992; Hayward et al. 2015). Competition for game animals between humans and
414 large carnivores (Virgos and Travaini 2005) may affect predator energy states and
415 consequently predation patterns. Conversely, anthropogenic food provisioning, such as at
416 refuse (Ciucci et al. 1997), urban (Rodewald et al. 2011) or hunting sites (Selva et al. 2014)
417 may alter predation risk trade-offs and interactions between species, potentially decoupling
418 interspecific relationships (Rodewald et al. 2011). Where anthropogenic foods dominate
419 predator diet, impacts of large carnivores upon wild herbivores could become minimal or
420 alternatively could increase due to inflated predator numbers, energy or time resources.

421 3.1.3 Landscape

422 Landscape-scale or micro-habitat predation patterns of large carnivores can impact upon local
423 vegetation communities. Wolf predation of deer can impact habitat heterogeneity through the
424 creation of nutrient pulses at kill sites (Bump et al. 2009). Wolf predation success and prey
425 vulnerability may be dependent on the amount of open grassland adjacent to streams
426 (Kauffman et al. 2007). If large herbivores are preyed more successfully and forage less in
427 high risk areas (Crossmary et al. 2012; Fortin et al. 2005; Ripple and Beschta 2004), one
428 might expect woody plant regeneration and vegetation succession (Berger 1999; Berger et al.
429 2001a; Hebblewhite et al. 2005).

430 In Yellowstone National Park's northern winter range, elk *Cetartiodactyla Cervidae Cervus*
431 *canadensis* movement preference for vegetative cover types was influenced by the spatial
432 distribution of wolves (Fortin et al. 2005). Risk driven habitat preferences may be responsible
433 for observed reductions in aspen *Malpighiales Salicaceae Populus tremuloides* browsing
434 pressure by elk in the presence of wolves (Fortin et al. 2005; Ripple and Larsen 2000; Ripple
435 et al. 2001). The extent of the impacts behaviourally-mediated trophic cascades have on
436 aspen recruitment in Yellowstone has however been debated (Beschta et al. 2014; Kauffman
437 et al. 2010; Winnie 2014; Winnie 2012). Trophic cascades may be more complicated than the
438 three tiered systems proposed; in complicated food webs interactions can go up, across and
439 down the trophic web (Polis et al. 2000; Strong 1992). In Yellowstone, interactions between
440 environmental productivity, habitat features, human activities outside the park, predators and

441 herbivores, as well as contributing impacts of engineers, such as beavers *Rodentia Castoridae*
442 *Castor canadensis*, are likely to contribute and interact to affect vegetation communities
443 through both behaviourally- and density-mediated mechanisms (Marshall et al. 2013; Painter
444 et al. 2015).

445 Anthropogenic landscape alterations such as higher road densities, fire regimes and housing
446 developments can have negative impacts on the presence and activity of large carnivores
447 (Haskell et al. 2013; Hebblewhite et al. 2009; Theuerkauf et al. 2003). Anthropogenic
448 disturbance may span further than expected, with activities outside protected areas having
449 strong effects on species within reserves (Parks and Harcourt 2002). Even human landscape
450 modification intended to conserve (e.g. fenced reserves) may alter natural predator-prey
451 dynamics through consequent changes in prey vulnerability and predator behaviour (Davies-
452 Mostert et al. 2013). Human landscape alteration can also create new landscapes of fear for
453 large herbivores (Semeniuk et al. 2014). Such interferences could inhibit desirable ecological
454 interactions.

455 3.1.4 Predation risk

456 Through behavioural mechanisms predators can influence prey species landscape use
457 (Laundré et al. 2001; Laundré et al. 2014; Willems and Hill 2009) and consequently the
458 impacts of herbivores upon habitat structure (Fortin et al. 2005; Kuijper et al. 2013). How
459 populations and individuals respond to predation risk is unlikely to be consistent across
460 contexts. Behavioural responses to environmental cues of predation risk may be sensitive to
461 fluctuations in predation pressure (Berger 1999) but can also remain stable in its absence
462 (Chamaille-Jammes et al. 2014). The strength of response to risk and the relative influence of
463 predation risk to a predator's overall limiting effect is likely to be affected by the
464 environment as well as predator and prey characteristics (Creel 2011). It is suggested that
465 prey species respond to overall risk rather than predator abundance alone (Heithaus et al.
466 2009). In some circumstances, prey species escape probability, habitat use and consequently
467 resource exploitation can be higher where predators are more abundant (Heithaus et al. 2009).
468 Individual factors such as gender (Laundré et al. 2001) and the presence of offspring (Wolff
469 and Horn 2003) can also influence investment in anti-predatory responses like vigilance.

470 Risk of predation can cause prey to be more cautious in how they forage, becoming more
471 vigilant (Altendorf et al. 2001; Halofsky and Ripple 2008; Wolff and Horn 2003), more
472 mobile, thereby reducing predictability (Fortin et al. 2009), alter habitat use (Creel et al.
473 2005; Fortin et al. 2005; Laundré et al. 2001), respond to risk cues (Berger 1999; Mella et al.
474 2014), forage less in risky patches (Andruskiw et al. 2008; Brown 1988; Koivisto and
475 Pusenius 2006) or at restricted times (Brown and Kotler 2007), forage in larger groups
476 diluting risk (Fortin et al. 2009; Hebblewhite et al. 2002; Isvaran 2007) or in smaller groups
477 reducing detection (Fortin et al. 2009; Hebblewhite et al. 2002). In any one circumstance a
478 myriad and combination of these antipredator tactics may be implemented.

479 Behavioural responses by prey also encourage countermeasures in predators such as stealth,
480 boldness and space-time use selection (Brown and Kotler 2007; Hopcraft et al. 2005). Fear

481 and predation risk create somewhat of a tactical predator-prey foraging game. “Prey face
482 different risks from predators with different tactics, and their antipredator responses vary
483 accordingly” (Creel 2011). Predator specific strategies in prey may also promote coexistence
484 among predator species, if employing vigilance or avoidance strategies against one sort of
485 predator causes the forager to be more vulnerable to another (Sih et al. 1998).

486 Variation in response to predators may be driven by local selective pressures. Predator
487 hunting strategies, foraging behaviour and social organisation of herbivores alongside
488 environmental variables will lead to context-dependent herbivore response to predation risk
489 (Samelius et al. 2013). Prey species response to predation risk in turn impacts lower trophic
490 levels in what is ambiguously known as a trophic cascade (Polis et al. 2000).

491 Human activities can also impact patch predation risk, landscapes of fear and habitat use by
492 both predators and large herbivores (Hebblewhite et al. 2009; Rogala et al. 2011; Sibbald et
493 al. 2011). Non-consumptive (Blanc et al. 2006; Frid and Dill 2002; Leighton et al. 2010) and
494 consumptive (Ciuti et al. 2012; Proffitt et al. 2013; Sand et al. 2006) human interactions with
495 large herbivores can affect predation risk responses. Whether an elk was harvested by
496 humans or not in North America was found to be a consequence of individual response to a
497 human mediated landscape of fear (Ciuti et al. 2012). Older female elk generally adopted
498 habitat preferences and the use of a running or hiding strategy that lead to their survival (Ciuti
499 et al. 2012).

500 In the absence of human hunting pressures large herbivores may adjust their behaviour in
501 response to large carnivores (Berger et al. 2001b). Human interactions with ungulates may
502 sometimes benefit large carnivores (Kilgo et al. 1998). However, anthropogenic selection can
503 also impact behavioural evolution and herbivore learning in a different and opposing manner
504 to that of large carnivores, potentially negating their impacts (Ciuti et al. 2012; Sand et al.
505 2006).

506 Individual behaviour, learning and the selective pressures of large carnivores and humans
507 over time may be important drivers of large herbivore behaviour and its potential cascading
508 effects. It is essential to know whether human interactions yield desired outcomes or interfere
509 with the impacts of large carnivores through intensified or competing selection pressures.

510 **4. Conclusions**

511 Interactions between species are complicated. Suppression of one species by another can be
512 driven by a varying intensity of both density- and behaviourally-mediated mechanisms.
513 Impacts from large carnivores will not be homogenous across contexts. Factors intrinsic to
514 prey, predators and the given system (species composition, environmental productivity,
515 landscape, and predation risk) will culminate to produce the resultant dynamics in a given
516 context. The mixture of variables yielding interspecific relationships with large carnivores in
517 a given context will in turn interact with additional features at lower trophic levels, dictating
518 further interspecific interactions, ecosystem services and the presence of trophic cascades
519 from large carnivores.

520 Human-induced changes could have cascading effects for the entire carnivore community, on
521 prey communities of both apex and mesopredators and consequently habitat structure and
522 biodiversity (Fig.1). The impacts of humans on other species, the types and intensity of
523 human activity in a given context could alter the direction or severity of other interspecific
524 interactions (Table 1). Humans can remove large carnivores from systems altogether,
525 undesirably influence large carnivore activity, disrupt foraging, reduce survival success or
526 breeding capability, suppress habitat use and ultimately interfere with trophic interactions.

527 An understanding of whole ecosystems and the processes that maintain them is key to
528 ensuring sustainability. If we are to understand ecological systems, it is important for basic
529 monitoring of common as well as rare species to be undertaken alongside novel experimental
530 approaches. Whilst managers, politicians and the public might desire standardised answers,
531 blanket assumptions of the role of large carnivores across contexts and inflexible or
532 misinformed approaches to their management are damaging. In order to take appropriate
533 management and conservation action in any given context, interspecific interactions, the
534 outcome of human interference and the trade-off between ecosystem services and
535 anthropogenic land uses must be informed by robust experimentation and analysis. It is
536 imperative that the consequences of intervention, particularly predator control are understood.

537 **Acknowledgements**

538 We would like to thank Bangor University and the University of Zagreb for their support of
539 the authors. Both Haswell and Kusak would also like to thank The UK Wolf Conservation
540 Trust, Nacionalni park Sjeverni Velebit and Nacionalni park Plitvička jezera for their
541 continued assistance and support of research efforts with the study of large carnivores in
542 Croatia. We are grateful to Dr. B. Allen and Dr. S. Creel for their useful comments on the
543 manuscript. The authors declare that they have no conflict of interest in the authorship of this
544 article.

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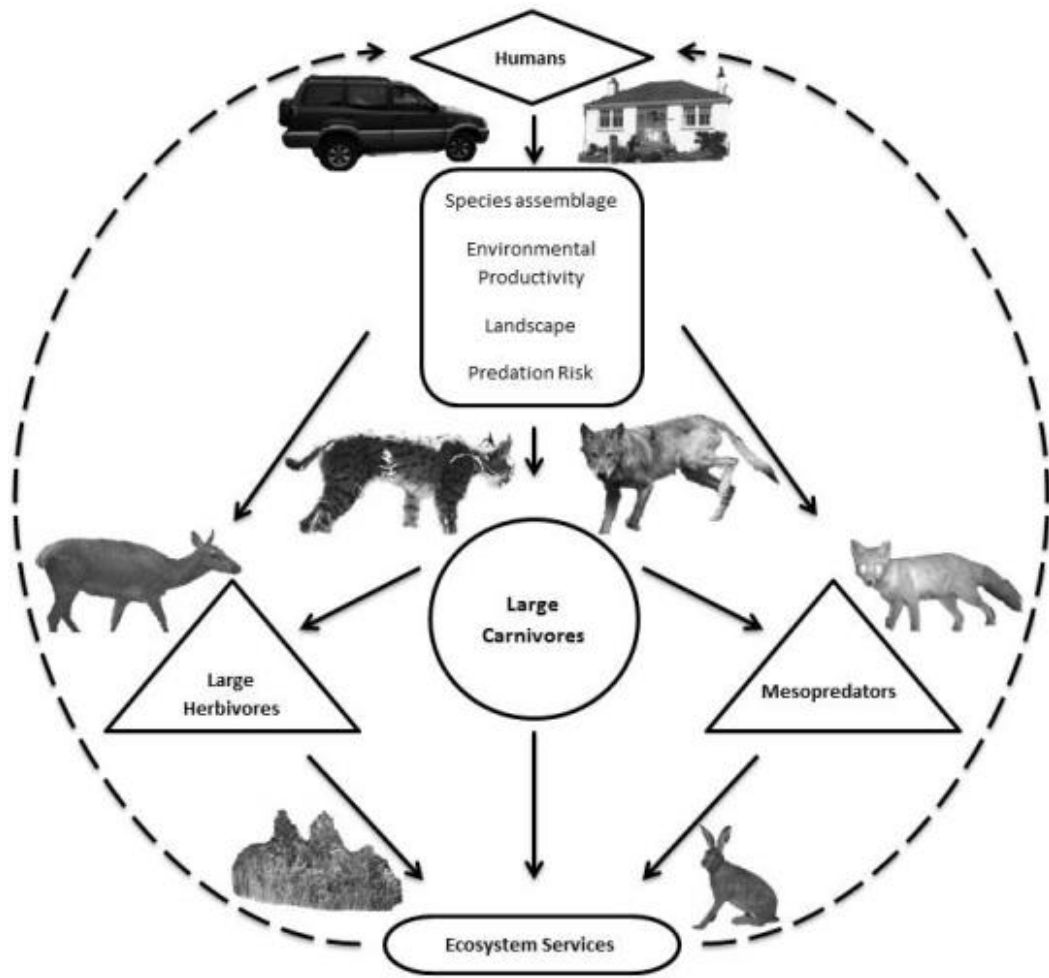


Fig.1. Benefits derived from large carnivores could be dependent on human context. As the most dominant landscape and resource user on the planet, humans have the potential to influence ecosystems and the organisms that inhabit them. The impacts of humans on other species in a given context could alter the direction or severity of consumptive and non-consumptive interactions between species. Humans can affect top down control from large carnivores which can have trickle down effects through trophic interactions, affecting habitat use and foraging behaviour with consequences for ecosystem services (solid arrows). These services can in-turn feedback to affect humans (dashed arrows). This figure represents a simplified flow diagram of how context affects the impacts from large carnivores; additional mechanisms have been excluded for clarity.

Table.1. Human impacts and their potential consequences to trophic systems. Both direct influences and consequent alterations to interspecific interactions can affect ecological processes. The positive (+), negative (-) or neutral (=) impacts of human interventions on a guild of organisms are likely to vary dramatically and will be dependent on context. Human interactions with apex predators can alter mesopredator release (MR), large herbivore release (LHR), predation (P), competition (C), food availability (F), seed predation (SP) and seed dispersal (SD). Negative human influences on large carnivores can release those species they suppress. This could in turn have cascading effects, potentially increasing (↑) or decreasing (↓) pressure on other species further down the food chain.

Human-wildlife interaction	Large Carnivores	Large herbivores	Mesopredators	Small herbivores	Vegetation
Hunting Large Carnivores	- (↑ P)	- (↑ P of young, MR) + (adults ↓ P)	+ (↓ C) - (↓ consistency of F, scavenging)	- (↑ P, MR)	- (↑ P, LHR) - (↓ SD, MR) + (↓ SP)
Hunting large herbivores	- (↓ F)	- (↑ P)	- (↓ F, scavenging & young herbivores) + (↓ C)	- (↑ P, MR) + (↓ P, ↓ C)	- (↓ SD, MR) - (↑ SP, MR) + (↓ P) + (↑ SD) + (↓ SP)
Alien predators	- (↑ C) = =	- (↑ P) = + (↓ P)	- (↑ C) = + (↓ C)	- (↑ P, MR) = + (↓ P, ↓ C)	- (↑ P, LHR) - (↓ SD, MR) - (↑ SP, MR) = + (↓ P) + (↑ SD) + (↓ SP)
Alien herbivores	- (↓ F) = + (↑ F)	- (↑ C) = + (↓ P)	- (↑ C) = + (↓ C) + (↑ F)	- (↑ C) = + (↓ P)	- (↑ P) - (↓ SD, MR) - (↑ SP, MR) = + (↓ P) + (↑ SD) + (↓ SP)
Food provisioning (predators)	+ (↑ F)	- (↑ P) = + (↓ P)	- (↑ C) + (↑ F) + (↓ C)	- (↑ P, MR) + (↑ F) + (↓ P)	- (↓ SD, MR) - (↑ SP, MR) + (↓ P) + (↑ SD) + (↓ SP)
Food Provisioning (herbivores)	+ (↑ F)	+ (↑ F)	- (↑ C) + (↑ F)	- (↑ P) + (↓ P) + (↑ F)	- (↑ P) - (↓ SD) - (↑ SP) = + (↓ P) + (↑ SD) + (↓ SP)
Habitat loss	-	-	-	-	-
Habitat fragmentation	-	- + (↓ P)	- + (↓ C)	- - (↑ P, MR) + (↓ P)	- - (↑ P) - (↓ SD) - (↑ SP) + (↑ SD) + (↓ SP)
Disturbance (risk)	- + (↑ F)	- - (↑ P) + (↓ P)	- - (↑ C) + (↓ C)	- - (↑ P) + (↓ P)	- (↑ P) - (↓ SD) - (↑ SP) = + (↓ P) + (↑ SD) + (↓ SP)